Scientific evaluation of the status of the Northern Spotted Owl

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Executive summary

This report consists of a critical review and synthesis of recent information on the status of the Northern Spotted Owl. The report has been prepared to support the US Fish and Wildlife Service in their 5-year status review process, as set out in the Endangered Species Act. This report does not make recommendations on listing status, or on management, and is solely focused on identifying the best available science, and the most appropriate interpretations of that science. The focus is on new information developed since the time of listing (1990).

The review process was comprehensive and critical, and involved a core panel of 8 scientific experts, plus 9 other contributing scientists. Four public meetings were held to discuss and analyze results and their interpretation. Over 1100 documents were read, critiqued, and discussed. Outside input was solicited, and external peer review was also obtained. Some new analyses were commissioned, and additional information was collected at our request. The final report represents a synthesis of all the available information, including a full discussion of points where data are conflicting, or where there is uncertainty in interpretations. In general the panel members, having discussed and argued over issues, came to a consensus; on those few areas where there was not complete consensus, the report makes clear the diversity of opinion, and the reasons for it.

Central to understanding the status of the subspecies is an evaluation of its taxonomic status. The panel is unanimous in finding that the Northern Spotted Owl is a distinct subspecies, well differentiated from other subspecies of Spotted Owls.

The panel did not identify any genetic issues that were currently significant threats to Northern Spotted Owls, with the possible exception that the small Canadian population may be at such low levels that inbreeding, hybridization, and other effects could occur.

The use of habitat and of prey varies through the range of the subspecies. These two factors interact with each other and also with other factors such as weather, harvest history, habitat heterogeneity etc, to affect local habitat associations. While the general conclusion still holds that Northern Spotted Owls typically need some late-successional habitat, other habitat components are also important (at least in some parts of the range).

The available data on habitat distribution and trends are somewhat limited. Development of new habitat is predicted under some models. However our ability to evaluate habitat trends is hampered by the lack of an adequate baseline. Given these caveats, the best available data suggest that timber harvest has decreased greatly since the time of listing, and that a major cause of habitat loss on federal lands is fire. In the future, Sudden Oak Death may become a threat to habitat in parts of the subspecies' range.

Barred Owls are an invasive species, that may have competitive effects on Northern Spotted Owls (as was recognized at the time of listing). Opinion on the panel was divided on the effects of Barred Owls. While all panelists thought this was a major threat, some panelists felt that the scientific case for the effects of Barred Owls remained inconclusive; other panelists were more certain on this issue.

The demography of the Northern Spotted Owl has been recently summarized in a meta-analysis (Anthony et al 2004), which is the most appropriate source for information on trends. Although the overall population, and some individual populations show signs of decline, we cannot determine whether these rates are lower than predicted under the Northwest Forest Plan (since there is no baseline prediction under that plan). However the decline of all four Washington state study populations was not predicted, and may indicate that conditions in that state are less suitable for Northern Spotted Owls. Several reasons for this pattern are plausible (including harvest history, Barred Owls, weather).

There is currently little information on predation on Spotted Owls, and no empirical support for the hypothesis, advanced at the time of listing, that fragmentation of forest after harvest increases predation risk.

West Nile Virus is a potential threat, but of uncertain magnitude and effect.

In general, conservation strategies for the Northern Spotted Owl are based on sound scientific principles and findings, which have not substantially altered since the time of listing (1990), the Final Draft Recovery Plan (1992) and adoption of the Northwest Forest Plan (1994). Nevertheless we identify several aspects of conservation and forest management that may increase both short and medium term risks to the species. These are typically due to failures of implementation.

A full evaluation of the uncertainties of the data, the conclusions that can be drawn from them, and of the perceived threats to the subspecies, are shown in the summary of individual panelist responses to a questionnaire.

Major threats to Northern Spotted Owls at this time include: the effects of past and current harvest; loss of habitat to fire; Barred Owls. Other threats are also present. Of threats identified at the time of listing, only one (predation linked to fragmentation) does not now appear well supported.

The review concludes with a discussion of the information that would be needed for a more definitive status review in the future. We note that if current monitoring efforts are not maintained, scientists in the future may be less able than we were to assess status. We also identify key information, currently unavailable, that could greatly affect our ability to understand and conserve Northern Spotted Owls.

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Volume Two: Appendices

SCIENTIFIC EVALUATION OF THE STATUS OF THE NORTHERN SPOTTED OWL

CHAPTER ONE

Introduction

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INTRODUCTION

1 STATUS REVIEWS

Status Reviews are prepared for species being evaluated by the US Fish and Wildlife Service (USFWS or Service hereafter), including species either being considered for listing under the Endangered Species Act (ESA) or species already listed as threatened or endangered. Four Status Reviews or their equivalents have been prepared for the Northern Spotted Owl in 1982, 1987, 1989, and 1990. Each Status Review differed in scope, focus and length (29, 36, 96, and 61 pp respectively), and in emphasis. The 1990 review, for instance, explicitly identified habitat loss as 'the problem', and devoted most attention to this issue, but only one paragraph to the effect of the Barred Owl, for which little evidence was then available. Note that major reviews of Northern Spotted Owl biology were additionally prepared by the Interagency Scientific Committee to Address the Conservation of the Northern Spotted Owl (ISC or Thomas et al., 1990 hereafter), and by the Northern Spotted Owl Recovery Team (Final Draft Recovery Plan, FDRP or USDI 1992 hereafter). The ISC report was published prior to the 1990 Status Review, and is referenced therein. The ISC and the FDRP remain major resources and summaries on the biology of the Northern Spotted Owl.

Despite their importance in making decisions concerning listing status, Status Reviews do not always make recommendations on listing actions (only one Spotted Owl review, that of 1990, made a specific recommendation on listing status, although the proposal of the USFWS to list the subspecies as threatened followed the 1989 Status Review Supplement). Indeed, there are no specific guidelines on the processes to follow in developing a Status Review (e.g. public involvement), or on the level of details that are to be included. This follows from the fact that Status Reviews fill several functions, and that 'Status Review' is not a statutory or regulatory term. Hence, Status Reviews vary in methods, scope, and recommendations.

Under Section 4 (c) (2) of the ESA, the purpose of a five year Status Review is to evaluate information on a listed species, and to:

> "(A) conduct, at least once every 5 years, a review of all species included in that list which is published pursuant to paragraph (1) and which is in effect at the time of such review; and (B) determine on the basis of such review whether any such species should – (i) be removed from such list; (ii) be changed in status from an endangered species to a threatened species; or (iii) be changed in status from a threatened species to an endangered species."

In essence the purpose of a review is to determine:

- Whether new information suggests that the species population is increasing, decreasing, or stable
- Whether existing threats are increasing, the same, reduced, or eliminated
- If there are any new threats

- If new information or analysis calls into question any of the conclusions in the original listing determination

Hence, five year Status Reviews are focused on the five listing factors used by USFWS in making listing decisions:

A. The Present or Threatened Destruction, Modification, or Curtailment of Its Habitat or Range.
B. Over-utilization for Commercial, Recreational, Scientific, or Educational Purposes.
C. Disease or Predation.
D. The Inadequacy of Existing Regulatory Mechanisms.
E. Other Natural or Man-Made Factors Affecting Its Continued Existence.

In this scientific evaluation, we will be focusing on factors A., B., C., and E. The USFWS will evaluate D., regulatory mechanisms as part of their process, and also make a final evaluation on status, based on all five factors.

We will also be focusing on changes in threats since the time of listing, and the most recent Status Review (1990).

2 SUSTAINABLE ECOSYSTEMS INSTITUTE

Sustainable Ecosystems Institute (SEI) is a public benefit, non-profit organization, founded in 1992 by Dr. Deborah Brosnan. The goal of the Institute is to provide impartial scientific support for conservation decisions; the Institute is non-partisan, and seeks science-based, cooperative solutions to environmental issues. The organization has previously carried out extensive work on endangered species conservation and management, and has developed the use of peer review in such situations (Brosnan 2000).

3 REVIEW PROCESS

The overall goal of this review is to provide a comprehensive, and critical evaluation of all important information regarding the status of Northern Spotted Owls. Ultimately, this evaluation will be used by USFWS as part of its materials in making a determination on listing status under the Endangered Species Act. However, the SEI evaluation team will not be making recommendations on listing actions, or indeed on any management or policy decision. These are appropriately the responsibility of USFWS. Our process is restricted to summarizing, critiquing, analyzing, and synthesizing all available science.

The process adopted was to set up a panel of experts drawn from a range of different academic backgrounds relevant to the status review. These experts read the materials that were available or that were developed, and in a series of public meetings and other discussions, evaluated the strengths and weaknesses of the various data, hypotheses and opinions. This panel of experts was supported by a staff of scientists who developed materials for their use. In addition, some other scientists helped with particular chapters where their expertise was useful.

3.1 SCIENTIFIC STAFF

Overall project lead was Dr. Steven Courtney, Vice-President of SEI, who has expertise in endangered species research and management, and in the application of peer review processes to natural resource management issues.

Panel members and their particular expertise in the review were:

Dr. Richard Bigley	Habitat Distribution and Trends
Prof. Martin Cody	Inter-specific interactions
Dr. Robert Fleischer	Genetics and Systematics
Dr. Alan Franklin	Spotted Owl biology
Prof. Jerry Franklin	Forest ecology
Prof. Rocky Gutiérrez	Spotted Owl biology
Dr. John Marzluff	Endangered species biology; disease ecology
Dr. Jack Dumbacher	Genetics and Systematics

Dr. Dumbacher originally was part of the genetics sub-team (see below), but subsequently assumed most of the duties of a full panel member, and participated in discussions and manuscript preparation etc.

All panelists discussed all materials (not just their narrow subject areas), and are equally authors of all the chapters presented in this report. Curriculum vitae of all panelists are shown in the Appendix.

In addition to the overall panel, other team members were:

Dr. Jennifer Blakesley	Habitat associations, demography
Dr. Andy Carey	Prey
Mr. William La Haye	General biology
Mr. David Kennedy	Barred Owl
Prof. Barry Noon	Extinction risks and population models

Prof. Craig Moritz	Genetics
Dr. W. Monahan	Morphology
Ms. Lisa Sztukowski	Prey

These additional team members provided information, and helped prepare individual chapters. However, they did not participate in the writing of all the chapters as did the main Review Panel.

Team members were organized into particular sub-groups, addressing particular subject areas. These sub-groups took the lead in discussing and writing chapters. Sub-groups were:

Systematics and Genetics:
- Fleischer
- Dumbacher
- Moritz
- Monahan
- Gutiérrez
- Courtney

Prey:
- Sztukowski
- Courtney
- Carey

Habitat Associations:
- Blakesley
- Gutiérrez
- Marzluff

Habitat Trends:
- Bigley
- J. Franklin
- Courtney

Barred Owls:
- Cody
- Gutiérrez
- Marzluff
- Courtney
- Kennedy

Demography:
- Blakesley
- A. Franklin

Courtney
Noon

3.2 INFORMATION

Information for the review was obtained in several ways. USFWS sought public input through a comment period; all materials (papers and comments) received by USFWS were made available to SEI. USFWS staff also prepared some preliminary analyses and summaries, which were very useful in the initial phases of the review. Tracey Fleming and collaborators had also developed a database of publications on the Northern Spotted Owl; this became the kernel of our own database.

Panelists and SEI staff also actively sought out information, through publication requests, interviews etc. Such information included the details of existing analyses, requests for new analyses, natural history observations, clarifications on techniques etc. These data and personal communications were added to the database.

SEI also requested information from the USFWS, notably analyses of habitat trends (this forms a large part of the work analyzed in chapter 6). The Service also, at our request, prepared summaries of other material, including monitoring data from HCPs, and collated information on the occupation of Spotted Owl areas after temporary occupancy by Barred Owls.

The public continued to submit material to the panel until mid July 2004. All such material was logged, and included in the review. Notable data include papers by R. Pearson, and analyses by AFRC (2004), and the genetics group of San Jose State University.

The panel members also generated new reviews and data themselves. Notable in this regard is the work in chapter 7 synthesizing information on competition and size differences in owls (by Cody), and the statistical analyses of A. Franklin (also in Chapter 7).

Finally, the panel commissioned several pieces of research and synthesis. Several appendices (e.g. chapters 3, 4, and 8) were prepared at the request of the panel. These appendices remain the sole work of their respective authors, and should not be seen as carrying the approval of the entire panel, or reflecting their authorship. They do not form part of the Status Review per se; however, they were very useful to the reports' authors, and are included with this report as background material.

In total, some 1100 documents and communications were received, and form the basis for this review, together with the transcripts from public meetings, copies of presentations, etc.

3.3 PUBLIC MEETINGS

An important part of the work of the science team was the public examination of scientific materials. Four public meetings were held (over a total of six days), during which time there was both formal presentation and discussion of scientific materials, and also structured debate on the best interpretation of these data. The goals of these meetings were to ensure that all scientific opinions were heard, and that the pros and cons of alternative viewpoints were vigorously and transparently debated. Much useful information was obtained through these meetings. The transcripts of discussions and the scientific presentations themselves are also part of the record of this review.

As a consequence of discussions during public meetings, several individuals and organizations prepared new materials for submission to the panel. These iterative interactions between the panelists and other scientists ensured that all information was presented and discussed, and that subjects were explored openly and fully.

3.4 OPINION

This report is to a very large extent a work of consensus. Initial draft chapters were circulated among the panel, and debated extensively by e-mail, conference call, and in meetings. Despite many initial differences of expertise and opinion, panelists were largely able to agree on the best interpretation of information, and on the relative uncertainty regarding different opinions, hypotheses and data. However, no attempt was made to enforce unanimity among the panel. On a few issues, despite vigorous and lengthy debates, several opinions remained. Throughout this document, we have indicated the degree of unanimity of the panel on different topics, and ensured that where there is a diversity of opinion this is clearly stated. As noted, on very few topics was there substantive disagreement – this may reflect on the relative certainty of many of the findings of the panel.

Nevertheless, some diversity in opinion did occur. In order to capture such variation, we include in chapter 10 a questionnaire that sets out individual responses to many key issues, including those of information quality and of uncertainty. This chapter should be referred to throughout a reading of the rest of the report, as it documents the relative unanimity of the panel on each topic.

4 SCIENTIFIC INFORMATION AND DATA QUALITY

Science proceeds as information is gathered, but also as theories develop and change. Scientific opinion, particularly in young and developing fields, is rarely static or unanimous – differences in opinion may be the fuel for the preparation of key experiments or observations. Any practicing scientist recognizes this inherent uncertainty; it is indeed the very stuff of science. Hypotheses are not proven, but disproven; initial models are replaced by better models; all scientific opinion is provisional. Chapter 10 discusses the growth of scientific information and uncertainty in more detail.

The Endangered Species Act, the Data Quality Act, and other laws affecting resource management, set out requirements for the use of science. These legal standards are important in making practical use of scientific information. However, there is no objective scientific definition for terms such ‘best available scientific information’. Sometimes, for instance, conflicting hypotheses may be equally well supported. It is important to note that science usually relies on ‘most widely accepted science’ or a majority opinion, but that very often an initial minority opinion subsequently becomes most favored.

Peer review is the primary means by which scientific information is evaluated – it is scientific 'quality control'. Usually (but not always), peer review is carried out at the point when information is published in a scientific journal or similar publication. A journal editor tries to ensure that external reviewers scrutinize methods, analysis, interpretation etc., in order to determine whether the work is of sufficient scientific standard to warrant publication. However, peer review is not infallible: mistakes in review do occur, and the fact that a paper has been peer-reviewed is no guarantee of infallibility. Brosnan (2000) provides a lucid explanation of some of the difficulties that arise when applying peer review approaches to resource management decisions.

In this report, we have striven to provide an objective assessment of the information available on each topic. This includes frank discussion on the uncertainty inherent in some observations and data, and our opinions on the quality of the information presented. We have distinguished between peer-reviewed information and other information. Generally, we have held a stronger regard for data and hypotheses that have already received review; however, we have also recognized that such data are not sacrosanct, and have maintained a critical attitude to the published literature. At several points in this review we point out errors in published, peer-reviewed information.

The panel discussed whether to exclude from consideration all information that has not been peer-reviewed. Eventually, we decided to include non-peer-reviewed data, because these were sometimes the only data available on a topic (and hence 'best available science'). Examples include the monitoring data on habitat trends presented by USFWS. Some such data were also excellent, and rigorously analyzed. For instance, the meta-analysis of demographic trends was not reviewed at the time we read it – yet it represents one of the crown jewels of conservation biology. To exclude such high-quality information would have been to ignore the 'best available information'. Nevertheless, the panel decided to distinguish all data or observations that were not peer-reviewed – these are italicized in the text thus: *Anon (2004).*

The panel also made other judgments on scientific quality. Essentially, simple observations, or personal communications were weighed less heavily than rigorous data collection. We valued more highly those hypotheses that had been subjected to experimental test, and regarded untested hypotheses as exactly that. We also looked critically at the use of statistics, including whether there was adequate statistical power to reject hypotheses (a common error is to falsely reject ideas on the basis of weak tests that lack adequate power to detect an effect). We made no hard and fast rules about levels of statistical significance; the 95 or 99% confidence intervals widely seen in scientific literature are essentially conventions, not hard rules. Hence, when a test suggested a result that just failed to meet such levels we noted this as weak evidence, and considered the power of the test when making our evaluation. We also emphasized rigor in interpretation of statistical analyses; for instance, correlation of two factors or effects does not necessarily imply a causative relationship (effects through a third factor may explain such results). Throughout the review we attempted to consider alternative hypotheses and valued evaluations including approaches that compared alternatives (e.g. goodness of fit modeling approaches).

Nevertheless, we recognize that the highest standards were not always met by the data available; we provided our frank evaluation of such material, including an explicit discussion of the strengths and weaknesses of the information. In chapters 10, 11, and 12 we discuss in more depth the uncertainties of information on the Northern Spotted Owl, and the risks posed by managing under such uncertainties.

5 PROCEDURES FOLLOWED

The drafting authors of each chapter (identified as such at the front of each chapter) were responsible for the initial reading and evaluation of all material on a particular topic. Each paper was read by several panelists or authors, and was critiqued and examined for errors or weaknesses. Such information was recorded and entered into the database. The 'type' of data or paper was also noted (peer-reviewed or not, type of publication, etc.).

The drafting authors then prepared a review chapter, which was circulated to the entire panel, often with key papers. Panelists often asked for further publications to be sent for examination. These drafts were then subject to multiple revisions, following arguments and debate. This constituted a form of internal 'peer review' where the drafting authors were responsible for responding to the other panelists in a new draft.

Many of the chapters were also subject to external peer review. The coordinator of the project, Courtney, selected reviewers for their impartiality and expertise. These external peer reviews were then sent to the drafting authors, who re-crafted the chapters in response to reviewers' critiques. We accepted and made changes to the manuscript in response to comments on editorial matters (clarity etc.,) analysis, overlooked publications, alternative hypotheses, and errors in interpretation. The manuscript is stronger for these reviews. However, not all criticisms were accepted. Reviewers' comments and our responses to them are presented in the Record.

We also sought USFWS commentary on the draft chapters. We accepted comments on editorial issues (particularly ease of understanding and use by Service personnel), analysis, and overlooked publications. Although we clarified our positions in response to USFWS queries, we did not modify any of our opinions or evaluations in response to USFWS comments. Hence, this scientific evaluation represents our own impartial opinions, and is independent of any USFWS opinion regarding the Northern Spotted Owl.

6 ORGANIZATION OF REVIEW

The final decision of the USFWS on the status of the Northern Spotted Owl will be made with reference to the five factors used in listing decisions (see above). We have elected not to follow this pattern, but to organize our report along biological lines. Nevertheless, our report can be readily evaluated in reference to the listing factors:

A. The Present or Threatened Destruction, Modification, or Curtailment of Its Habitat or Range.

Addressed in chapters 5 (habitat associations), 6 (habitat trends), and 8 (demography)

B. Over-utilization for Commercial, Recreational, Scientific, or Educational Purposes.

Regarded (as in 1990) as unimportant, and not addressed in depth in this report

C. Disease or Predation

Addressed in sections of Chapter 8 (demography)

D. The Inadequacy of Existing Regulatory Mechanisms.

Not formally addressed in terms of regulatory sufficiency (outside our agreed scope of work). Chapter 9 (conservation science) evaluated the extent to which existing conservation measures are based on sound science. Chapter 11 (threats) evaluates the likelihood of continuing threats under current conditions.

E. Other Natural or Man-Made Factors Affecting Its Continued Existence

Addressed in chapters 3 (genetics), 7 (Barred Owls), parts of 8 (demography).

As noted above, our main approach throughout this review has been to compare information available now to that at the time of listing (1990), and to update the evaluation of 1990 where appropriate.

7 GENERAL ACKNOWLEDGEMENTS

This scientific evaluation of the Northern Spotted Owl has involved the work of many scientists. Although the authors of this report are responsible for all the opinions expressed herein, the review itself is only possible because of the extraordinary efforts of the hundreds of individuals who have studied, monitored, and managed Northern Spotted Owls. The strengths of the review derive directly from this unprecedented effort in conservation biology.

We thank all the many biologists, managers and members of the public who participated directly in this review, by attending meetings, making presentations, providing data, answering questions, and engaging in debate. Again, this review benefited greatly from such input. There are so many contributors of note that it would be unfair to single out any one individual for their scientific input. However, we do thank in particular Tracey Fleming for making available his database on Spotted Owl literature that formed the basis for our own database.

Several biologists and foresters provided external peer review on our report. These reviews are discussed in detail in the Record.

We also thank our colleagues in the USFWS. In addition to providing much initial information and synthesis, USFWS staff, particularly Mr. Barry Mulder, Ms. Robin Bown, Dr. Danielle Chi, and Dr. Karl Halupka, have courteously assisted our process at every stage, while carefully respecting our independence. Ultimately, if this review is useful to the Service in its future deliberations on Spotted Owl status, such success is due in part to the easy cooperation showed by the Service personnel assigned to the project.

SCIENTIFIC EVALUATION OF THE STATUS OF THE NORTHERN SPOTTED OWL

CHAPTER TWO

Northern Spotted Owl Biology

Drafting Author:
W. La Haye

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1 INTRODUCTION

The Spotted Owl (*Strix occidentalis*) occurs in western North America from southwestern British Columbia, Canada, to central Mexico (Gutiérrez et al. 1995). Throughout its range it is primarily associated with older age forests having relatively closed canopies (Forsman et al. 1984, Ganey and Balda 1989, Bart and Forsman 1992, Bias and Gutiérrez 1992, Call et al. 1992, Gutiérrez et al. 1995, Seamans and Gutiérrez 1995, Moen and Gutiérrez 1997, LaHaye and Gutiérrez 1999, Peery et al. 1999). The only major exceptions to this generalization are in the southwestern United States, where it sometimes occupies deep, steep-walled canyons (Rinkevich and Gutiérrez 1996), and in some portions of the Pacific Northwest, where it occurs in relatively young forests (*Irwin et al. 1991*, *Anderson and Farnum 1993*, Diller and Thome 1999, Thome et al. 1999, Folliard et al. 2000).

For more than a century since this species was described, the Northern Spotted Owl (*S. o. caurina*) was considered a rare, seldom-seen resident of the vast, virgin forests of the Pacific Northwest (Bent 1938). By the mid 1970s, new research in this region indicated a more widespread distribution, a higher population density, and a strong association between this species and late-successional stage forests (*Forsman 1976*, 1977, *1980*; Gould 1977; Forsman et al. 1984). This new information, coupled with rapid logging of virgin forests following World War II, resulted in concern for the conservation status of this owl (USDI Fish and Wildlife Service 1973, 1982, 1987, 1989, 1990, Dawson et al. 1985, Anderson et al. 1990, Gutiérrez 1994).

When continuing research indicated that this species probably required many hectares of old-growth forest of high commercial value, much controversy ensued over proper management of this species. This controversy centered on the conservation needs of the owl and economic and social needs of the timber industry. This controversy made Spotted Owls one of the most studied birds in the world (Dixon and Juelson 1987, Lôhmus 2003). The political controversy that evolved (Simberloff 1987, Doak 1989, Wilcove and Murphy 1991) spawned numerous management plans for this species (e.g., Marcot et al. 1986, USDA-PNW 1988, Thomas et al. 1990, Noon and Murphy 1997, USDI 1993, Noon and McKelvey 1996, Marcot and Thomas 1997, *Washington Department of Natural Resources 1997*). These developments highlighted the complexities of managing a rare, but currently wide-spread species which appeared to require large tracts of older forest for its continued existence (Gutiérrez et al. 1995). Over time, it became clear a solution to this complex problem would require advances in population analysis, forest-wildlife relationships, forestry, as well as adaptability of the timber industry and federal, state, and local governments (Salwasser 1987, Gutiérrez et al. 1995, Noon and Murphy 1997).

2 PHYSICAL CHARACTERISTICS

The Northern Spotted Owl is a medium-sized owl about 0.5 m in length with a wing span around 1.0 m (Dawson 1923, Gutiérrez et al. 1995). It has dark eyes, chocolate-brown plumage with white spots, and no ear tufts (Gutiérrez et al. 1995). The sexes have similar plumage, but are sexually dimorphic in size (Johnsgard 2002, Blakesley et al. 1990). Females are typically 10-20% larger in mass than males (540-850 g versus 490-690 g, respectively).

The Barred Owl is similar in appearance, but can be distinguished from Spotted Owls by its slightly larger size, ashy-gray coloration, horizontal bars on its breast, and vertical streaks on its abdomen (Gutiérrez et al. 1995, Mazur and James 2000). During the last several decades, the Barred Owl has expanded its range into the Pacific Northwest (Campbell 1973, Hamer et al. 1994, 2001, Dark et al. 1998, Herter and Hicks 2000, Pearson and Livezey 2003) where it is known to displace (Dunbar et al. 1991, Iverson 1993, Kelly et al. 2003), hybridize with (Hamer et al. 1994, Herter and Hicks 2001, Peterson and Robins 2003), and possibly kill Northern Spotted Owls (Leskiw and Gutiérrez 1998). Hybrids generally appear like large, light-colored Spotted Owls. The head and tail feathers are most similar to those of Barred Owls and the breast and abdomen appear intermediate with white patches separated by brown streaks and bars (Gutiérrez et al. 1995).

3 DISTRIBUTION

The Northern Spotted Owl is found from southwestern British Columbia, western Washington and Oregon, into northwestern California south to Marin County (*American Ornithological Union 1957*, *Forsman 1976*, Forsman et al. 1984, Gutiérrez et al. 1995). The range of the Northern Spotted Owl does contact the range of the California Spotted Owl (*S. o. occidentalis*) in northern California near the southern end of the Cascade Range (Thomas et al. 1990, USDI 1992, Barrowclough et al. 1999, Haig et al. 2001).

4 VOCALIZATIONS

Vocalizations of the Spotted Owl include an array of hoots, whistles, and barks (*Forsman 1976*, Forsman et al. 1984, *Fitton 1991*, Gutiérrez et al. 1995). Thirteen different calls have been described and are used by both sexes. Female and male calls can be identified by the pitch of the call. Females have distinctively higher-pitched calls than males for all vocalizations. The following is a brief description of the most common vocalizations used by this species, including comments on the perceived use of each call. For a thorough discussion of Spotted Owl vocalizations, see *Forsman (1976)*, Forsman et al. (1984), *Fitton (1991)*, Gutiérrez et al. (1995), *Waldo* (*2002*), and *VanGelder* (*2003*).

The *four-note location call* is used to announce territoriality, locate a mate, or announce prey deliveries. Phonetically it is described as *hoo—hoo-hoo—hooo*. Other commonly used hoots are *agitated location calls* (*hoo—hoo-hoo-ow*) and *series location calls* which are extended versions of the four-note location call lasting 7-15 notes and are most often used for territorial defense. Both agitation and series location calls are used to convey aggression and males tend to use them more often than females.

Contact calls are hollow whistles ending in an upward inflection (*cooo-weep*) and are typically used by females to announce their locations to mates. Males use this call infrequently except when presenting prey to their mate or young. Agitated contact calls are a louder, shriller form of the contact call and are most often used by females during territorial defense.

Bark series calls are 3-7 note calls (*ow!-ow!-ow!-ow!-ow!-ow!*) used primarily during territorial disputes and most commonly by females. *Begging calls* are employed by young of the year and sounds like a raspy contact call. Phonetically, it is a gravelly *cooo-weep* or *sweeeet*. Females may exhibit similar behavior and calling patterns during the nesting season using a soft contact call to stimulate delivery of prey from their mate.

5 BEHAVIOR

5.1 LOCOMOTION

The Spotted Owl spends virtually its entire existence beneath the forest canopy. Thus, its flight pattern shows adaptations to maneuverability rather than strong, sustained flight (Gutiérrez et al. 1995). Most daily movements are accomplished by numerous short flights, using a series of wing-beats followed by gliding (Gutiérrez et al. 1995). Upslope flight appears labored and unhurried.

5.1.1 NON-FLIGHT MOVEMENTS

Occasionally, Spotted Owls will walk along limbs or on the ground for short distances to chase prey, cache prey, or change roost locations (Gutiérrez et al. 1995). This owl walks with an ambling, rolling gate occasionally flapping its wings to maintain balance when running. Before juvenile owls are capable of flight, they can walk or climb using their feet and bill (Kristan et al. 1996).

Spotted Owls forage by moving from perch to perch through the forest. They are classified as perch and pounce predators because once on perch they sit, look and listen for prey activity and then attack the located prey (*Forsman 1976, Forsman 1980*, Forsman et al. 1984, Gutiérrez et al. 1995). Prey can be detected by sound as prey species move among branches or through forest litter. Spotted Owls have the morphological characteristics associated with owls that hunt primarily using sound localization: a well-developed facial disk, asymmetrical positioning of ear openings and large preaural folds (Norberg 1977, Volman and Konishi 1990). Prey can also be detected by sight.

Upon satiation, Spotted Owls will cache surplus food for later use (*Forsman 1976*, Forsman et al. 1984, Gutiérrez et al. 1995). The majority of the time, this involves placing the remaining portion of the prey item in a partially concealed location on the limb of a tree. However, other suitable locations include cavities in trees, broken tree stubs, on the ground at the base of a tree, and on the ground near logs. Alternatively, owls may simply roost with surplus prey in their talons or placed immediately beside them on the branch where they are roosting. Concealment of cached prey may have evolved in response to kleptoparasitism by other species, particularly birds (Hunter et al. 1993).

5.2 SELF-MAINTENANCE

5.2.1 PREENING, SCRATCHING, CLEANING

Spotted Owls often preen themselves while they are roosting. Spotted Owl pairs are very social and often allopreen with their mates when roosting together. They also preen their young regularly.

5.2.2 ROOSTING AND THERMOREGULATION

Spotted Owls select sheltered roosts to avoid inclement weather, summer heat, and predation (*Forsman 1976*, *1980*, Barrows and Barrows 1978, Barrows 1981, Forsman et al. 1984, *Ting 1998*). This owl has a narrow thermal neutral zone (Ganey et al. 1993, Weathers et al. 2001) and during summer months selects cool, shady roosts to minimize exposure to warm temperatures (*Forsman 1976*, *1980*, Barrows and Barrows 1978, Barrows 1981, Forsman et al. 1984, *Solis 1983*, *Ting 1998*). During warm weather, Spotted Owls seek roosts in shady recesses of understory trees and occasionally will even roost on the ground (Barrows and Barrows 1978, Forsman et al. 1984, Gutiérrez et al. 1995). In winter, they roost relatively high near the bole of canopy trees with overhanging branches to shelter themselves from precipitation. On sunny winter days they occasionally seek roosts with sun exposure (*Sisco 1984*). During the course of a day, Spotted Owls may move short distances in response to temperature changes or to avoid direct sunlight (*Ting 1998*). Once an owl becomes overheated, it will gular-flutter, followed by standing erect, exposing its legs, and partially spreading its wings (*Ting 1998*). Both adult and juvenile Spotted Owls have been observed drinking. Drinking has been observed primarily during summer and is possibly associated with thermoregulation (Gutiérrez et al. 1995). However, Weathers et al. (2001) suggested that this owl requires more water than most birds and may obtain nearly 40% of its required water by drinking.

5.2.3 PELLET DEPOSITION

Spotted Owls usually swallow an entire prey animal whole if it is small, or a sizeable portion if it is a large prey. On occasion they may remove viscera of larger small mammals, but they generally eat prey whole. As a consequence, the undigested portions of prey (e.g., claws, hair, bones) are regurgitated as a compact pellet. Little is known about the frequency or timing of pellet regurgitation (*Smith et al. 1999*). However, pellets are regularly found near roosts during the breeding season, but less so during the winter. In spring and summer, pellets are most commonly cast in the late afternoon or evening (Gutiérrez et al. 1995). However, they often regurgitate pellets to make room for recently captured prey and may commonly regurgitate pellets while foraging.

5.2.4 GENERAL DAILY ACTIVITY PATTERN

Spotted Owls are primarily nocturnal (Forsman et al. 1984). They forage between dawn and dusk and sleep during the day. Peak activity occurs during the two hours after sunset and the two hours prior to sunrise (Forsman et al. 1984, Gutiérrez et al. 1995, Delaney et al. 1999).

However, this owl will readily take advantage of opportunities to capture vulnerable prey near their roosts during daylight hours (Laymon 1991, Sovern et al. 1994).

5.2.5 AGONISTIC BEHAVIOR

Spotted Owls become alert when roosting whenever large birds fly over the canopy or when potential predators enter nest or roost stands (*Forsman 1976*, Gutiérrez et al. 1995). They will actively defend their nests and young from avian and mammalian predators, including biologists (*Forsman 1976*, Gutiérrez et al. 1995). Defensive behavior includes agitated calling, posturing, flying, and if sufficiently provoked, physical attack. Attacks involve repeated strikes where the owl attempts to talon the head and upper body of the intruder (Gutiérrez et al. 1995).

5.3 TERRITORIALITY

Spotted Owls are highly territorial and regularly confront conspecifics with aggressive vocal displays (*Forsman 1976, 1980*; Forsman et al. 1984, Gutiérrez et al. 1995, Franklin et al. 1996). In extreme cases, physical confrontations may occur but are thought to be rare and of short duration. They apparently learn to recognize their neighbor's voices and calling patterns and respond to them much less vigorously (*Fitton 1991*, *Waldo 2002*). Because of their strong territoriality, survey protocols have been developed for this species (Forsman 1983). In the past decade, it has been noted that Spotted Owls seem to respond less when Barred Owls are present and several incidences of Barred Owls replacing Spotted Owls have been recorded (Iverson 1993, Hamer et al. 1994, Gutiérrez et al. 1995, Dark et al. 1998, Kelly et al. 2003). It is possible that Spotted Owls exhibit reduced response rates when Barred Owls reside nearby (Gutiérrez et al. 1995).

5.4 SEXUAL BEHAVIOR

5.4.1 MATING SYSTEM

Spotted Owls are generally monogamous and primarily mate for life. While divorce does occur (Forsman et al. 2002), the majority of Spotted Owls exist with a single mate throughout their lives (Gutiérrez et al. 1995). Pair bonds can last a decade or longer.

5.4.2 PAIR ACTIVITIES

Pairs begin roosting together 4-6 weeks prior to egg-laying in late February or early March (*Forsman 1976*, Gutiérrez et al. 1995). Pairs commonly roost together from March to June and less frequently the remainder of the year. Spotted Owls regularly roost side-by-side during the breeding season and often allopreen (Gutiérrez et al. 1995, Forsman et al.1984). Copulation begins 2-3 weeks before egg-laying and becomes more frequent immediately prior to laying (*Forsman 1976*, Forsman et al. 1984).

6 INTERSPECIFIC INTERACTIONS

6.1 NONPREDATORY

Spotted Owls are regularly mobbed by smaller birds (Gutiérrez et al. 1995). Mobbing is primarily done by social corvids, such as Steller's Jays. However, numerous diurnal bird species may also participate. Most species that mob Spotted Owls have been recorded in this owl's diet and this may partially explain mobbing. Red-tailed Hawks (*Buteo jamaicensis*) and ravens (*Corvus corax*) have been documented kleptoparasitising Spotted Owls (Hunter et al. 1994), and Barred Owls will displace Spotted Owls (*Hamer 1988*).

6.2 PREDATION

Predation on Spotted Owls has not been directly observed. However, Northern Goshawks (*Accipiter gentiles*), Cooper's Hawks (*Accipiter cooperi*), Red-tailed Hawks, and Great Horned Owls (*Bubo virginianus*) have been implicated as potential avian predators (*Johnson 1992*). Leskiw and Gutiérrez (1998) may have recorded predation of a Spotted Owl by a Barred Owl (*Strix varia*). Fisher (*Martes pennanti*) have been seen climbing in Spotted Owl nest trees and may eat Spotted Owl eggs and young (Gutiérrez et al. 1995).

7 BREEDING

7.1 PHENOLOGY

7.1.1 PRENESTING BEHAVIOR AND NEST SELECTION

Pairs begin to roost together from February to early March and regularly call to each other and interact at dawn and dusk (*Forsman 1976*, Forsman et al. 1984, Gutiérrez et al. 1995). Similar to most owls, Spotted Owls do not construct their nests. Suitable nesting platforms are selected and the owls do little except minor reshaping of the nest surface. Eggs are typically laid between the middle of March and the middle of April (*Forsman 1976*, Forsman et al. 1984, Gutiérrez et al. 1995). Occasionally, clutches are initiated later than mid-April (inferred by late fledging and estimated age of juveniles). However, it is unknown whether these are late-starting first clutches or attempts to renest after an initial failure. Although renesting has been reported (Lewis and Wales 1993, Forsman et al. 1995) it is rare, and production of a second brood has not been documented for this species.

7.1.2 INCUBATION, BROODING, AND FLEDGING

Incubation lasts about 30 days and is performed exclusively by the female (*Forsman 1976*, Forsman et al. 1984, Gutiérrez et al. 1995). Brooding is also done exclusively by the female and she provides constant attention to the young until they are 8-10 days old (*Forsman 1976*). At this time, the female begins to leave the nest for short periods of time to forage. During incubation and the first 10 days of brooding, the male provides all food for himself, his mate, and their young (Forsman et al. 1984).

Brooding continues until the nestlings are around 35 days old (*Forsman 1976*, Forsman et al. 1984, Gutiérrez et al. 1995). The female spends less time in the nest as the young grow and develop. However, she can almost always be found in close proximity to the nest during this time and regularly roosts on the closest available perch, often within a couple meters. At about 35 days old, the young fledge but are incapable of flight (*Forsman 1976*). They either hop out of the nest to nearby branches or jump to branches below the nest or to the ground. The growth rate of juvenile bills and feet far exceeds that of other body structures and appears to be adapted to handling prey and climbing to safe perches (Kristan et al. 1996).

7.1.3 FLEDGLINGS

Once they have left the nest, fledglings spend the remainder of spring and summer moving from branch to branch gaining mass and developing their flight feathers (*Forsman 1976*, Forsman et al. 1984, Gutiérrez et al. 1995). By August, parents spend substantially less time attending their young, while fledglings begin to forage opportunistically but clumsily (Gutiérrez et al. 1995). By September, parents feed their young irregularly and some juveniles begin to disperse. Most young have dispersed by early November (Gutiérrez et al. 1985, Forsman et al. 2002).

8 PLUMAGE CHARACTERISTICS

Hatchlings are sparsely covered with white natal down until they are about 10 days old (Forsman 1981). The prejuvenal molt is completed in 34 to 36 days (Forsman 1981). Retrices reach full development by 75 days of age (Forsman 1981). The prebasic I molt begins at 8 to 9 weeks of age and is completed by late September or October (Forsman 1981). Plumage color is chocolate brown. The retrices and remiges are retained from the juvenal plumage (Forsman 1981, Moen et al. 1991). The tips of the retrices are white with pointed, downy tips and subadults are distinguished from adults by this characteristic (Moen et al. 1991). Juvenal retrices and remiges are molted at 26 months of age (Forsman 1981). Adult plumage characteristics are similar to Basic I plumage except for the tips of the retrices, which are rounded and mottled after this molt.

9 DISEASES AND PARASITES

Very little is known about diseases affecting Spotted Owls (Gutiérrez et al. 1995). However, Thomas et al. (2002) documented a case of spirochetosis and there is considerable concern that Spotted Owls may be susceptible to West Nile Virus (Rapploe et al. 2000, Komar et al. 2003, Male 2003).

The documentation of parasites in Spotted Owls is more substantial. These include ectoparasites (Young et al. 1993, Hunter et al. 1994, and Morishita et al. 2001), endoparasites (Hoberg et al. 1993), and hematozoa (Gutiérrez 1989).

10 SURVEY METHODS

10.1 PRESENCE-ABSENCE SURVEYS

Spotted Owls are very territorial and the majority of territory defense is accomplished through vocalizations (*Forsman 1976*, 1977, 1983). Thus, surveying known Spotted Owl sites or potential habitat can be accomplished by imitating Spotted Owl calls (Forsman 1983, Ward et al. 1991, USFWS 1993, Franklin et al. 1996, Reid et al. 1999).

Surveys are usually designed to cover an entire area thoroughly. Imitated calls can be heard for at least ½ kilometer from a survey point or route (Forsman 1983, Franklin et al. 1996). Thus, surveys are spaced to avoid gaps in coverage. Most surveys are accomplished by using a series of call points from which imitated or tape recorded owl calls are broadcast. Call points are established throughout an area of interest such as along existing roads and trails at a spacing that avoids or minimizes gaps in coverage (Forsman 1983, Franklin et al. 1996).

A complete survey is defined as the effort needed to access and survey all areas that could reasonably be expected to be included within a Spotted Owl territory (USFWS 1993). The current survey protocol requires three complete surveys per year for two consecutive years or six complete surveys during a single year (USFWS 1993).

10.2 SURVEYS TO ASSESS REPRODUCTION

Surveys to assess Spotted Owl reproduction are performed once presence-absence surveys have determined that a site is occupied and the project requires information on the reproductive activity of the owls occupying the site (Forsman 1983, USFWS 1993, Franklin et al. 1996). First, the owls must be visually located. Second, the owls must be fed mice to stimulate the owls to feed their young, if present (Forsman 1983, USFWS 1993, Franklin et al. 1996).

Standard minimum effort requirements include: attempting to visually locate the owl(s) on at least four occasions, feeding the owls a minimum of two mice per occasion, and attempting to verify the results of the first successful reproductive survey with a repeat survey (USFWS 1993). Some flexibility is required when attempting to complete reproductive surveys, because, the owls do not always cooperate fully.

10.3 CAPTURE TECHNIQUES

Capturing Spotted Owls is usually attempted during daylight hours when the owls are roosting (Forsman 1983, Franklin et al. 1996). Nighttime captures are also possible, but the owls are more active and have the advantage of superior night vision. In general, this species is approachable and appears somewhat tame. A common practice is to present a mouse or rat to them, which distracts them while a capture is attempted (Forsman 1983, Franklin et al. 1996). While this is typically accomplished using a live rodent, fur-covered toys, dead rodents and tethered raptors have also been used as lures.

The most commonly used capture techniques used with Spotted Owls are mist nets, snare poles, noose poles, and by hand. The use of mist nets is based on the premise that Spotted Owls prefer to fly down-slope after capturing prey. Nets are positioned down-slope from a lure accessible to the owl such that the owl flies down-slope into the net after attempting to capture the lure (Forsman 1983, Franklin et al. 1996). Once the owl hits the net, the owl is quickly restrained and removed from the net.

A snare pole is a long (6-8 m) modified fishing pole with a snare (a noose that self-tightens when pulled against resistance) on one end (Forsman 1983, Franklin et al. 1996). Snare poles are used to capture owls while they are perched on branches at their roost or in a position where they were available for capture. Once the owl is in position, one person distracts the owl using a lure while another person slips the snare over the owl's head and onto its neck. When the snare has been placed in the correct position on the owl, it is drawn tight onto the owl's neck feathers by applying tension to the snare. Once the snare is snug on the owl's neck feathers, the owl is lowered to the ground and restrained. The snare pole is currently the most common technique used to capture owls.

Noose poles are similar to snare poles, except that the noose must be drawn tight by the operator. This is accomplished by the noose cord extending the length of the pole to the operator's hands. Once the noose is in position on the owl, the noose cord is pulled which closes the noose on the owl's neck feathers. Capturing owls with a noose pole is accomplished in the same manner as described for the snare pole.

SCIENTIFIC EVALUATION OF THE STATUS OF THE NORTHERN SPOTTED OWL

CHAPTER THREE

Assessment of the Subspecies and Genetics

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1 SUBSPECIES STATUS

1.1 SUMMARY STATEMENT

*Here we review available data that may offer insight into the subspecies status of the Northern Spotted Owl (*Strix occidentalis caurina). *These data include morphological (morphometric and plumage), behavioral (vocalizations), and genetic characters (including allozyme, RAPD, mitochondrial DNA sequence, and microsatellite markers). Mitochondrial DNA and microsatellite allele frequencies provide the greatest power to resolve the Spotted Owl subspecies, while morphology, vocalizations, allozymes and RAPDs provide less informative variation. Both mitochondrial DNA and microsatellites provide adequate information to distinguish the geographically defined Northern and California Spotted Owl subspecies under standard subspecies definitions, and support the current subspecific designations. There is a relatively low percentage of mitochondrial haplotype mixing near to the geographical boundary of the two subspecies in Northern California and southern Oregon; this is often observed and expected between valid subspecies. Although the present data do not allow us to draw conclusions about the history, directionality, and the eventual outcome of this mixing, we present alternative ways to interpret this and suggest that future studies investigate genetics along this hybrid zone. Under FWS guidelines, these data suggest that Northern Spotted Owls are both genetically significant and discrete from other subspecies.*

The Northern Spotted Owl (*Strix occidentalis caurina*) was listed as a threatened subspecies under the U. S. Endangered Species Act (ESA) on June 26, 1990 (55 FR 26194). Early forms of the ESA afforded protection only to named species and subspecies. In 1978, the ESA was amended to include "distinct population segments" of vertebrates in order to protect reproductively isolated populations that have unique genetic attributes ["Any subspecies of fish or wildlife or plants, and any distinct population segment of any species of vertebrate fish or wildlife which interbreeds when mature" (Endangered Species Act, Sec. 3 (15))]. The Spotted Owl currently includes three subspecies, *S. o. caurina*, *S. o. occidentalis*, and *S. o. lucida*, the Northern Spotted Owl, California Spotted Owl, and Mexican Spotted Owl. There has been substantial criticism of the subspecies concept (e.g., Wilson and Brown 1953, Selander 1971, Zink 2004), and some response to this criticism (Smith and White 1956, Parkes 1982, Patten and Unitt 2002), but this taxonomic level was included in the U. S. ESA, and the Northern Spotted Owl was originally listed as threatened at this taxonomic level. Thus we address whether existing data support designation of the Northern Spotted Owl as a distinct subspecies. We are not, however, limited from also addressing whether the data support designation at other taxonomic levels or conservation unit definitions. In Part I, we evaluate evidence pertaining to the validity of the subspecies designation of the Northern Spotted Owl (*S. o. caurina*). We compare the available and relevant morphological, ecological, and genetic data to established criteria for designating subspecies. In addition, we discuss, and evaluate the data in light of the criteria of other potential defined units of conservation, including phylogenetic species (Cracraft 1983), distinct population segments (DPS), evolutionarily significant units (ESU), and management units (MU) (Waples 1991, Vogler and DeSalle 1994, Moritz 1994, Crandall et al. 2000).

1.2 DEFINITIONS

Below we summarize taxonomic and conservation unit definitions. The reader should bear in mind that there is a diversity of opinion among biologists about such definitions and their application. For example, some biologists might advocate that subspecies never need to be defined; if taxa are diagnosable then they should be considered separate phylogenetic or evolutionary species. In addition, while some of these are classical taxonomic units (e.g., subspecies, biological species), others were not initially defined in a taxonomic context and represent a unit that was defined instead for conservation management purposes (e.g., ESU, DPS, MU). Also, these units do not necessarily nest into a hierarchy of levels. While there are many definitions of taxonomic and conservation units, there is a consensus opinion among conservation and evolutionary biologists that diagnosable genetic and taxonomic diversity is important and requires preservation.

1.2.1 TRADITIONAL SUBSPECIES

Subspecies are considered to be recognizably different but interbreeding populations of the same biological species in different geographical areas. A subspecies may be considered "a collection of populations occupying a distinct breeding range and diagnosably distinct from other such populations" (Mayr and Ashlock 1991). Amadon (1949) derived the "75% rule" for delineation of subspecies, in which 75% of a population must be distinct or diagnosably different from 75% of the individuals of the other population. Patten and Unitt (2002) proposed formalizing the 75% rule, and provided a quantitative method for determining the validity of subspecies. Under their methods, “to be a valid subspecies 75% of a population must lie outside 99% of the range of other populations for a given defining character or set of characters.” For characters that occur as separate states, such as presence or absence of a plumage pattern or mtDNA haplotype or clade, the test involves a simple contingency table analysis. For continuously varying, normally distributed traits, such as measurements of body size, the rule involves comparison of the two distributions via their means, standard deviations and the expectation of 75% non-overlap from a t-distribution. Thus, unlike the biological species concept, this taxonomic level does not require reproductive isolation (i.e., a defined small level of hybridization or gene flow is allowed between subspecies). This rule has been applied sporadically, but increasingly, in the literature (e.g., Patten and Unitt 2002, Meijaard and Groves 2004), and it provides a quantitative method to evaluate distinctiveness and in which to make subspecies designations (Patten and Unitt 2002). Relevant morphological, genetic and ecological information about the Spotted Owl subspecies will be compared to the criteria of these definitions in order to ascertain the support for the subspecies status of the Northern Spotted Owl.

1.2.2 PHYLOGENETIC SPECIES DEFINITIONS

The phylogenetic species concept defines a species on the basis of phylogenetic history and diagnosability. The argument for using them over subspecies or ESUs is that “species” are traditional taxonomic entities. Cracraft (1983) defines a species as “the smallest diagnosable cluster of individual organisms within which there is a parental pattern of ancestry and descent” or later (Cracraft 1989) as “an irreducible (basal) cluster of organisms, diagnosably distinct from other such clusters, and within which there is a parental pattern of ancestry and descent”. A more history-based definition by Baum and Donoghue (1995:567) states that a species is “a basal group of organisms all of whose genes coalesce more recently with each other than with those of any organisms outside the group”. They claim that this is because "species are defined solely on genealogical history rather than on characters." We evaluate the data on the Northern Spotted Owl on the basis of both genealogical history and diagnosability.

1.2.3 DISTINCT POPULATION SEGMENT DEFINITIONS

A distinct population segment (DPS) is not well described in the ESA, but some definitions have been developed over the past decade. The National Marine Fisheries Service (NMFS) developed criteria for salmonid populations to be considered a DPS:

> (1) It must be substantially reproductively isolated from other conspecific population units; and
> (2) It must represent an important component in the evolutionary legacy of the species.

The U.S. Fish and Wildlife Service acknowledged these criteria, and noted that most Evolutionarily Significant Unit (ESU) definitions (see below) would qualify as a DPS. They developed the following policy as regards DPS (USFW- *The Federal Register* for Wednesday, February 7, 1996 (Vol. 61), p. 4722):

> “Three elements are considered in a decision regarding the status of a possible DPS as endangered or threatened under the Act. These are applied similarly for addition to the lists of endangered and threatened wildlife and plants, reclassification, and removal from the lists:
> 1. Discreteness of the population segment in relation to the remainder of the species to which it belongs;
> 2.The significance of the population segment to the species to which it belongs; and
> 3.The population segment's conservation status in relation to the Act's standards for listing (i.e., is the population segment, when treated as if it were a species, endangered or threatened?).
>
> *Discreteness*: A population segment of a vertebrate species may be considered discrete if it satisfies either one of the following conditions:
> 1. It is markedly separated from other populations of the same taxon as a consequence of physical, physiological, ecological, or behavioral factors. Quantitative measures of genetic or morphological discontinuity may provide evidence of this separation.
> 2. It is delimited by international governmental boundaries within which differences in control of exploitation, management of habitat, conservation status, or regulatory mechanisms exist that are significant in light of section 4(a)(1)(D) of the Act.
>
> *Significance*: If a population segment is considered discrete under one or more of the above conditions, its biological and ecological significance will then be considered in light of Congressional guidance (see Senate Report 151, 96th Congress, 1st Session) that the authority to list DPS's be used "...sparingly" while encouraging the conservation of genetic diversity. In carrying out this examination, the Services will consider available

scientific evidence of the discrete population segment's importance to the taxon to which it belongs. This consideration may include, but is not limited to, the following:
1. Persistence of the discrete population segment in an ecological setting unusual or unique for the taxon,
2. Evidence that loss of the discrete population segment would result in a significant gap in the range of a taxon,
3. Evidence that the discrete population segment represents the only surviving natural occurrence of a taxon that may be more abundant elsewhere as an introduced population outside its historic range, or
4. Evidence that the discrete population segment differs markedly from other populations of the species in its genetic characteristics.

Because precise circumstances are likely to vary considerably from case to case, it is not possible to describe prospectively all the classes of information that might bear on the biological and ecological importance of a discrete population segment.

Status: If a population segment is discrete and significant (i.e., it is a distinct population segment) its evaluation for endangered or threatened status will be based on the Act's definitions of those terms and a review of the factors enumerated in section 4(a). It may be appropriate to assign different classifications to different DPS's of the same vertebrate taxon."

Therefore, in this case, the DPS definition contains criteria of several definitions of ESUs (see below), although some criticisms of equating DPS with ESU have been made (e.g., Pennock and Dimmick 1997). We will compare data available for the Northern Spotted Owl with relevant applied ESU definitions.

1.2.4 EVOLUTIONARILY SIGNIFICANT UNIT DEFINITIONS

Several definitions for "evolutionarily significant units" (ESUs) have been proposed in the scientific conservation literature (Ryder 1986, Waples 1991, Moritz 1994a, b, Vogler and DeSalle 1994, Barrowclough and Flesness 1996, Moritz and Faith 1998, Crandall et al. 2000, Moritz 2002). Perhaps the most stringent definition is that of Vogler and DeSalle (1994), in which an ESU is "delimited by characters that diagnose clusters of individuals to the exclusion of other such clusters" (one that is similar in its criteria to the phylogenetic species concept, see above). An early definition of ESUs required assessment of characters that may be adaptive to local environments (Waples 1991), but evidence of this sort can be very difficult to obtain, and other methods based more on maintenance of evolutionary history over adaptability became more widely accepted. In this vein, Moritz' (1994b) definition was developed, and relies largely on the determination of reciprocal monophyly in mtDNA sequences (each geographically based population coalesces to a common mtDNA haplotype ancestor) and significant differentiation of nuclear gene allele frequencies. This definition has been used widely in conservation biology, and is perhaps the definition most often applied to assess avian ESUs (e.g., Fleischer 1998, Lovette et al. 1999, Tarr and Fleischer 1999, Zink et al. 2000). A more recent method for defining ESU's incorporates information from morphological and ecological traits, as well as molecular characters (Crandall et al., 2000). These all agree on two essential points. First, to be defined as a unique unit, a Spotted Owl subspecies must have diverged sufficiently in diagnosable characteristics to allow identification of one population from another. Second, these characteristics should have some heritable or genetic component. We note that it is not necessarily these characteristics that we are trying to protect or conserve. Rather, these measurable characteristics are a proxy for identifying populations that have shown significant evolutionary change while isolated from other such populations. This broader ESU concept is in many ways similar to the phylogenetic species concept (Cracraft 1989; Baum and Donoghue 1995).

ESUs do not necessarily need to meet the criteria for "biological species" (Mayr 1963), which define actually or potentially interbreeding populations as the same species. Thus, while the biological species concept relates to the future potential for genetic mixing, the ESU (and phylogenetic species) concept is related to the past evolutionary relationships and recognizing groups that have broadly significant genetic differences (including differences in adaptation or genetic attributes). We acknowledge that there may be significantly different ESUs that deserve conservation attention, and at the same time there can be some amount of measurable gene flow among these groups. Indeed, many threatened and endangered species are listed (esp. plants) despite genetic introgression from other species.

1.2.5 MANAGEMENT UNITS

Management units (MUs) are populations or sets of populations that are demographically independent (Moritz 1994, 1995). They are usually defined by having significant differences in allele frequencies. MUs are usually smaller units than ESUs and are appropriate units to use for monitoring impacts of management (Moritz 1995).

1.3 SPOTTED OWL HISTORICAL TAXONOMIC OVERVIEW

The taxonomic committee of the American Ornithologists' Union previously identified *S. o. caurina*, *S. o. occidentalis*, and *S. o. lucida* as valid subspecies from 1910 through 1957, after which the checklists stopped providing subspecies summaries (*American Ornithological Union 1957*). A fourth named subspecies, *S. o. huachucae* (the Arizona Spotted Owl; Swarth 1910; Swarth 1915), was not formally recognized by the ornithological community (*American Ornithological Union 1957*). Subspecific designations have traditionally been based on research and expert opinion, and the Birds of North America species account for the Spotted Owl (which also is an AOU publication) provided a brief discussion of the three previously recognized subspecies (Gutiérrez et al. 1995). The two subspecies of primary interest for this review are *S. o. caurina* (Northern Spotted Owl) and *S. o. occidentalis* (California Spotted Owl).

1.4 MARKERS USED AND EXPECTED PATTERNS

Several types of characters can use be used to define and distinguish taxa. For very distantly related groups, characters such as morphology and nuclear DNA coding sequences (including allozyme analysis) are often useful. However at the intraspecific level, markers must be carefully chosen so as to provide the necessary variation to distinguish closely related taxa or populations. In the past decade, the field of intraspecific phylogenetics and phylogeography was revolutionized by the application of high-resolution genetic markers such as mitochondrial DNA sequences and microsatellite loci. Over the period during which Spotted Owl systematics research has been conducted, a variety of markers have been used, including morphological characters, behavioral characters, allozymes, Randomly Amplified Polymorphic DNA (RAPD) markers, mitochondrial DNA and microsatellites. Here we summarize potential strengths and weaknesses inherent in each marker type, and we critically evaluate the available data and the published interpretation of these data.

Before evaluating the available data, we further address how patterns of character variation and levels of genetic divergence can inform us about subspecies diagnosis and validity. To be able to draw conclusions about differentiation, one needs to identify markers that show variability. For example, many protein coding nuclear genes are identical or nearly identical between humans and chimps. We cannot, therefore, on the basis of these genes, conclude that chimps and humans are the same species. Instead, we need to find a gene that shows variability, and examine the way that the variation is distributed between humans and chimps. Thus, genes that show little or no variation are normally considered uninformative about the question of subspecific variation. To support the subspecies designation, we must find a character of a trait that generally has one state in the one subspecies and another state in another. In other words, we have to find some "diagnostic character or group of characters" that can be used to distinguish clearly one subspecies from another. This character can be morphological, protein, DNA, or behavioral, but it should have some heritable basis. Alternatively, to refute subspecies status, we need to find a suite of characters that varies, but the variability is "shuffled" among the geographically defined subspecies or populations, showing that there has been no divergence, or there has been significant mixing subsequent to divergence. The degree to which the character states are subdivided or are mixed tells us how much genetic distinctness or genetic mixing is taking place. If however, a large sample of appropriate genes or other characters are examined and they show no differentiation, there would be little or no support for the designation of separate subspecies or other taxonomic units.

1.5 MORPHOLOGICAL PATTERNS

Strix occidentalis was described by Xanthus in 1859, and *S. o. caurina* by Merriam in 1898. Merriam remarks (1898:40), "Comparison of the northwestern Spotted Owl with the type specimen of *S. occidentale* shows it to be a well-marked subspecies, differing, like so many birds of the same region, in darker and richer coloration". Coues (1903) described the Northern Spotted Owl as possessing smaller white markings, especially on the head and back, as well as darker primary tips and tail bands. Ridgeway (1914:650) concluded that the Northern Spotted Owl was similar to the California Spotted Owl, but "decidedly darker, the brown darker in tone and greater in area, the white spotting correspondingly reduced, and the legs more heavily mottled." According to Pyle (1997), the Northern Spotted Owl exhibited smaller spots on the central upper breast contour feathers, darker wing and tail bars, and darker leg feathering. Barrows et al. (1982) also identified slight differences among Northern Spotted Owl and California Spotted Owl in the number and patterns of tail bars. Both recent studies (Barrows et al. 1982 Pyle 1997) include illustrations demonstrating the observed patterns of spotting and barring; however there are no statistical analyses to evaluate them and no examination of additional specimens to test their conclusions.

In addition to describing plumage characters, Ridgeway (1914) measured the total length of study skin, wing, tail, and culmen. He found an Northern Spotted Owl male (*n* = 1) was slightly larger than California Spotted Owl males (n = 6), but Northern Spotted Owl females (n = 4) were slightly smaller than a California Spotted Owl female (n = 1). He presented only the range and the mean, and his sample sizes are probably too small to demonstrate statistically significant differences. Gutiérrez et al. (1995) recorded similar measurements from field studies in which wild birds were captured, measured, and released. Barrowclough (1990) quantified morphological differences/similarities among subspecies using multivariate (principal components [PCA]) analyses, but did not report his original data, details of sample sizes, or univariate means or variances (it is not standard practice to include such data in conference proceedings). Clear differences emerged in multivariate space between the Mexican Spotted Owl and Northern Spotted Owls/California Spotted Owls, however variation in plumage color and pattern between Northern Spotted Owl and California Spotted Owl was shown to be clinal. The cline in coloration followed a well-known phenomenon called "Gloger's rule" (Orr 1971) where darker individuals inhabit areas of higher humidity. Thus the coloration may be adaptive for the owls (Barrowclough and Flesness 1996). Clines often occur in species in relation to clinal variation in some physical feature of the environment (temperature, rainfall, ecotones), but can also be generated by secondary contact and hybridization (Endler 1977). They can present complications in defining taxonomic entities, especially if they are smooth (which is the case in Spotted Owl morphological measurements), as opposed to step, clines. Adaptive variation is important for managers to maintain, but if clinally distributed, creates difficulties when defining management boundaries.

In the literature reviewed here, clear discrepancies exist between the qualitative and quantitative morphological data. While the existing qualitative accounts indicate that the Northern Spotted Owl is different from California Spotted Owl in appearance, the quantitative studies suggest that the observed patterns of morphological variation fail to cluster individuals according to the two traditionally named subspecies. Nevertheless, only Oberholser (1915) has recommended joining Northern Spotted Owl and California Spotted Owl into a single subspecies (on the basis of his examination of 31 specimens). He points out that multiple "California birds" are indistinguishable from the Northern Spotted Owl. Bent (1938) criticizes Oberholser's work because Oberholser based his findings on a single Northern Spotted Owl specimen (the *S. o. caurina* type specimen).

In an effort to build upon previous research aimed at quantifying differences and similarities among Northern Spotted Owls and California Spotted Owls, we conducted a new morphometric study using 62 museum specimens (Table 3.1, Table 3.2A,B) collected throughout western North America (methods in Appendix 1). Subspecific differences between the Northern Spotted Owl and the California Spotted Owl were minimal for all eight characters examined (Table 3.2). This was also true for comparisons between Northern Spotted Owl and far northern Northern Spotted Owl specimens collected north of the zone of mitochondrial introgression extending up into central Oregon (Table 3.2). Subspecies exhibited considerable overlap in component space (Fig. 1), suggesting that Northern Spotted Owl and California Spotted Owl are relatively undifferentiated for the characters examined. Neither PC1 nor PC2 was significantly correlated with latitude (Fig. 2). In summary, both the univariate and multivariate results establishing the lack of diagnostic differences between Northern Spotted Owl and California Spotted Owl are in accord with Barrowclough (1990) and Barrowclough and Flesness (1996). However, given the rather small sample sizes and number of characters included in the new analyses reported here, these findings do not mean that Northern Spotted Owl and California Spotted Owl are morphologically identical. They are simply indistinguishable according to the quantitative characters considered in the study.

In **conclusion**, the ornithological community has since the early 1900s consistently recognized Northern Spotted Owl, California Spotted Owl, and Mexican Spotted Owl as valid Spotted Owl subspecies based on phenotypic differences in coloration and size as well as geographical ranges. Despite difficulties with actually quantifying morphological differences and delineating distributional boundaries between Northern Spotted Owl and California Spotted Owl, several studies have identified a series of qualitative plumage characters for assigning individuals without a priori knowledge of geography. Hence, morphological criteria for distinguishing subspecies have been suggested, although to our knowledge these have not been tested rigorously. The characters that were identified in earlier studies appear not to clearly diagnose all three subspecies, although body size does differentiate the Mexican Spotted Owl from the other two subspecies. In addition, some clinal patterns of variation have been found for plumage between the Northern Spotted Owl and the California Spotted Owl. Understanding the historical and evolutionary underpinnings of these patterns requires consideration of the associated molecular and ecological data.

1.5.1 BEHAVIORAL MARKERS

Behavioral markers such as song have been useful in distinguishing subspecies and in some cases cryptic species (Irwin et al. 2001, Isler et al. 2002, Groth 1988). A recent study of the Spotted Owl four-note location call evaluated various correlates of song variation. *Van Gelder (2003*) found that the model that best explained variation in Spotted Owl calls was a model inferring that all three subspecies are distinct. This model had the lowest Akaike value and accounted for 83.6% of the Akaike weight, which indicates strong fit of these data to the model. These data additionally suggest that the subspecies have significant differences in song.

1.6 GENETIC MARKER PATTERNS

Genetic studies have explored variation and its geographic distribution in Spotted Owls using several common genetic markers, including allozymes (Barrowclough and Gutiérrez 1990), mitochondrial DNA (Barrowclough et al. 1999, Haig et al. 2004a; *Chi et al., unpublished*), Randomly Amplified Polymorphic DNA or RAPDs (Haig et al. 2001), microsatellite markers (*Henke et al., unpublished,* Thode et al. 2002), and Amplified Fragment Length Polymorphism or AFLPs (Haig 2004b). These genetic markers provide different insights into the evolutionary processes leading to present day patterns of variation. They also vary in statistical power, and in appropriateness for the type of question being asked. Here we describe and compare these datasets and discuss their ability to provide inference about subspecies designations in the Spotted Owl. We conclude with an assessment of the most appropriate inference given the data. We also make simple predictions and suggest additional studies.

1.6.1 ALLOZYMES

Allozymes are protein variants of a single genetic locus that are distinguished by gel electrophoresis and specific staining. Proteins will move through a starch, polyacrylamide or cellulose acetate matrix depending on their size, charge and conformation. Particular types of proteins, mostly enzymes involved in cellular processes, can be specifically stained in the gel and the pattern interpreted as genotypes and alleles at genetic loci. If the band of a protein (whose amino acid sequence is produced by the DNA sequence of a genetic allele) differs in position in the gel from another, the genetic locus is considered polymorphic. Allozyme variants are rarely confirmed to conform to Mendelian expectation, but when tested, usually are. They have not been widely used in population and conservation genetics since the early 1990s.

The first published study of Spotted Owl genetics was Barrowclough and Gutiérrez's 1990 investigation of 23 blood protein loci in 107 individuals. Twenty-two of 23 loci were monomorphic across all populations; only one protein locus (Esterase-D) was variable. Polymorphism occurred only in the Mexican Spotted Owl subspecies, where the frequency of the most common Esterase-D allele was 0.389. The authors commented that although it was rare to find so little variation with 23 allozymes and sample sizes of over 100 individuals, these results were neutral or non-informative about the question of Northern and California Spotted Owl genetic differentiation (note this is analogous to the situation described above for the small sample of birds and variables measured in morphological studies).

In addition, many factors can make allozymes uninformative. First, proteins used in allozyme population studies are generally encoded in nuclear genes. The animal cell nucleus has several mechanisms to find and correct mutations, so mutations are relatively rare. In addition many mutations that occur are synonymous (they do not change the amino acid sequence), and thus do not change the protein. Those that do change the protein (non-synonymous) can disrupt the function of the protein so that it is removed rapidly by natural selection from the population. Furthermore, only a proportion of changes in the amino acid sequence translate to changes in electrical charge or size of the final folded molecule, and it is these two characteristics that determine the rate of mobility of proteins in a controlled electrical field such as an electrophoresis experiment. Thus, it is possible in allozyme studies to detect little or no informative variation even when several allozyme loci are screened, and even when significant variation is present at the gene level. In addition, the use of blood samples, rather than tissues, also substantially reduces the number of loci available to be screened (Fleischer 1998), however, because Spotted owls are threatened, only blood samples were available. Thus, this allozyme analysis provided a relatively low-resolution methodology for inferring intraspecific phylogenies, and is mostly uninformative for Spotted Owl subspecies.

1.6.2 MITOCHONDRIAL DNA

Mitochondrial DNA (mtDNA) makes up the genome of an intracellular organelle, the mitochondrion, and is a very commonly used marker in evolutionary, population and conservation genetic studies. MtDNA sequences have several genetic characteristics that make them useful for population studies. First, mitochondrial genes evolve at faster rates than nuclear genes. This provides more variation that can be evaluated in population studies. Second, mitochondrial genes have low effective population sizes, roughly 1/4 the size of nuclear gene copies. Thus, if populations are isolated and evolving independently, then mitochondrial genes are expected to show monophyly or reciprocal monophyly in roughly one-fourth the time that it takes for nuclear genes. Third, each DNA base can be clearly identified within each sequence of bases. Thus homology of characters and identity of character states can be more accurately inferred. Fourth, examining DNA sequence makes a greater proportion of variation visible, and even synonymous or "silent" mutations can be detected and scored. Fifth, our understanding and models of sequence evolution may allow more sophisticated estimation of evolutionary dates, rates of gene flow, and other population parameters.

Mitochondrial genes have several disadvantages as well. First, there is no recombination, so the entire mtDNA molecule is effectively only one single locus. As only one locus, it is difficult to discern whether its history is representative of the entire organism's genome. Second, mitochondria are passed only from females to offspring. Therefore population processes that can normally be tracked using genetics (such as dispersal, population bottlenecks, etc.) are only tracked in the female lineage. This can be a problem in special cases, such as when only one sex disperses or a disease attacks only one sex. Although these situations can occur, in practice, it is rare for a mitochondrial intraspecific history to be incongruent with a nuclear DNA intraspecific history (Avise 2000). Third, another concern with mtDNA is the possible amplification and sequencing of nuclear copies of mtDNA (termed NUMTs) (Soren and Fleischer 1996) – copies of the mtDNA sequence that have been transposed to the nuclear genome. Thus care must be taken to ensure that sequences obtained represent mitochondrial and not nuclear copies. Although there are a couple minor disadvantages, the advantages are also many, and so mitochondrial markers have become extremely useful for designating evolutionarily significant units (Moritz 1994a; Moritz 1994b; Moritz 1995; Avise 2000) and validating subspecies (Zink 2004).

BARROWCLOUGH ET AL. (1999)

These authors examined 1105 bases of the highly variable mitochondrial DNA control region from 73 individuals representing all three described Spotted Owl subspecies. They recovered 37 individual haplotypes, roughly one for every two individuals, and this provided sufficient variation to address the subspecies status of the owls. Their data revealed that every haplotype but one was unique to only one subspecies, which suggests little recent mixing. The various haplotypes showed nearly complete reciprocal monophyly of all three subspecies based on geographical positioning of samples, suggesting that each currently recognized subspecies is valid. Furthermore, they found that the California Spotted Owl is a sister subspecies to the Mexican Spotted Owl, and that the Northern Spotted Owl is more distantly related to these two. They found a single individual out of 20 sampled in the range of Northern Spotted Owl that had a California Spotted Owl haplotype, but no cases of Northern Spotted Owl haplotypes in the California Spotted Owl range. Their sample size along the Northern Spotted Owl - California Spotted Owl boundary was insufficient to address the extent or directionality of this introgression, but it does suggest that genetic mixing or introgression has occurred between the two subspecies, and that it may be directional (see Haig 2004a, results below). Coalescent theory (Hudson 1990) can be used to estimate the expected time that it would take for mitochondrial genes to segregate completely into three monophyletic subspecies, given present demographic parameters (Barrowclough and Coats 1985). This theory suggests that the subspecies have been separated on the order of more than ten thousand years. These are only rough estimates with unknown confidence intervals, but they offer some idea of the amount of time since these populations were mixed. The distribution of haplotypes suggests that there is substantial gene flow within, but little among, subspecies. Overall, we find that this study is carefully conceived, sample sizes are adequate to address subspecies divergence questions, the analyses are appropriate and the conclusions well formulated.

HAIG ET AL. 2004A

This study uses similar methodology (mtDNA control region sequencing) as Barrowclough et al. (1999), and comes to some similar conclusions, and others that differ. Haig et al. (2004a) used sequences of 522 base pairs of control region from 213 individuals from 30 local breeding areas, representing all three Spotted Owl subspecies. The sample includes the 73 Spotted Owl sequences from Barrowclough et al. (1999) and 140 new sequences. While their study has more individuals than Barrowclough et al. (1999), it also has fewer bases sequenced (1105 vs. 522). However, they have similar numbers of variable sites (63 in Haig et al., 2004a, and 61 in Barrowclough et al.), but some of the sites not included in the sequences of Haig et al. (2004a) are potentially informative ones for subspecies diagnosis (e.g., sites 2, 972 and 984). Thus the Haig et al. (2004a) analyses may have more power to detect introgressed haplotypes, but they may have reduced power for accurately resolving the intraspecific phylogeny. Haig et al. (2004a) found 63 unique haplotypes; 34 of these were recovered only from geographically-defined Northern Spotted Owl populations, five were recovered only from California Spotted Owl populations, 23 were recovered only from Mexican Spotted Owl populations, and only one haplotype was found in both Northern Spotted Owl and California Spotted Owl populations. This particular haplotype was the most common California Spotted Owl haplotype, and was found in 29 California Spotted Owl individuals as well as two individuals collected north of the traditional subspecies boundary. Thus, the subspecies were mostly represented by unique haplotypes (independent of clade structure of the haplotypes, see below), but clearly showed mixing in two individuals (less than 1% of all Spotted Owl individuals, or mixing in two of 168 Northern Spotted Owl + California Spotted Owl or 1.2%). The level of introgression is on the same level as that found by Barrowclough et al., even given the limited sample sizes of the previous study.

In addition to the haplotype distribution, we can also examine the genetic relationships of the haplotypes, as this can give additional information regarding from where the haplotypes may have been derived and historical population mixing. Haig et al. (2004a) reconstructed a phylogeny that suggests the same pattern of divergence between Northern Spotted Owl and California Spotted Owl populations that Barrowclough et al. (1999) also recovered, providing some evidence for the existence of the traditional subspecies. However, their phylogeny also suggested some historical mixing because some Northern Spotted Owl haplotypes appeared to be closely related to California Spotted Owl haplotypes. We note that bootstrap values on this portion of their phylogeny are weak (64% at the base of the California Spotted Owl - Mexican Spotted Owl clade in a neighbor-joining tree, Figure 2 of Haig et al., 2004a), so relationships among these haplotypes are not well supported by the data. This may be due to the smaller number of bases sequenced in this study than in Barrowclough et al. 1999, although it may be due to homoplasy in these control-region sequences. It is suggestive that there may have been some degree of historical mixing, or that these mitochondrial haplotypes are still sorting in this part of the range, or that there are not enough data at present to adequately resolve the phylogeny. All subsequent analyses (including the nested clade analysis performed by Haig et al. 2004a) are therefore tenuous at best. Because of this, we believe that Haig et al. (2004a) may err in too liberally assigning Northern Spotted Owl birds as having California Spotted Owl ancestry. Nonetheless, even under this liberal designation, there are 15 of 131 Northern Spotted Owl birds that are considered to have California Spotted Owl ancestry, and this is 11.5%. Thus, the Northern Spotted Owl and California Spotted Owl subspecies would still be considered valid under the 75% rule.

CHI ET AL., UNPUBLISHED

A preliminary analysis of Spotted Owl mtDNA sequences from four California populations was provided to the committee by T. Chi, A. Henke, C. Brinegar and J. Smith (San Jose State University, CA). This paper is an unpublished report based upon ongoing research, and is part of Master's Degree requirements for Chi and Henke. The populations examined included two in the traditional Northern Spotted Owl range (along the California coastal ranges in Marin County and Mendocino National Forest); and two in the California Spotted Owl range (in the El Dorado National Forest of the Sierra Nevada, and the Ventana Wilderness in Monterey County). The sample sizes per locality are adequate although the geographic sampling is restricted (Marin n = 19 individuals; Mendocino n = 19; El Dorado n = 14; Monterey n = 8), but the patterns observed do support and confirm the results of both Barrowclough et al. (1999) and Haig et al. (2004a). First, all 22 of the geographically defined samples of California Spotted Owl (that is, those from El Dorado and Ventana) can be found within a single well-supported (bootstrap = 96%) clade (their "California Spotted Owl clade"). The sister clade to this is also strongly supported (bootstrap = 96%), and includes all of the Marin samples and 16 of the 19 Mendocino samples (and is considered their "Northern Spotted Owl clade"). Two of the Mendocino samples have haplotypes that are unique to Northern Spotted Owl and yet cluster more closely with the California Spotted Owl clade, and a third matches the most common California Spotted Owl haplotype that presumably represents gene flow from California Spotted Owl into Northern Spotted Owl. The designation of separate subspecies based on the 75% rule is upheld, with only one of 38 birds collected in the Northern Spotted Owl range having California Spotted Owl haplotypes (2.6%) or three of 38 birds collected in Northern Spotted Owl range with haplotypes belonging to the California Spotted Owl clade (7.9%). An alternative way to look at this is that Northern Spotted Owl populations are at least 92.1% pure. **These subspecies differences are especially significant given the relative proximity of California Spotted Owl populations to the two Northern Spotted Owl populations evaluated in this study.** While these studies were not done precisely in the putative hybrid zone, all of the populations are located in Northern California where hybridization is more likely to be observed, if it is occurring.

To summarize and combine the results of these mitochondrial DNA sequences studies, **all studies agree that there are significant differences genetically between the Northern Spotted Owl and California Spotted Owl subspecies, and that these are more than 75% pure and diagnosable, and thus meet a quantitative subspecies definition. However, each**

study did also detect a small degree of haplotype mixing, mostly near the border of the California Spotted Owl and Northern Spotted Owl.

We might suggest three categories of mitochondrial evidence for historical mixing.

First, the strongest evidence consists of single haplotypes found to occur in both Northern Spotted Owl and California Spotted Owl ranges. This was detected in Barrowclough et al. (1999: one California Spotted Owl haplotype also occurring in Northern Spotted Owl range), Haig et al. (2004a, two California Spotted Owl haplotypes also found in Northern Spotted Owl range), and in *Chi et al. (unpublished)* (one California Spotted Owl haplotype also found in Mendocino).

Second, evidence of historical mixing might be found in haplotypes unique to Northern Spotted Owl or California Spotted Owl, but which cluster phylogenetically significantly within the clade of haplotypes from the range of the other subspecies. Barrowclough et al., found none of these, and likely had the greatest power to resolve the phylogeny due to the greatest number of bases sequenced. Haig et al. (2004a) found none of these, as no part of their California Spotted Owl clade is significantly supported (bootstrap support is less than 50% for every node related to the California Spotted Owl clade). *Chi et al. (unpublished)* found two additional Northern Spotted Owl individuals with haplotypes that clustered significantly with California Spotted Owl haplotypes (bootstrap support ~96%). While this is strong support, one of these haplotypes is basal and distantly related to other California Spotted Owl haplotypes, and may instead represent older historical mixing or incomplete lineage sorting since the subspecies were isolated.

Third, weak evidence for mixing might include finding haplotypes unique to Northern Spotted Owl or California Spotted Owl, but which cluster with haplotypes from the opposite range, despite lack of strong support for clustering. Haig et al. (2004a) found two haplotypes (KNLF 105 and HUMB118) that are only one base different from a California Spotted Owl haplotype, and three more that are two or more changes but weakly cluster with California Spotted Owl (WSPR21, ROSE76, and JACK86) despite also having similarities with Northern Spotted Owl haplotypes. Because this phylogenetic clustering is weak, this could alternatively be interpreted as evidence for genetic mixing, segregation, or an inaccurate tree; but is most honestly described as incomplete resolution of the tree, due to lack of data.

We note that finding a California Spotted Owl haplotype in a Northern Spotted Owl population does not necessarily mean that bird is a hybrid. These haplotypes could be evidence for 1) a long distance California Spotted Owl migrant, 2) a stray and confused bird that will eventually return to its former range (one can sometimes observe a rare individual far outside the normal species range), or 3) an individual with a mix of some Northern Spotted Owl and some California Spotted Owl alleles (a "hybrid"). *S. Haig (personal communication)* has noted that there are at least a few particular cases in which birds carrying what she describes as a California Spotted Owl haplotype have been mated with birds with an Northern Spotted Owl designated haplotype (although analysis of genotypes of offspring would be needed to confirm hybridization). Because a hybrid would have mixed ancestry and therefore genes from both Northern Spotted Owl and California Spotted Owl, this cannot be determined by looking solely at mitochondrial DNA. Multiple genetic loci must be screened to verify that a bird has hybrid origins. Such an analysis might include microsatellites or RAPD markers. We do believe, however, that the hybrid hypothesis is a reasonable and likely explanation for finding California Spotted Owl haplotypes in Northern Spotted Owl range.

We note that there is an important difference between biological ***classification*** and ***identification***. Two populations can be different enough to ***classify*** them as different entities (having different histories, different alleles, haplotypes, or allele frequencies, etc.), and there may be some individuals that cannot be clearly ***identified*** as members of one or the other group.

1.6.3 RAPD MARKERS

The RAPD method is "randomly amplified polymorphic DNA" and is a simple DNA analysis involving the Polymerase Chain Reaction (PCR), usually with a single small primer that amplifies random pieces of DNA from the entire genomic DNA sample. The resulting PCR products or fragments are run through an agarose gel and visualized with ethidium bromide staining as bands on the gel. The process produces from zero to dozens of bands or fragments. These are scored as variable if there is a band present at a particular point in the gel in at least one individual's lane that is absent in at least one other individual's lane. The differences are assumed to result primarily from changes in the priming sites. Thus, homozygote (++) and heterozygote (+-) each provide a band, and therefore cannot normally be distinguished on gels. This makes it difficult to accurately calculate allele frequencies without making additional assumptions. Furthermore, because there are multiple possible mutations that can eliminate bands, (-) alleles are not necessarily identical, and (--) individuals are not even necessarily homozygous. Combined with phenetic analyses, this can lead to clustering unlike individuals simply because they lack a band, despite the fact that there are many different "genetic character states" that are all scored as (--) in RAPD analyses. Nonetheless, RAPD analyses can indicate variable populations, and when interpreted carefully, can identify interesting populations for further study. RAPDs are thought to primarily target nuclear gene sequences, but unless one clones and sequences the genes, and determines what they are, their origins and inheritance are often unknown (and could even be derived from blood parasites or other commensal organisms). In general, these markers are expected to have lower mutation rates and hence lower evolutionary rates than mitochondrial genes. They, as putative nuclear genes, are also expected to take approximately four times longer to coalesce to a single ancestor than mitochondrial markers. Thus, population parameters that are being measured with RAPDs are averaged over longer time frames.

HAIG ET AL. (2001)

Haig et al. (2001) conducted a study to assess population genetics and geographic variation of Spotted Owls, mostly concentrating on very large samples of the Northern Spotted Owl, with smaller samples of California and Mexican Spotted Owls. Haig et al. (2001) scored and analyzed RAPD markers for 276 Spotted Owls. Using 400 RAPD primer pairs, they found 13 variable primer pairs with 17 bands. Six of these bands were sex-linked, and discarded from the analysis, leaving 11 remaining bands [or (+) alleles]. A variety of phenetic and statistical approaches were used to cluster and assign genotypes to particular groups. Although there were bands that clearly distinguished Mexican from California Spotted Owls, there were none that completely distinguished Northern Spotted Owls from either of the other subspecies. The number of variable bands was extremely low for RAPD studies, especially given the huge number of primer pairs tested (see discussion in Part III below).

Although Haig et al. (2001) state that their data conflict with those of Barrowclough et al. (Barrowclough et al. 1999), we do not believe that to be the case. We believe that the data are valid and consistent, but instead that an alternative and more plausible interpretation should be considered. The mitochondrial DNA data suggest that the subspecies have been evolving independently for more than 10,000 years, and this has allowed us to observe reciprocal monophyly in mtDNA among subspecies (although not strongly supported). Because the RAPD data did not recover the same evolutionary divisions, the nuclear RAPD data suggest that the subspecies separated less than 40,000 years (e.g., four times the coalescence time of the mtDNA), and genes are still segregating and show signs of that previous mixing. These observations are not mutually exclusive and, taken in combination, suggest that the subspecies began to evolve independently between 10,000 - 50,000 years ago.

Another possibility is that there is current gene flow between the Northern and California Spotted Owls. Unfortunately, these studies are unable to distinguish between current gene flow and historical (past) gene flow. Thus, the interpretation and implications of this are unclear and are in great need of further study.

Haig et al. (2001) also present cluster analyses in the form of "trees." There are reasons, however, to be cautious with the published interpretation of these RAPD data. First, the trees presented in this paper do not represent phylogenies in the traditional, or cladistic, sense, but are phenograms. Hence they do not necessarily imply genealogical relationships. Second, the RAPD trees were drawn using the Mexican Spotted Owl as an arbitrarily-chosen root, which then forces the Northern and California Spotted Owls to cluster together, and depicts Mexican Spotted Owls as a single "clade" by default. This depiction is not a result of the clustering analysis, but rather of an *a priori* rooting assumption made by Haig et al. (2001). (If these phenograms are more appropriately rooted, they can in some cases very closely resemble the phylogenies reconstructed from mtDNA.) Third, there is no bootstrap support greater than 50% for any of the important nodes. In other words, there is minimal support for any particular hypotheses in these analyses. Fourth, Barrowclough et al. (1999) as well as Haig et al. (2001, and in press a) both claim to document hybridization along the subspecies contact zone. Haig et al. (2001) treat this hybrid population as an "operational taxonomic unit" in their analysis, which provides a matrix of genetic distances and an analysis that is very difficult or impossible to interpret in terms of genetic relatedness of the individuals within the populations. As such, it is difficult to see how Haig et al.'s (2001) conclusions of genetic relatedness of individuals can be inferred from such analyses. Finally, only 25 California Spotted Owl samples are used in the analysis (and only 18 Mexican Spotted Owls), and 17 of the 25 are collected from an area very close to the contact zone between the Northern Spotted Owl and the California Spotted Owl. Because these are collected in an area near the contact zone (a zone of some unknown but potential hybridization), it may be unreasonable to use this one population to infer generalizations for the entire California Spotted Owl subspecies. Although Haig et al. (2001) failed to find significant structure at many levels, the molecular markers and analyses employed are not high resolution and are not likely to be well-suited for detecting structure among the subspecies. Thus, despite claims made in Haig et al. (2001), there is no obvious conflict between the mtDNA study of Barrowclough et al. and the RAPD data Haig et al. present. Because RAPDs segregate more slowly, one expects that they will not reveal recent divergences that are shown by mtDNA gene trees.

1.6.4 MICROSATELLITE LOCI

Microsatellites are usually nuclear DNA segments consisting of tandem repeats of 2-8 bases that appear in sets of a couple to several hundred repeats. The number of tandem repeats in microsatellites can evolve quickly, and so several different length alleles are often present in any given population. Variation is assessed by PCR amplifying across the repeat array and evaluating the size of the resultant fragments, usually on an automated sequencer. These markers have several advantages: they are fast evolving, usually autosomally inherited (ie. they are rarely sex linked), relatively easy to score, have many alleles at each locus, and tend to be useful for diagnosis at the subspecies level. Microsatellites are often used to infer patterns of nuclear gene flow and geographic subdivision in order to compliment mitochondrial studies, and are additionally useful for analyses of parentage, genetic census, and other fine-resolution issues.

Only one microsatellite study has been published on Spotted Owls, a paper by Thode et al. (2002). The purpose of this work is to identify several microsatellite loci that show variation within the Mexican Spotted Owl, and present primers and experimental conditions so that other labs can use these in genetic studies. This sort of paper is often referred to as a “primer note,” and is not intended to portray results of a major study. Although the microsatellite loci promise high variability and resolution for Mexican Spotted Owl studies, at least four of the loci also showed variability in the Northern Spotted Owl, indicating that these markers would be useful for other Spotted Owl subspecies.

A second, unpublished study by Henke et al. (*Henke et al., panel discussion*) has been provided to the committee. In this study, the authors analyzed four California populations of Spotted Owls: two in the Northern Spotted Owl range (along the California coastal ranges in Marin County and Mendocino National Forest); and two in the California Spotted Owl range (in the El Dorado National Forest of the Sierra Nevada, and the Ventana Wilderness in Monterey County). The authors used six of the loci provided by Thode et al. (2002); a seventh locus turned out to be linked to one of the others and was excluded from analysis. The sample sizes of individuals (per population mean of 38.2, range of 36-41) and loci (n = 6) are adequate for this type of study. This study was designed to address important genetic issues concerning population size and gene flow within and between the two subspecies, especially in the southernmost populations that have slightly different ecology and climate than the more northerly populations (see genetic variation section below). The results, while preliminary, suggest some microsatellite differences between the Northern Spotted Owl and California Spotted Owl populations. There are some unique, or nearly unique alleles, and major differences in allele frequencies. The authors provide estimates of both F_{ST} and G_{ST} for all pairwise comparisons among populations. G_{ST} provides a better estimator for divergent populations and subspecies (i.e., G_{ST} corrects for alleles divergent in size, and better represents evolutionary divergence than F_{ST}, which is calculated only from allele frequencies). All values were significantly different from 0, and some are quite large for microsatellite data. G_{ST} estimated within each subspecies is 0.055 for Northern Spotted Owl (between Marin and Mendocino) and 0.152 for California Spotted Owl (between El Dorado and Monterey). G_{ST} between subspecies averages 0.351 across the pairwise comparisons among subspecies, and ranges between 0.172 and 0.535. The major difference is between the Monterey population and all other populations (G_{ST} is 0.535, 0.407 and 0.288 for Monterey versus Marin, El Dorado, and Mendocino populations, respectively). In a clustering analysis, 150 of 153 birds clustered with others from their own subspecies, again supporting the 75% rule (figure 3.5). These researchers have also examined mtDNA sequences from the same populations (see *Chi et al., unpublished*, above) and have found concordance with the microsatellite results. Although these studies were not designed to specifically test the subspecies validity of the Northern Spotted Owl and the California Spotted Owl, they provide strong evidence that these particular Northern Spotted Owl and California Spotted Owl populations are genetically distinct and that gene flow is relatively low between them.

1.7 CONCLUSIONS FOR PART I: SUBSPECIES STATUS

Several studies have been performed that provide data that address the *discreteness* and *significance* (and hence the validity) of Spotted Owl subspecies. These have used morphological variables, vocalizations, allozyme loci, mitochondrial DNA markers, and nuclear DNA markers. Morphological markers show a great deal of variation; however, analyses of that variation have failed to demarcate clearly the geographically defined subspecies as currently named. We repeated these studies using characters that have been suggested as showing some variability, but again we found no significant patterns. Most nuclear genetic markers (allozymes and RAPDs) have shown remarkably low levels of variation, but some of this variation has been effective at distinguishing the Mexican Spotted Owl from the other two subspecies, and at showing some distinctions between the Northern Spotted Owl and California Spotted Owl (Barrowclough and Gutiérrez 1990; Haig et al. 2001). These studies also document some hybridization at or near the contact zone of the Northern Spotted Owl and California Spotted Owl. A recent study using six microsatellite loci provides evidence of significant differentiation between the California Spotted Owl and Northern Spotted Owl (*Henke et al., unpublished*), and again, some evidence for greater similarity of the subspecies closer to the area where they may come into contact.

Three recent studies using mitochondrial DNA sequence (Barrowclough et al. 1999, and Haig et al., 2004a, *Chi et al., unpublished*) show a genetic distinction between individuals classified by range or morphology as Northern Spotted Owl and California Spotted Owl birds. Furthermore, both datasets with the Mexican Spotted Owl included suggest that California Spotted Owl individuals are more closely related to the Mexican Spotted Owl than either is to the Northern Spotted Owl. All three studies separately and in combination support subspecies designations based upon the expectation of the 75% rule (Mayr and Ashlock 1991, Patton and Unitt 2002). Also, in a recent paper that criticizes many currently-named subspecies for having little, if any evolutionary significance, the Spotted Owl subspecies are held up as one of only a few cases where subspecies designations actually concur with genetic boundaries (Zink 2004).

Furthermore, mitochondrial sequences show reciprocal monophyly in our dataset with the greatest sequence length (Barrowclough et al. 1999) and near monophyly in others (Haig et al. in 2004a, *Chi et al., unpublished*), which suggests that the populations had been isolated at least on the order of N_e generations. This and the finding of significant divergence in nuclear allele frequencies (as shown by the *Henke et al., unpublished* microsatellite dataset, and in RAPD dataset of the Haig et al. 2001 paper) indicate that the two subspecies are likely ESUs under the Moritz (1994) definition (a widely utilized definition for ESUs), as well as those by Waples (1991) and Vogler and Desalle (1994). The evidence for, at least, clinal variation in coloration (Barrowclough 1990) and the results of the ecological niche models, suggest that there may also be adaptive differences between the Northern Spotted Owl and California Spotted Owl subspecies. This would indicate that the subspecies also match the definition of an ESU of Crandall et al. (2000). In addition, given the reliance of the DPS on an ESU definition (USFW-*The Federal Register* for Wednesday, February 7, 1996 (Vol. 61), p. 4722), the Northern Spotted Owl and California Spotted Owl would also qualify for DPS status. Based on the data we review, the Northern Spotted Owl clearly meets the first element required by USFWS for a DPS definition: genetic discreteness of the population segment. In addition, it seems clear to us that the Northern Spotted Owl meets the other two USFWS requirements of the DPS: significance and status. The data we evaluated do appear to confirm the discreteness and significance of all currently recognized Spotted Owl subspecies as subspecies, ESUs, MUs, and DPS (and some might argue phylogenetic species as well).

Both mitochondrial and nuclear genetic studies document some gene flow near the contact zone of Northern Spotted Owl and California Spotted Owl subspecies (see next section below), but the current low level and restricted range of introgression does not negate the subspecies status of the geographically defined taxa. For management purposes, it will be important to plan studies that can adequately document the future of this introgression, and better understand its causes and implications for Spotted Owl conservation.

2 SUBSPECIES HYBRIDIZATION AND GENE FLOW

The first known map illustrating the California ranges of the Northern Spotted Owl and California Spotted Owl showed a major disjunction between the two subspecies and provided no indication of contact (Grinnell and Miller 1944). Later maps and discussions of range show considerably wider range distributions and an area of potential contact that occurs in Northern California along the Sierra Nevada/Cascade Range axis. The range of the California Spotted Owl extends North to at least central Shasta County (Gutiérrez et al. 1995); the range of the Northern Spotted Owl south along the Cascades into Northern California in the Klamath and Shasta regions, and also in coastal forests south to Marin County (Gutiérrez et al. 1995). Thus the area of greatest potential for contact between the subspecies is in the Shasta-Klamath region on the California and Oregon border.

We wish to repeat, as we noted in section I, that **finding a California Spotted Owl haplotype in a Northern Spotted Owl population does not necessarily mean that bird is a hybrid**. These haplotypes could be evidence for 1) a long distance California Spotted Owl migrant, 2) a stray and confused bird that will eventually return to its former range, or 3) an individual with a mix of some Northern Spotted Owl and some California Spotted Owl alleles (a "hybrid"). We do believe, however, that the hybrid hypothesis is a reasonable and likely explanation for finding California Spotted Owl haplotypes in Northern Spotted Owl range. In addition, for some of the California Spotted Owl haplotype individuals in the Northern Spotted Owl range there is evidence that these birds are residents and have behaviorally mated with owls with Northern

Spotted Owl haplotypes (*S. Haig, personal communication*). We discuss the movement of genes in the following sections as if it is successful introgression, i.e. that they are found either in hybrid individuals or newly dispersed individuals whose descendents are likely to have mixed ancestry.

2.1 EXTENT OF GENE FLOW

There is no well-documented estimate of hybridization levels between Northern Spotted Owl and California Spotted Owl individuals based on field observation (other than the anecdotal cases noted above by S. Haig), perhaps because cases identified on the basis of plumage (and not on geographic location) are not likely to be made in the field. Morphological analyses do suggest clinal variation in ranking (dark to light brown) from the Northern Spotted Owl to the South into the California Spotted Owl, and then inland into the Mexican Spotted Owl (Barrowclough 1990). In the same study, no similar cline in measurements or overall body size was evident in the Northern Spotted Owl and California Spotted Owl, but the Mexican Spotted Owl was significantly smaller than both the Northern Spotted Owl and California Spotted Owl.

Genetic analyses have indicated varying levels of overlap or gene flow between the Northern Spotted Owl and the California Spotted Owl, but each of the studies thus far reported have aspects that make them less than ideal for assessing the level of introgression or hybridization. Barrowclough et al. (1999) used mtDNA control region sequences to show that geographically defined samples of Northern Spotted Owl and California Spotted Owl were largely confined to distinct clades, but did find that one out of 20 Northern Spotted Owl individuals had a haplotype that fell within the California Spotted Owl clade (5%). Limiting the sample to the 10 northern California individuals indicated a 10% rate of overlap or introgression. Haig et al. 2001 showed more extensive mixing between California Spotted Owl and Northern Spotted Owl based on RAPD analyses (perhaps as many as 35% of 234 Northern Spotted Owl individuals were assigned to the California Spotted Owl pool and 28% of 25 California Spotted Owl individuals assigned to the Northern Spotted Owl pool). The analysis is biased by the fact that nearly a quarter of the individuals genotyped were from the Klamath region where contact and hybridization is most likely, and where a stable hybrid zone may exist (see below). In addition, for many of the reasons noted above in the subspecies section of the report, RAPDs may not be the ideal markers to use for this type of analysis. In fact, subsequent mtDNA sequence analysis of 213 owls by Haig et al. (2004a) indicates a considerably lower rate of gene flow into the traditional geographic range of the Northern Spotted Owl (at most, 15 or 11.5% of 131 owls). If the analysis is limited to the Klamath region, this value goes up to 12 or 20.3% of 59 birds, suggesting most of the overlap is in the area surrounding the zone of contact between the two subspecies. Given the greater median dispersal distance of female Northern Spotted Owls (Forsman et al. 2002), mtDNA (as a female to female inherited marker) indicates a liberal estimate of the extent of introgression, and the overall extent of introgression would be likely to be even less.

The microsatellite analyses by *Henke et al. (unpublished)* provide an additional source of information on the question of gene flow in California. This study includes four populations, including two Northern Spotted Owl populations in Marin and Mendocino counties, and two California Spotted Owl populations in Placer and Monterey counties. Divergence, as measured by F_{ST} or G_{ST} values among the four populations, shows higher values among subspecies than within. However, divergence between the Placer and Mendocino populations appears to be nearly half of that between the Placer and Marin populations, suggesting that there may be more historical mixing between California Spotted Owl and Mendocino Northern Spotted Owl populations.

Both the limited Barrowclough et al. (1999) study, and the Haig et al. (in press a) study indicate that most gene flow is directional from the California Spotted Owl northward into the historical range of the Northern Spotted Owl in the Klamath region of northern California and southern Oregon (Haig et al. 2001, in press a; Barrowclough et al. 1999). In particular, Haig et al. (2004a) found no Northern Spotted Owl haplotypes outside of the geographical range of the Northern Spotted Owl, but 15 California Spotted Owl haplotypes within the historical range of the Northern Spotted Owl. We note, however, that *G. Barrowclough (personal communication)*, with recent and improved sampling in the California Spotted Owl range, has also documented Northern Spotted Owl gene flow into California Spotted Owl geographic ranges.

It is unclear whether this gene flow among the subspecies is increasing, stable, or decreasing over time. It is very difficult to determine, without proper sampling and a surfeit of markers, the history of a zone of probable secondary contact between two taxa (Endler 1977). One option we can suggest for future work is an assessment of museum specimens of owls from this region to examine changes in haplotype frequencies and introgression over time (assuming these are available).

2.2 POTENTIAL FOR FUTURE HYBRIDIZATION BETWEEN SUBSPECIES

At the present time, the level of introgression appears to be below a level that would engender any changes to the subspecies, ESU or DPS status of the Northern Spotted Owl. It is unclear whether the current gene flow is increasing, decreasing, non-existent, or constant, and whether the contact zone represents a stable zone of limited hybridization, as found for some other avian and non-avian species (e.g., *Corvus corone*x *C. cornix* hybrid zone in Europe, Risch and Anderson 1998). The ecological niche models presented for the Northern Spotted Owl and California Spotted Owl suggest the existence of intermediate or ecotonal habitat at the subspecies boundary. If there has been local adaptation, then gene flow between the two subspecies may be limited to the ecotonal region, but not much beyond it. On the other hand, there could be genetic incompatibilities unrelated to habitat, and hybrids may be less fit than pure types. If this is the case, the contact or hybrid zone will be a sink, and will remain a narrow zone unless pre-mating isolating mechanisms evolve. Alternatively, because the Spotted Owl is facing new challenges from disease (West Nile Virus) and competition (Barred Owl invasion), one might argue that increased genetic diversity may be important for tackling these challenges. Along contact zones, hybrid individuals offer unique combinations of genes from both Northern Spotted Owl and California Spotted Owl populations, and could lead to hybrid vigor. This could result in a spreading or growing hybrid zone and increased population in this area. **Our existing data do not allow us to distinguish among these alternatives or provide any judgment about whether hybridization is good or bad or to make guesses about the ultimate fate of the**

contact zone. At this point therefore, it is impossible to say whether hybrids would be beneficial (and perhaps receive extra protection) or detrimental.

The region of contact between the two valid subspecies must be monitored and reassessed in the future in order to determine whether the subspecies will continue to exist as separate entities, and to evaluate what impact genetic mixing may have on the fitness of hybrids and each subspecies.

2.3 CONCLUSIONS FOR SUBSPECIES HYBRIDIZATION AND INTROGRESSION

There is concrete evidence in every available dataset that there is some mixing of individuals of California Spotted Owl into Northern Spotted Owl geographic regions and possibly evidence of the converse. At this time, it is unclear whether this represents temporary movements, natal dispersal, or hybridization, but some nuclear DNA datasets and a few field observations suggest that hybridization is occurring in these areas of overlap. Other aspects of the overlap zone, such as its width, stability, the relative fitness of any hybrids within it, the net direction of gene flow, and its ultimate fate (stable, sink, or complete panmixia) are virtually unknown at present. Studies that can address these issues are of great importance to both Spotted Owl management as well as basic theoretical scientific interest. Some current day samples are available, but additional samples need to be obtained, and nuclear genetic markers must be analyzed. Some of these markers have been developed (AFLPs, Haig et al., 2004b; and microsatellites, *Henke et al., unpublished*), and there are several labs interested in working on these issues. Analyses of linkage disequilibrium and admixture using these nuclear markers will indicate the level of hybridization and backcrossing within the area of overlap, and introgression through and outside this region. In addition to modern or recently collected material, museum specimens collected over the past 100 years can be also be analyzed for mtDNA and microsatellites. If there is no evidence of California Spotted Owl haplotypes or alleles in the historical range of the Northern Spotted Owl and vice-versa, this would indicate that the gene flow suggested by the current datasets is due to very recent secondary contact and may be expected to continue. If the frequency of shared haplotypes in the older material is similar to that found today, the overlap zone may be older, and perhaps is stable and represents a suture zone or sink. Even if hybridization is occurring between the listed Northern Spotted Owl and the un-listed California Spotted Owl, there is the potential for protection of hybrids under the "similarity of appearance" clause of the ESA (Section 4e) (Haig and Allendorf, in press).

3 GENETIC VARIATION

3.1 CHARACTERIZATION OF GENETIC VARIATION AND DIFFERENTIATION

3.1.1 PATTERNS

The pattern of genetic divergence among and within the described subspecies likely reflects historic processes of long-term isolation and divergence, possibly in Pleistocene refugia (Soltis et al. 1997), although it is possible that divergence could have occurred *in situ* along a habitat gradient or ecotone (e.g., Smith et al. 2001). For example, the coalescence of mitochondrial

DNA haplotypes within each subspecies clade suggests a long period in isolation, as does the significant mtDNA divergence between each subspecies. The patterns of clade relationships shown in Barrowclough et al. (1999) and Haig et al. (2004a), as well as the relative levels of sequence divergence, indicate that the basal split is between a Northern Spotted Owl subspecies clade and a clade containing the California Spotted Owl and the Mexican Spotted Owl subspecies. This indicates that there was an older split between the northern and southern populations of the owls before there was a split between the eastern and western populations.

The nucleotide diversities for the mtDNA control region sequences, reported per subspecies by Barrowclough et al. (1999), are on the order of 0.5% in the Northern Spotted Owl and Mexican Spotted Owl, and much lower (<0.1%) in the California Spotted Owl. Such low values indicate relatively short coalescence times for mtDNA control region within each clade. Although Haig et al. (2004a) make an attempt to date the divergence, there apparently are no relevant calibration points for *Strix* or other owls to obtain a local rate, and it is likely too difficult to apply any sort of global rate calibration to mtDNA control region data given the variable rates within this sequence region. *S. Haig (personal communication)* recently also obtained sequence data from 936 bp of the mtDNA cytochrome b gene, considered a more appropriate marker than mtDNA control region for applying rate calibrations (Fleischer and McIntosh 2001). They used an often-applied rate of 2% sequence divergence per million years to estimate a divergence date of 125,000 years between the Northern and California Spotted Owl, which suggests a late Pleistocene divergence. They estimate a split date between the California and Mexican Spotted Owl of only 15,000 years. The pattern of differentiation among the three subspecies suggests past disjunction of Spotted Owl populations into three refugia, each corresponding to the present subspecies. The dichotomy of northern and southwestern lineages (Northern Spotted Owl and California Spotted Owl) is found in a wide variety of other taxa in the region, suggesting the strength of vicariance in facilitating genetic differentiation (Soltis et al. 1997).

3.1.2 LEVELS

Although there is some diversity of opinion on the matter, the consensus opinion of biologists is that genetic variability is considered important for the health of a population and for the maintenance of evolutionary potential, and that endangered species risk losing variation as a consequence of population size declines (Frankham et al. 2002 and references therein). Thus estimation of current genetic variation in Northern Spotted Owl populations and prediction of future losses from demographic and habitat changes is important for conservation management.

Mitochondrial control region variability within the Northern Spotted Owl is typical of that found in other bird species (13 haplotypes among 20 individuals [Barrowclough et al. 1999] and 34 haplotypes among 131 individuals [Haig et al., in press], and mean nucleotide diversities of 0.0045 and 0.024, respectively). For example, average nucleotide diversity for mitochondrial control region sequences of Yellow-billed Cuckoos (*Coccyzus americanus*, Fleischer et al., MS) was 0.020, for Chaffinches (*Fringilla coelebs*, Griswold and Baker 2002) it ranged from 0.005 to 0.019, for Great Tits (*Parus major, Kvist et al. 1999*) from 0.011 to 0.025; for redpolls (*Carduelis flammea*, Ottvall et al. 2002) it was 0.0030; for Great Bustards (*Otis tarda*, Pitra et al. 2000) it averaged 0.0032; for Bluethroats (*Luscinia svevica*; Zink et al. 2003) it averaged 0.023 (range of 0.0009 to 0.0042); and for MacGillivray's Warbler (*Oporornis tolmiei*, Mila et al.

2000) it averaged 0.0017 (range of 0 to 0.0063). On the other hand, mtDNA control region nucleotide diversity (0.0006) was considerably lower in the California Spotted Owl populations assessed, especially the ones outside of the Sierra Nevada (Barrowclough et al. 1999; *Chi et al., unpublished*). The degree of RAPD variation found for the Spotted Owl is remarkably low (11 variable bands from 450 surveyed primer sets, or thousands of bands scored; n.b. the exact number of bands scored was not reported in Haig et al. 2001). This low level of RAPD variation is similar perhaps only to a study of California Clapper Rails (Nusser et al. 1996) for which mtDNA and minisatellite variation were also found to be very low (Fleischer et al. 1995). It is very difficult to understand why RAPD variation was found to be so low in the Northern Spotted Owl and other Spotted Owl subspecies because variation in mtDNA (Barrowclough et al. 1999, Haig et al. 2004a) and microsatellites (*Henke et al., unpublished*) in the Northern Spotted Owl are generally typical of other avian taxa. Unfortunately, Haig et al. (2004b) do not report the level of variation within Spotted Owls in their AFLP analysis. This would provide the best comparison to the RAPD data of Haig et al. (2001). Interestingly, the microsatellite diversity in the study by *Henke et al. (unpublished)* also revealed lower variability in the California Spotted Owl relative to the Northern Spotted Owl, especially in the Monterey county populations which appear to have undergone a historical bottleneck (observed heterozygosity for Northern Spotted Owl in Mendocino and Marin counties are 0.66 and 0.56, for California Spotted Owl in Placer and Monterey are counties 0.58 and 0.29).

3.2 FACTORS AFFECTING GENETIC VARIABILITY

3.2.1 INBREEDING

Although some evidence for mating between close relatives (usually parent with offspring) has been documented for the Northern Spotted Owl (Carlson et al. 1998, Forsman et al. 2002), it is generally a rare event, and not likely to result in genetic problems under normal circumstances. Mating between more distant relatives is likely to occur (Forsman et al. 2002), but the extent and fitness consequences of these activities are unknown. Likewise, natal dispersal data suggest substantial long distance dispersal in the Northern Spotted Owl (median for males of about 14 km; median for females of about 23 km; Forsman et al. 2002). The range was from 0.6 to 111.5 km, indicating that long-distance dispersal is possible. This would greatly reduce the chances of inbreeding.

Based on the assortment of genetic markers used in the Northern Spotted Owl, there is no evidence of reduced genetic variation and past bottlenecks (Barrowclough et al. 1999; Haig et al. 2001, in press; *Henke et al., unpublished*), but there is significantly lower variability documented in some populations of the California Spotted Owl, in particular those in Monterey County and further south (Barrowclough et al. 1999, *Henke et al., unpublished*). The microsatellite data gave no indication of deviations from Hardy-Weinberg expectations in the two Northern Spotted Owl populations (*Henke et al., unpublished*), suggesting that inbreeding is not occurring in their Northern Spotted Owl study populations. The California Spotted Owl population in the Sierra Nevada (El Dorado National Forest) showed significantly lower heterozygosity than expected by Hardy-Weinberg equilibrium, and high values of the inbreeding coefficient F_{IS}, suggesting possible inbreeding or Wahlund effects. The other California Spotted Owl population in the study, in Monterey County, showed extremely low genetic diversity, and some indication of bottlenecks. While there is no evidence of significant inbreeding in Northern Spotted Owl populations at the present time, monitoring of that possibility in the future, especially in small, isolated populations (as in the southern California Spotted Owl populations, Carlson et al. 1998) should be maintained.

3.2.2 EFFECTIVE POPULATION SIZE

Estimates of effective population size have been made from demographic prediction (Barrowclough and Coats 1985). Such estimates can also be made directly from genetic data, either from standing variation or from comparisons of allele frequencies over time (Frankham et al. 2002). Examination of existing patterns of genetic variation using microsatellite and mtDNA data suggest that local deme or effective population sizes are relatively large in the Northern Spotted Owl, but may be considerably smaller in certain populations of the California Spotted Owl (*Henke et al., unpublished*). Barrowclough and Coates (1985), using preliminary demographic data, including dispersal, survivorship, fecundity, variation in reproductive success, and sex ratio, estimated local deme size to be approximately 220 individuals. The amount of the types of data used in this paper has increased several-fold since 1985, and calculation of effective size estimates and other genetic parameters should be recalculated using a more up-to-date dataset.

3.2.3 FRAGMENTATION IMPACTS

Natal and breeding dispersal are likely impacted by forest fragmentation. For example, Forsman et al. (2002), in a very detailed study of juvenile and adult dispersal in Northern Spotted Owls, never found cases of owls crossing large segments of unsuitable habitat such as the non-forested Willamette, Rogue and Umpqua Valleys, or large bodies of water. Thus it is expected that deforestation could impact the movements of owls, the rates of recolonization of suitable habitat, and therefore the local effective population or deme size. Fragmentation is predicted to result in reduction of deme size through reduction of population density as well as through reduced dispersal. Therefore, any additional fragmentation of habitat or reduction of Northern Spotted Owl densities from Barred Owl territorial usurpation would likely have negative impacts on genetic variability within populations and result in increased levels of inbreeding. It is also not clear whether fragmentation of Northern Spotted Owl populations will modify the probability and extent of hybridization and introgression between Northern Spotted Owl and California Spotted Owl.

3.2.4 A NOTE ON GENETIC ISSUES FACING CANADIAN POPULATIONS OF NORTHERN SPOTTED OWLS

Canada has a small, but significant, population of Northern Spotted Owl. This population is relatively isolated and is apparently declining sharply and is absent from significant areas of apparently-suitable habitat. Breeding populations have been estimated at fewer than 33 pairs and may presently be declining as much as 35% per year (*Harestad et al. 2004*). Although the population is under Canadian jurisdiction and responsibility, it is still listed under the US ESA. Much less is known about its genetics, including how it is related to US populations, the amount of gene flow among US and Canadian populations, and whether the population acts as a demographic source, sink, or as a relatively independent unit. With this level of annual decline and with such small population sizes, it is possible (but not necessarily the case) that these populations may be more adversely affected by issues related to small population sizes including, inbreeding depression, genetic isolation, and reduced genetic diversity, hybridization with Barred Owl, and these issues require further investigation. These populations are certainly more vulnerable, however, to stochastic fluctuations in population size or reductions of habitat due to fire, disease, etc. Overall, the Canadian population of Northern Spotted Owl is critically endangered. Canadian authorities convened a workshop in early 2004 to discuss these and other concerns (*Zimmerman et al. 2004*). The workshop proceedings set in full detail the particular circumstances faced in Canada, the conservation challenges that are posed, the problems with conservation and management, the uncertainties in information, and the role of science in the overall coordinated strategy.

4 OVERALL SUMMARY

We review morphological (morphometric and plumage), behavioral (vocalizations), and genetic characters (including allozyme, RAPD, mitochondrial DNA sequence, and microsatellite markers). These data provide adequate information to distinguish the geographically defined Northern and California Spotted Owl subspecies under standard subspecies definitions, and support the current subspecific designations. The Northern Spotted Owl is considered genetically significant and discrete under a variety of definitions, including subspecies, ESU, DPS, MU. Although a low degree of gene flow between Mexican Spotted Owls and California Spotted Owls would suggest that Spotted Owls remain classified as a single Biological Species, Northern Spotted Owls, California Spotted Owls, and Mexican Spotted Owls appear to be properly classified as subspecies and could even be considered as phylogenetic species. There is a relatively low percentage of mitochondrial haplotype mixing near to the geographical boundary of the two subspecies in Northern California and southern Oregon; this is often observed and expected between valid subspecies.

5 TABLES

Table 3.1.: List of Specimens Measured (see Appendix for list of characters)

ID	Species	Sex	Season	LWING	RWING	TAIL	TBAR	ISLANDS	LTC	RTC	LWBAR	RWBAR
MVZ82187	C	F	1	301	300	174	7.25	1	24.5	23.5	NA	NA
UWBM7974	C	F	1	310	311	193	7.75	0	22.5	21.5	6.67	6.67
MVZ97114	C	F	1	312	320	191	6.75	1	22.0	22.0	NA	6.67
MVZ54547	C	F	1	313	320	194	8.00	1	22.5	21.5	6.67	6.67
MVZ67972	C	F	1	315	315	200	8.00	0	22.5	22.5	6.67	6.67
MVZ63297	C	F	1	315	319	202	7.50	1	21.5	21.0	6.67	6.67
MVZ63298	C	F	1	317	321	189	7.25	0	22.0	22.0	6.67	6.67
MVZ81270	C	F	1	317	317	198	NA	1	22.0	NA	6.67	6.67
UWBM68173	C	F	1	318	NA	201	6.50	1	NA	23.0	6.33	NA
MVZ5941	C	F	1	319	320	198	7.00	1	24.0	22.0	6.00	6.00
MVZ46149	C	F	1	319	321	201	7.75	1	20.5	21.5	6.67	6.67
MVZ60997	C	F	1	322	320	196	7.75	0	22.5	21.5	6.33	6.33
MVZ83381	C	F	1	322	322	197	6.50	1	22.5	22.5	6.67	6.67
MVZ17211	C	F	1	322	317	201	6.75	0	23.0	23.0	7.00	6.67
MVZ89750	C	F	1	324	325	206	6.75	0	22.5	NA	7.00	6.67
UWBM48265	C	F	1	325	324	203	7.00	1	22.0	22.0	7.00	7.00
UWBM48266	C	F	1	NA	NA	192	7.00	1	22.0	NA	6.67	6.33
UWBM62998	C	F	1	NA	NA	192	7.00	1	NA	NA	6.00	6.00
UWBM53433	C	F	1	NA	NA	200	NA	1	22.0	NA	6.67	6.33
UWBM62766	C	F	1	NA	NA	NA	NA	NA	NA	NA	NA	3.00
MVZ90348	C	F	2	313	315	197	7.00	1	23.5	23.5	6.67	6.67
UWBM62999	C	F	2	315	NA	202	7.75	0	NA	NA	6.67	6.67
UWBM48269	C	F	2	316	NA	193	8.00	1	21.5	22.0	6.67	6.33
UWBM40526	C	F	2	320	322	186	7.75	1	22.0	22.5	6.67	6.33
UWBM17107	C	F	2	320	322	194	8.00	0	24.5	22.0	6.67	6.67
MVZ60998	C	F	2	320	321	195	7.75	0	22.5	22.5	6.67	6.67
UWBM62058	C	F	2	321	NA	197	7.00	0	21.5	NA	6.67	6.33
MVZ88914	C	F	2	325	323	196	6.75	1	24.5	24.5	6.67	6.67
MVZ101802	C	F	2	326	324	202	7.75	0	25.0	24.0	6.67	6.67
UWBM63001	C	F	2	NA	NA	193	6.50	1	22.0	NA	6.67	6.67
UWBM47929	C	F	2	NA	NA	204	6.75	0	22.0	NA	6.67	6.67
UWBM47931	C	F	2	NA	NA	NA	NA	NA	NA	NA	6.67	NA
UWBM62059	C	F	2	NA	NA	NA	NA	NA	NA	NA	NA	6.67
MVZ117602	C	M	1	292	290	189	5.25	1	NA	22.5	NA	NA
MVZ44221	C	M	1	298	300	176	6.00	1	21.0	22.0	6.67	6.33
MVZ97113	C	M	1	304	303	183	5.50	1	20.5	21.5	6.33	6.00
MVZ87462	C	M	1	309	310	184	5.25	1	23.0	22.5	NA	NA
MVZ83379	C	M	1	310	312	185	3.50	1	21.0	21.5	6.33	6.67
MVZ101803	C	M	1	310	311	196	6.00	1	22.0	23.0	6.33	6.00
MVZ81271	C	M	1	311	314	189	4.25	1	21.5	21.0	6.33	6.00
MVZ87461	C	M	1	312	309	184	5.50	1	22.5	22.0	6.00	5.67
MVZ83380	C	M	1	314	315	196	4.75	1	20.5	21.0	6.33	6.33
UWBM8900	C	M	1	316	322	204	6.75	0	23.0	23.0	6.67	6.67
UWBM63000	C	M	1	NA	NA	NA	NA	NA	NA	NA	NA	6.67
UWBM48270	C	M	2	298	NA	197	6.50	1	18.5	NA	6.33	6.33
MVZ70360	C	M	2	308	309	185	4.75	1	21.0	22.0	6.33	NA
MVZ31270	C	M	2	320	316	202	6.75	0	22.5	22.5	6.67	7.00
UWBM47930	C	M	2	NA	NA	194	NA	0	NA	NA	6.33	6.33
UWBM48268	C	M	2	NA	NA	NA	NA	NA	NA	NA	6.33	NA
UWBM62057	C	M	2	NA	NA	NA	NA	NA	NA	NA	NA	6.33
MVZ143689	L	F	1	294	289	187	6.50	1	20.5	20.5	NA	NA
MVZ143690	L	F	1	311	306	200	7.00	1	21.0	20.5	7.00	7.00
MVZ143688	L	F	1	319	NA	207	7.25	0	21.0	21.0	6.67	NA
MVZ139383	L	F	1	321	321	192	6.00	1	22.5	22.5	6.67	6.67
MVZ119367	L	M	1	295	295	183	NA	1	19.5	20.0	NA	5.33
MVZ135445	L	M	1	304	306	179	NA	1	20.0	20.0	6.67	6.67
MVZ143691	L	M	1	310	307	186	5.50	1	20.0	20.0	6.67	6.50
MVZ139381	L	M	1	310	309	191	4.75	1	20.0	20.5	5.67	5.67
MVZ101805	L	M	1	312	313	195	7.00	1	19.0	NA	7.33	7.33
MVZ119366	L	M	1	318	317	NA	NA	NA	20.5	21.5	6.67	7.33
MVZ139382	L	M	1	323	320	198	6.25	1	19.5	19.0	6.67	6.67
MVZ140533	O	F	1	310	316	NA	NA	NA	21.5	NA	6.67	6.67
MVZ43236	O	F	1	312	311	187	6.00	0	19.5	19.5	6.67	6.67
MVZ140532	O	F	1	315	326	200	7.00	1	24.0	23.0	6.33	6.67
MVZ25536	O	F	1	322	322	187	7.75	0	20.0	20.0	6.67	6.67
MVZ40705	O	F	1	324	325	198	6.75	1	22.5	22.0	6.00	6.67
MVZ106975	O	F	2	318	319	202	8.25	0	23.5	23.5	6.67	NA
MVZ32322	O	F	2	322	322	186	6.50	0	23.5	24.5	6.67	6.67
MVZ25887	O	F	2	322	322	195	7.75	1	24.0	24.5	6.67	6.67
MVZ68787	O	M	1	310	310	183	5.75	1	20.5	19.5	6.67	6.33
MVZ74640	O	M	1	310	313	192	5.50	1	NA	19.5	6.00	6.33
MVZ27187	O	M	1	317	317	200	6.25	0	22.5	22.5	6.00	6.67
MVZ79355	O	M	1	318	316	190	5.75	1	NA	20.0	6.67	6.67
MVZ32323	O	M	2	310	310	192	5.25	1	22.5	21.5	NA	6.33

Table 3.2. ANOVA results comparing Northern Spotted Owl and California Spotted Owl (A) as well as "pure" Mexican Spotted Owl and California Spotted Owl (B). Putative "pure" northern individuals were collected from Washington.

A

		F						
Character	***n***	**Subsp**	**Sex**	**Molt**	**Subsp x Sex**	**Subsp x Molt**	**Sex x Molt**	**Subsp x Sex x Molt**
LWING	51	0.7277	22.8913***	1.1259	1.4607	0.0103	0.5625	0.4236
RWING	46	1.0933	21.8387***	0.9275	0.399	0.6591	0.0444	0.3303
MTAIL	56	0.5444	6.5827*	0.596	0.7399	0.0155	1.0612	0.365
TBAR	53	0.4347	76.2119***	2.0308	0.7647	0.0134	0.1009	2.7482
LTC	50	0.0077	7.4604**	2.1091	0.4831	4.096*	3.0576	0.0322
RTC	45	3.6511	7.0332*	15.1242***	4.6061*	5.9317*	2.1444	0.6923
LWBAR	54	1.1396	12.1952**	1.0577	0.1673	0.6596	0.0507	NA
RWBAR	55	0.8934	0.6949	1.2472	0.0597	0.5012	0.0072	0.0401

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

B

		F						
Character	***n***	**Subsp**	**Sex**	**Molt**	**Subsp x Sex**	**Subsp x Molt**	**Sex x Molt**	**Subsp x Sex x Molt**
LWING	23	0.6179	10.8152**	0.0295	0.7445	1.5059	7.5611*	1.2951
RWING	20	0.0281	6.393*	0.0775	0.9547	1.0931	0.5857	NA
MTAIL	27	0.8697	0.1164	0.3407	0.1907	0.0158	0.0619	0.0147
TBAR	26	0.1882	23.8957***	1.5267	0.2476	0.176	0.0086	2.6208
LTC	23	0.4176	3.5755	1.0603	0.6702	5.5168*	2.8653	0.5546
RTC	19	0.3305	4.9444*	6.5484*	2.9232	2.2917	1.3483	NA
LWBAR	29	0.4028	5.5395*	1.1876	0.0432	0.4429	1.3389	NA
RWBAR	31	1.2187	0.0848	1.1048	0.9099	0.846	2.3182	0.6811

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

6 FIGURE LEGENDS

FIGURE 3.1. Principal component scores 1 and 2 plotted for morphometric analyses involving *caurina* (c) and *occidentalis* (o). Results presented separately for males (A) and females (B). Arrows identify component loadings.

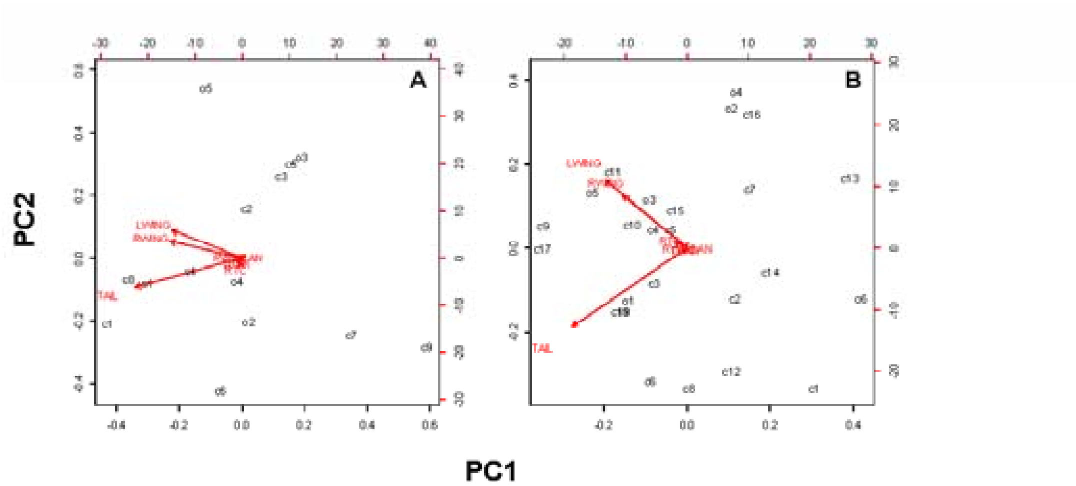


FIGURE 3.2. Linear regressions of male (A) and female (B) principal component scores 1 (circles, solid line) and 2 (squares, dashed line) on latitude. Males: PC1: $Y = 1.52X - 48.67$ ($P = 0.19$); PC2: $Y = 0.15X - 16.02$ ($P = 0.60$). Females: PC1: $Y = 0.21X - 7.69$ ($P = 0.56$); PC2: $Y = -0.25X - 10.10$ ($P = 0.42$).

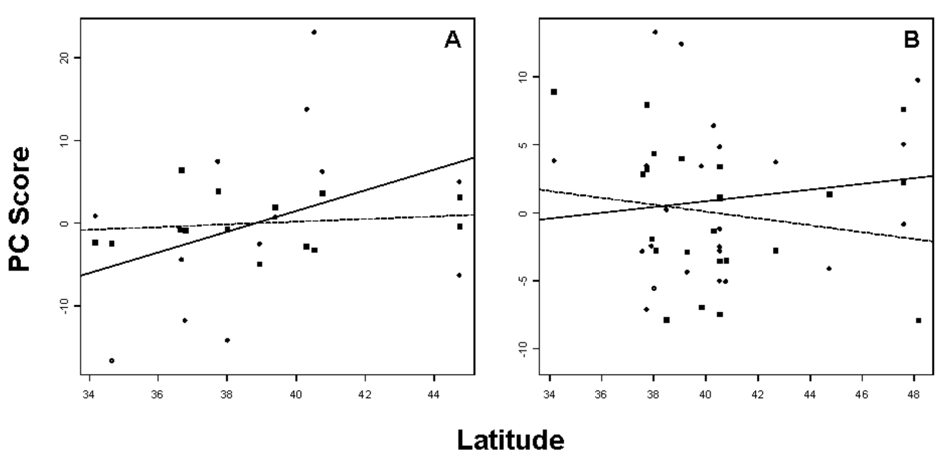
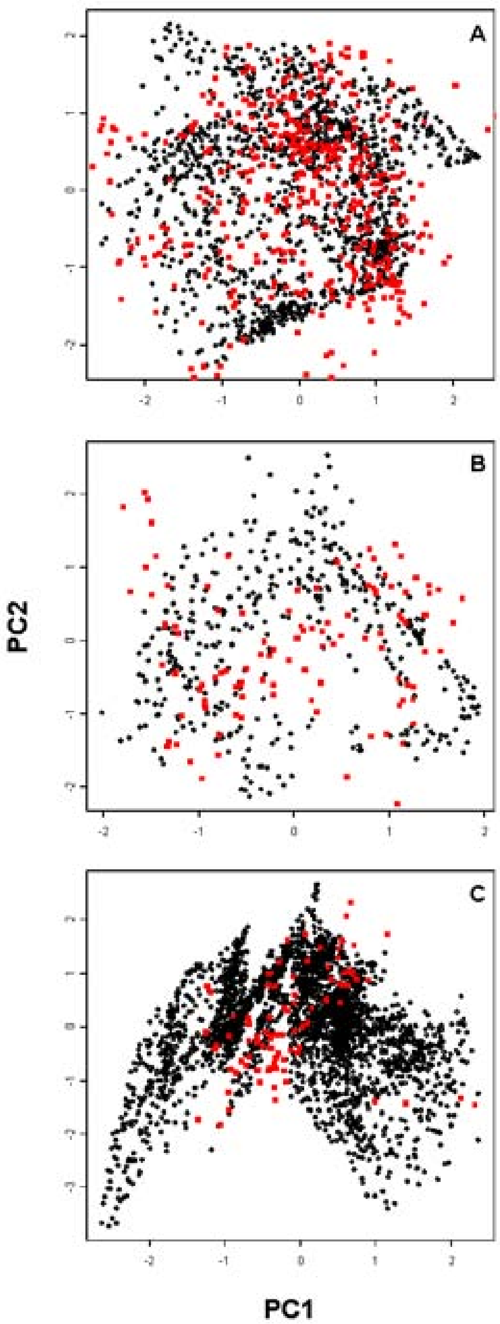


FIGURE 3.3. Extent of Spotted Owl sampling in multivariate climate space for *caurina* (A), *occidentalis* (B), and *lucida* (C). Principal component scores 1 and 2 plotted for existing point localities (red squares) and all points within the geographic range of each subspecies at 10 km^2 spatial resolution (black circles).



SCIENTIFIC EVALUATION OF THE STATUS OF THE NORTHERN SPOTTED OWL

CHAPTER FOUR

Prey

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"The ecology of a predator cannot be understood without knowledge of the ecology of its primary prey"

Waters and Zabel 1995: 858

1 BACKGROUND

1.1 INTRODUCTION

Prey identity, abundance, distribution, and habitat associations have major effects on the habitat selection and demographic parameters of predator populations (Ranazzi et al. 2000). Indeed, there are many studies of the relationship of prey to the ecology of owls (see reviews in Mikkola 1983, Cramp 1985), including *Strix* owls (Southern 1970, Hirons 1982). In this section, we review and summarize current knowledge on the relationship between prey and Northern Spotted Owls. We do this in primarily with respect to information available at the time of listing and the information that has accumulated subsequent to listing. Specifically, we examine the interaction between diet, habitat associations, demographic parameters, and environmental effects. We will also summarize the available information on the different prey species (Appendices).

1.2 KNOWLEDGE AT THE TIME OF LISTING

At the time of listing, it was recognized that:

> "Spotted owls are perch-and-dive predators and over 50 percent of their prey items are arboreal or semiarboreal species. Spotted owls subsist on a variety of mammals, birds, reptiles, and insects, with small mammals such as flying squirrels (*Glaucomys sabrinus*), red tree voles (*Arborimus longicaudus*) and dusky-footed woodrats (*Neotoma fuscipes*) making up the bulk of the food items throughout the range of the species (Solis and Gutiérrez 1982, Forsman et al. 1984, Barrows 1985)."
>
> Federal Register 55: 26114
>
> "It has been suggested that fluctuations in reproduction and numbers of pairs breeding may be related to fluctuations in prey availability (Forsman et al. 1984, Barrows 1985, Gutiérrez 1985)."
>
> Federal Register 55: 26115
>
> "The relative abundance of different prey in old-growth and in different kinds of young-growth has not been studied well enough for clear patterns to emerge…The Service agrees that the issue of prey abundance in different habitat warrants additional research."
>
> Federal Register 55: 26156

> "The Service concurs that recent summaries of prey abundance (Thomas et al. 1990) do not support a generalization that prey are more abundant in old than in younger forests. Rather, abundance of prey species by forest age varies with the species of prey, geographic region, and probably year. The fact remains that spotted owls forage disproportionately in older forests with the clear inference that they obtain prey in proportion to the time spent in the various age classes of forest."
>
> Federal Register 55: 26170
>
> "The relationship of spotted owl reproduction to abundance of prey has not been well established. The reported positive association between reproduction and the frequency of large prey in spotted owl diets may represent either differential capture or differential transport of large prey to the nest; this issue is unresolved. The Ward and Gutiérrez (1989) study was unable to demonstrate differences in prey abundance between reproducing and nonreproducing owls by sampling prey at foraging sites used by the male owls (Thomas et al. 1990). Small mammal populations vary greatly from location to location and from year to year. It is not surprising, therefore, that investigators in different regions, and often in different years, report differing measures of abundance of the same or different species over a variety of forest types and age classes. "
>
> Federal Register 55: 26171

As noted above, the primary summary of information on prey at the time of listing was Appendix J of the report by Thomas et al. (1990). This remained the most complete summary available for the development of the Final Draft Recovery Plan (USDI 1992), and the Northwest Forest Plan.

Major conclusions of Thomas et al. (1990) were:

- Spotted Owls eat a wide variety of prey, but nocturnal, arboreal or semi-arboreal small mammal species predominate in diets.
- At individual study sites, a high proportion of the diet is composed of just one or two species – typically Northern Flying Squirrels, Dusky-footed or Bushy-tailed Woodrats, and lagomorphs.
- Pocket Gophers, Red Tree Voles and Deer Mice may be regionally important.
- Flying Squirrels are the dominant prey in Western Hemlock/Douglas Fir forests; woodrats are more important in drier, mixed-conifer/mixed-evergreen forests.
- This association of prey use with habitat type is mirrored by geographic trends (Flying Squirrels predominating in diets from northern areas, woodrats in drier southern forests), local distribution (again woodrats predominating in more xeric forests), and (in some areas) elevational differences (Flying Squirrels being more abundant at higher elevations).
- Seasonal shifts in diet mirror shifts in prey abundance or vulnerability.
- Since most small mammal populations 'fluctuate notoriously in abundance over time', short-term studies will be insufficient to establish broad ecological relationships.

- There was no conclusive association of flying squirrels with older forest types.
- Dusky-footed Woodrats are most abundant in early seral stages, when hardwoods were present and in riparian areas.
- Bushy-tailed Woodrats are associated with talus and outcrops.
- Red Tree Voles appear to be associated with older forests based on limited data.

We note that of the major hypotheses to explain the association of Northern Spotted Owls with old-growth habitat, proposed that owls selected prey that were more abundant in older forest (Carey 1985), or that they were more available to owls (Gutiérrez 1985).

1.3 INTRODUCTION TO PREY SPECIES

In the appendices, we review the current information on individual prey species, emphasizing studies carried out since the time of the Northern Spotted Owl listing in 1990. We report data for each species' ecology, abundance, habitat preference, and possible limiting factors of population, when available. Several main prey species have been identified - Northern Flying Squirrels, 2 species of woodrats, 2 species of Red-backed Voles, Red Tree Voles, 2 species of Deer Mice, and 2 species of lagomorphs. Although some species such as *Peromyscus* species and lagomorphs form only a small or seasonal component of the diet, they may be important to owl survival or reproduction.

Factors affecting the distribution and abundance will vary with species, season, biotic community (i.e., forest type and seral stage), geographic location, and sympatric species of competitors and predators. Indices of abundance indicate large fluctuations in species populations for several spotted owl prey species, which is not uncommon for small mammals.

Please refer to the Appendices for species descriptions and ecology.

1.4 PREDATION IN CONTEXT

Forests of the Pacific Northwest support one of the most diverse mammal faunas in the United States, with mammals comprising >25% of the vertebrate species in this area (>70 species of mammals on the Olympic Peninsula) (Corn and Bury 1991, Norse 1990, Songer et al. 1997). This diverse mammal community supports a prey base not only for Northern Spotted Owls, but for a variety of predators including coyotes (*Canis latrans*), foxes (*Vulpes vulpes* and *V. velux*), bobcats (*Lynx rufus*), martens, weasels and skunks (Mustelidae), hawks and other birds of prey (Falconiformes), and owls (e.g. Great Horned Owls) (Strigiformes). These predators all consume small mammals (see Ingles 1965, Maser et al. 1981, and Carey 1991 for overviews or Carey et al. 1992, Carey and Kershner 1996, Wilson and Carey 1996 and Watson et al. 1998 for specific examples, Carey et al. 1999c, Carey et al. 1999a, Martin and Anthony 1999). Hence, although Northern Spotted Owls are often regarded as quasi-specialist on larger small mammals, many other predators also take these same prey species in various proportions.

The prey species themselves have diverse dietary requirements. Some species are herbivores (e.g. Red Tree Voles, woodrats, lagomorphs), while others consume mostly fungi and lichens (Flying Squirrels). Therefore, it is probable that environmental factors affecting one prey species will act differently on other species. For instance, environmental factors affecting fungal fruiting body production are likely to differ from those affecting seed production. Prey species may also interact, directly or through competition for food and other resources.

Northern Spotted Owls occupy a niche in a complex web of interactions. However, it is not known whether this interaction web is composed of many diffuse relationships, with weak linkages between the abundance of different species, or a more structured system where each species is linked to the abundance and effects of a few key populations. However, numerous ecological studies suggest single-factor linear relationships are rare in temperate forests. As noted, although Northern Spotted Owls take many arboreal and semi-arboreal prey, these same species are also eaten by other flying, terrestrial (weasels), or arboreal predators. For instance, Northern Flying Squirrels are prey of mustelids (long-tailed weasels, fishers, and martens) and raptors, notably Great Horned Owls (*Carey pers. comm.)*. Moreover, we know that Spotted Owls take many very small mammals, and more of them during high reproductive years (Rosenberg et al. 2003, Ward 2001). Therefore, while the Spotted Owl is a purported specialist, the dynamics of other species may be important to the owl as well. Hence, understanding the relationship between Northern Spotted Owls and prey populations must include all factors that effect prey populations, including predation. Given that Great Horned Owls are also a presumed major predator of Northern Spotted Owls, these interactions may be quite complex.

2 FORAGING ECOLOGY OF NORTHERN SPOTTED OWLS

Northern Spotted Owls usually forage at night, primarily on arboreal or semi-arboreal species (Anthony et al. 1998, *Carey 1993*, *Forsman Presentation 2004*, Forsman et al. 1984, 2001, 2004, Gutiérrez et al. 1995). Numerous studies of individual foraging behavior (e.g. Solis and Gutiérrez 1990) have shown that owls select among habitat types, and selection can be correlated with various vegetation variables (e.g. tree density, shrub cover). Solis and Gutiérrez found that canopy closure (as defined by the total cover of all plant growth forms above a point on the forest floor) was highest in roosting habitat, and lowest in areas infrequently used for foraging (typically on the edge of a home range). (Note that Carey et al. 1992 described roosting cover as being high overhead and lateral cover around the roosting owl and high foliage height diversity within the roosting stand.) Highest use areas were typically those areas with large conifers and high hardwood density. "Shrub and herb cover were highest in areas used infrequently for foraging" (Solis and Gutiérrez 1990:744). These results suggest, but do not demonstrate, that Northern Spotted Owls may respond behaviorally to structure of vegetation when selecting foraging areas. They hypothesized that maneuverability of the owl within a forest may be a significant factor affecting individual habitat selection. Solis and Gutiérrez noted that smaller males and larger female owls may forage in different habitats, perhaps in response to differing tree density that might differentially affect the flight capability of the different-sized sexes. An alternate explanation is this may allow a pair of owls to partition and more effectively track prey resources or allow the male to forage further from the nest grove.

The average prey size of the Northern Spotted Owl was 116±6.5g in Oregon, 111.4±1.5g on the Olympic Peninsula, 74.8±2.9g in the Western Washington Cascades, and 91.3±1.7g in the Eastern Washington Cascades, which is large when compared to the owl's body mass (Forsman et al 2001, 2004, *Forsman Presentation 2004*). As noted in the *Federal Resister*, Spotted Owls appear to select larger prey.

Tables 4.1 and 4.2 summarize data on diet of Northern Spotted Owls in different geographic areas. As noted above, Flying Squirrels and woodrats usually form the bulk of the diet. Indeed, Flying Squirrels are the most important prey (by biomass) in 16 of 17 studies in Table 4.2. However, other prey types, including a variety of small to medium sized mammals, are often a major component of diet (Forsman et al. 2004). Other prey items include birds, reptiles, amphibians, and insects, which usually comprise < 15% of the diet by frequency and < 5% of the biomass (Anthony et al. 1998, *Forsman Presentation 2004*, Forsman et al. 1984, 2001, 2004, Gutiérrez et al. 1995).

Forsman et al (2001, 2004), *Forsman* (*Presentation 2004*), and Anthony et al. (1998) discuss variation in diet composition over time. For instance, Forsman et al. (2004:220) found that:

> "Composition of the diet varied among years ($P < 0.05$) at 25 of 56 territories where we collected ≥20 prey in 2 or more years. In most cases, the differences were relatively small, but there were notable exceptions. For example, at two territories, the percent of tree voles and flying squirrels in the diet varied dramatically among years… At the Oak Creek territory, deer mice varied from 0% of the diet in one year to 79% of the diet in another year…"

In some cases there may have also been decreased use of voles, possibly due to declines in vole abundances or availability (Anthony et al. 1998).

Diet composition varies with distribution and abundance of prey, and habitat type. The data shown in Tables 4.1 and 4.2 essentially confirm patterns reported by Thomas et al. (1990):

- In any area, a few prey species predominate, typically Flying Squirrels and woodrats, but also Deer Mice, Red Tree Voles, Western Red-backed Voles, and lagomorphs (seasonally) in some areas.
- Flying Squirrels are the dominant prey in more mesic Western Hemlock/Douglas Fir forests; woodrats are more important in drier, mixed-conifer/mixed-evergreen forests.
- 'Minor' prey items, such as insects, may still occasionally be important (insects constitute 15.4% of the diet (by prey frequency) in the drier habitat of the eastern Cascades of Oregon).

Spotted Owl diet shows considerable variation regionally, seasonally, annually, and locally, which is likely in response to prey availability (Laymon 1988, Ganey 1992, Verner et al. 1992, Ward and Block 1995, Duncan and Sidner 1990, Forsman et al. 2001, *Carey 1993*). However *Carey* (*1993*) proposes that prey may be selected based on prey mass (100-400 g), a preference for arboreal or semi-arboreal prey, and social behavior. These characteristics may have more influence on the diet than either numerical abundance or total biomass (*Carey 1993*).

As noted by Thomas et al. (1990), there is a clear geographic pattern of diet, paralleling differences in habitat. While Northern Flying Squirrels and woodrats are usually the predominant prey both in biomass and frequency (Barrows 1980, Forsman et al. 1984, *Ward*

1990, *Bevis et al. 1997*, Forsman et al. 2001, 2004, *Forsman, Presentation 2004*), these species have a general north-south trend, with Flying Squirrels comprising a large percentage of the diet in the north, while woodrats become an increasing portion of the diet in the southern range of the Spotted Owl (Table 4.1). Flying squirrels and woodrats are co-dominant in the diet through the southwest interior of Oregon (Table 4.1, Forsman et al. 2001, 2004).

Though their sample sizes was small, Cutler and Hays (1991) suggest small mammals notably voles (*Microtus* spp. and *Clethrionomys occidentalis*) are important prey items at higher elevation, as their abundance and seasonal availability to the owls in some areas may be greater than the generally selected prey species (Northern Flying Squirrel or woodrats). This is consistent with the results of Ganey (1988) for Mexican Spotted Owls in Arizona and Forsman et al (1984) in southwestern Oregon, except that western Red-backed Voles are more prevalent than *Microtus* spp. in Oregon (Cutler and Hays 1991). Increases in the presence of Red-backed Voles and gophers in the diet of Spotted Owls were positively correlated with elevation in Oregon Cascades (Forsman et al 2004). However, in the Central Cascades, predation on Red Tree Voles declines with increasing elevation; the occurrence of Red Tree Voles in the diet in other regions in Oregon was limited regardless of elevation (Forsman et al 2004). Note that if Northern Spotted Owls are displaced into higher elevation areas by Barred Owls (suggested by Gremel (presentation 2003) and others). This may cause changes in diet (see Chapter 7 on Barred Owls).

Relatively few studies have focused on the diet of Northern Spotted Owls outside of the breeding season. This is likely due to the necessity of radio-tracking owls during winter, which is time consuming and expensive. Owls expand their home ranges during winter and do not consistently roost in the same place, which makes pellets more difficult to find (Forsman et al. 1991, Carey et al 1992). Similar problems are associated with non-territorial owls (juvenile and sub-adult owls also know as the "floater" population). Therefore, little is know about their diet, and most of the data presented here are from territorial owls.

Studies that include fall and winter diet analysis have found that "species that hibernated or spent the winter under the snow (e.g. chipmunks, pikas) were absent from the diet from approximately October-March" (Forsman et al. 2001). Insects, terrestrial mammals, birds, and juvenile large mammals were also seasonal (mainly spring, summer and early fall for some species) (Forsman et al. 2001, 2004). Forsman et al. (2001, 2004) suggests adult large mammals and birds, like snowshoe hares, rabbits, mountain beavers, and grouse, are largely absent from the diet because they are difficult to capture due to their size. This increases predation pressure on other species still available to the owl, as revealed by a slight increase in the proportion of flying squirrels in the diet (Forsman et al. 2001).

Rosenberg et al. (2003) have discussed prey switching by Northern Spotted Owls. In their study area, the abundance of different prey species (small mammals) varied independently of each other, perhaps promoting switching in owls to the most abundant prey at any one season or year. Prey switching may occur in other owls when primary prey become rare (Wendland 1984, Petty 1999) or when secondary prey irrupt (Ward 2001).

2.1. ENERGETICS, DIET AND HOME RANGE

Energetic requirements have not been studied directly in the Northern Spotted Owl, although data are available for the similar Mexican and California Spotted Owls (Ganey et al. 1993, Weathers et al. 2001 respectively), and Ward et al. (1998) has extrapolated some of these data to calculate Northern Spotted Owl energetic costs. Note that Weathers et al. (2001) critiqued the calculations of Ganey et al. (1993), and that this criticism has apparently been accepted (*R. Gutiérrez pers. comm.*).

In calculating the effects of energetic needs on owl foraging behavior and biology, it is important to recognize that, for instance, average captures rates, which influence total energetic need, may be influenced by target prey species, habitat type, and stand age and structure. Additionally, Franklin et al. (2000) pointed out that the most energetically demanding season for owls may well be the breeding season rather than the winter (Wijnandts 1984, Meczewa 1986). Energetic stress due to reproductive effort will be additive with maintenance metabolic costs, increasing the risks of starvation. In addition, the male is providing food for both himself and his mate.

Forsman et al. (2004) estimated the average adult spotted owl needs 73.2g of prey per day (12% of its body mass of 610 grams) or 26,718g per year. Using the proportion of biomass of each species then dividing by the species mean mass, the number of prey items captured per year can be estimated. The East Cascades show the highest estimate of total prey captured per year because of the high proportion of insects and miscellaneous prey items that Northern Spotted Owls consume in that region. This may be an underestimate due to the remains of insects being less likely to be found in pellets compared to vertebrate remains (Ganey 1992). The estimated number of prey items that would be taken per year by owls in the south coast and southwestern interior regions of Oregon are 222.4 and 217.4, respectively (Forsman et al. 2004, *Forsman Presentation 2004*). (Estimated number of prey consumed by owls is also discussed in section 4 of this chapter.) This compares to the results of Weathers et al. (2001), who estimated that on average, California Spotted Owls feeding young can meet their own needs by consuming one Northern Flying Squirrel every 1.8 days or one Dusky-footed Woodrat every 3.7 days based on the FMR data, assimilated efficiency of 77% and the body composition of prey species. *Forsman* (*Presentation 2004*) estimated an average of 270.6 flying squirrels per year (0.7 squirrels a day) and 58 woodrats per year for a pair of owls with two young in Oregon. These estimates include the consumption of other prey in their average proportions. Non-nesting owls are estimated to capture an average 0.6-1.0 prey items per day, which includes the East Cascades where numerous insects are consumed relative to other areas in Oregon (Forsman et al. 2004).

Selection of large prey is energetically efficient, maximizing input over expenditure. Ward et al. (1998) estimate the energetic equivalency of alternative diet items. Ward et al.'s calculated energetic needs of a reproductive male owl (see above) are equivalent to 47 woodrats, 100 flying squirrels, 410 voles, 547 white-footed mice, or 2001 insectivores. While Northern Spotted Owls take many prey items, the hypothesized 'quasi-specialization' on large prey appears to make energetic sense.

Larger home ranges, especially at the northern extent of the range, suggest that when available prey density is low (Carey et al. 1992, Zabel et al. 1995) or there is an increased reliance on a single prey species (Northern Flying Squirrels), owls respond by increasing home range (and hence flight costs) (see habitat association section). Densities of Flying Squirrels generally tend to decrease toward the northern edge of the Spotted Owl's range (southern Coast Ranges and Western Cascades vs. Olympic Peninsula and North Cascades of Washington), with a few exceptions (Carey 1995a, 2000 Appendix X). Studies of the relationship between spotted owl home range size and prey requirements do support a general trend that prey abundance is negatively correlated with home range size (Carey et al. 1992).

Overall, the distribution of the Northern Spotted Owl does not encompass the entire range of some of its primary prey species. Northern Flying Squirrels range through parts of Canada and into Alaska. Deer Mice and Snowshoe Hares also occur over a wide region. Therefore, factors other than prey distribution must set limits to owl distribution. It is possible that the northern distribution limits of Northern Spotted Owls are set by energetic costs, since Spotted Owls likely have increased basic maintenances metabolic demands in those parts of the range; direct effects of temperature are, however, also a plausible limiting factor. *Forsman (pers. comm.)* has pointed out that Barred Owls (which must have somewhat similar metabolic needs to Northern Spotted Owls) have expanded rapidly into the interior mountain ranges of Idaho, Washington, Montana, British Columbia, and even into Alaska; this suggests that limits to the distribution of Northern Spotted Owls could be set by the relative abundance of preferred prey (such as flying squirrels). At this point, it can only be hypothesized that distribution may be affected by energetic needs, which increase with increased basal metabolic costs, and increased foraging costs (affected in turn by reduced prey diversity, reduced prey availability, forest fragmentation, and reduced habitat availability).

2.2. EFFECTS OF WEATHER AND CLIMATE ON OWL-PREY INTERACTIONS

Climate probably affects Spotted Owl population dynamics (see Demography chapter). Whether this effect is directly on the survival or reproductive success of the owl, an indirect effect through prey, or both is unclear. Reproductive success was reduced when weather was cold and wet during the late nesting period, while survival was negatively inmpacted by early nesting season precipitation (Franklin et al. 2000, *Olson et al. 2004*). These studies were from demographic study areas in Oregon and northern California. Therefore weather effects may be more pronounced in the northern parts of the range where seasonal variation is great, snow cover complicates prey acquisition, reduced prey availability, reduced prey diversity, and owls may be operating closer to their metabolic limits. Indirect effects could be through a reduction in prey abundance or availability, or through reducing the owl's hunting efficiency (Franklin et al. 2000). This appears to be the case for Northern Goshawks on the Olympic Peninsula where reproduction and survivorship were also reduced in cold, wet (la nina) years (Bloxton 2002). Associated with these demographic costs were reductions in avian and mammalian prey and greater ranging behavior by radio-tagged hawks (Bloxton 2002).

It is possible that noise from rain or wind may make it harder for Spotted Owls to hear their prey, thus directly influencing foraging success. Prey availability may also be a factor on foraging success. Flying Squirrels in North Carolina and Pennsylvania are known to delay nocturnal activity during high winds, mist and heavy rain (Weigl and Osgood 1974, Witt 1992). Flying

Squirrels in Washington exhibit behaviors suggestive of minimization of exposure to cold and rain in the winter as well as predator avoidance (see Carey et al 1997, Carey 2000). Flying squirrels may reduce their on-the-ground foraging for truffles in the winter, when truffles may be scarce, and spend more time foraging on lichens in trees and remaining in their dens.

Weather undoubtedly affect prey abundance both on short (direct) and long-term (indirect) scales. For instance, severe weather conditions may cause increased prey mortality. After an ice storm, the abundance of most shrew species and two species of Deer Mice declined (*Risenhoover et al. 2002*). However, after this same ice storm, Northern Flying Squirrel abundance increased, perhaps due to habitat changes induced by the storm (*Risenhoover et al. 2002*). Therefore, different species may respond differently to environmental stresses.

Weather also affects prey reproduction. In Prairie Deer Mice, weather affects the sexual composition and size of litters, and weight of young (Myer et al. 1985). Warm temperatures in autumn or heavy rain during early pregnancy in any season decrease litter size of Prairie Deer Mice, while unusually warm temperatures during early pregnancy increase reproductive output (Myer et al. 1985). Whether this also applies to Deer Mice in the Pacific Northwest or other Spotted Owl prey remains untested. Although it has been demonstrated that weather may influence the survival and reproduction of some small mammals, there are few data regarding the effects of weather on any of the primary prey of Northern Spotted Owls.

Weather may also have indirect effects on prey abundance by altering food availability. Increased moisture tends to increase the abundance of mycorrhizal fungi, a source of food for several prey species including western Red-backed Voles and Flying Squirrels (Tallmon and Mills 1994, Mills 1995, Carey 1991, Maser et al 1978, Maser et al 1985, Carey 1995a, Carey et al 1999, Colgan et al 1999, Carey et al. 2002). Fungal species differ in the moisture, temperature and nutrients gained from the mineral soil and organic matter (Molina and Trappe 1982, Perry et al. 1989, Molina et al. 1992, Carey et al. 1999a). "Fungal production drops in summer with drought…" (Franklin and Dyrness 1973, USDC National Oceanic and Atmospheric Association 1981, Villa et al. 1999:40). "Lichen litterfall biomass increased with increasing stand complexity and moisture" (Lehmkuhl 2004:381). Lichens are used by "…small mammals (Maser et al., 1985; Rosentreter et al., 1997; Zabel and Waters, 1997), mainly during the winter when plant and fungal food sources are at low levels or unavailable under deep snow" (Lehmkuhl 2004:381). If lichens provide critical nutrients and energy when species are most food stressed, lichen diversity and abundance may affect survival and be one factor in determining population levels of small mammals. Precipitation also plays a role in moving the spores, yeasts, and bacteria from feces "…into the soil where the fungi colonize new [tree] roots" and "…enhance the ability of trees to absorb water and nutrients…" (Carey et al. 2002:148). Vegetation would also be expected to differ in growth rates and seed production. Despite indications that precipitation may adversely affect some small mammals, it also appears necessary for their survival.

Rosenberg et al. (2001, 2003) found a positive correlation between Northern Spotted Owl reproductive success and Deer Mice abundance. This is somewhat surprising in that Deer Mice are not a primary prey of Spotted Owls (less than 2% by biomass in the study area), and hence a strong linkage of the two species' populations was not predicted. One possibility may be that

Deer Mice and owls responded similarly to weather and were simply correlated without direct causation. Alternatively, Deer Mice abundance may be correlated with that of presumed primary prey (whose densities are less easily measured with accuracy). Note that Fryxell et al. (1998) showed linkage of the abundance of many small mammal species (including Flying Squirrels and Deer Mice) over a 43-year period in eastern Canada. *Carey* (*pers. comm.*) speculates that such synchrony across the prey community could be driven by years of high conifer seed production, which triggers high reproduction in Douglas Squirrels and *Peromyscus*. In subsequent years, these elevated densities of seed eaters, lacking seeds, could compete heavily with mycophagous mammal species, resulting in community wide declines, and synchrony. This interesting hypothesis will require many more data to be adequately tested.

The interaction between Spotted Owls and their prey may be affected by weather in complex ways. Franklin et al. (2000) have shown that weather may interact with habitat characteristics. High territory quality, a function of habitat and other factors, can buffer the effects of bad weather on owls. Understanding such effects of weather (even though they cannot be controlled) may be critical to an understanding of viable population levels and in designing recovery strategies. The effects of weather may be exacerbated and confounded with diet and habitat differences, with complex consequences for owl reproductive success and survival.

Finally, we note that if weather affects prey and owl interactions, it is possible that systematic changes in weather, brought on by climate change (both long-term warming and cycling changes in temperature and precipitation characteristic of the Pacific coast), may affect Spotted Owls' survival and reproduction. This may be a fruitful area for exploration with predictive modeling—if and when adequate empirical data are available.

3 EFFECTS OF PREY ON SPOTTED OWLS

Predators are affected by the abundance and availability of their prey (e.g. Martin and Anthony 1999). "Numerous studies of strigids have shown positive correlations between prey abundance and either nest success or number of fledglings produced (reviewed by Verner et al. 1992)" (Ward et al. 1998). This suggests supplementing the spotted owl diet by increasing prey abundance may increase reproductive success as it has in many avian species including owls (Korpimäki 1989, Boutin 1990, Ward et al. 1998). Carey et al. (1992) provided empirical data on the effect of old-growth fragmentation and reduced prey abundance on stability and turnover in owl pairs. Carey and Peeler (1995) provide empirical evidence of the effects of forest fragmentation on spotted owl energetics in terms of prey base.

In the sections that follow we report information on the effects of prey on Northern Spotted Owl demographic performance and behavior. As noted above, prey type and availability also influence home range size, and interact with other factors to set limits of owl distribution (Carey et al. 1992).

Virtually all studies equate abundance with prey availability. However, factors other than prey abundance also affect availability, notably foraging opportunity. Some researchers have suggested that owls make less use of younger stands, because owls may be less maneuverable and, therefore, less able to catch prey there (Rosenberg and Anthony 1992, *Zabel et al. 1993*, Thome et al. 1999). Carey (1995b) disagrees with this interpretation, and suggests instead that lack of suitable perches limit foraging opportunities. This appears to agree better with data showing that owls use sapling stands, and densely vegetated riparian areas with woodrats (Carey et al. 1992, Carey and Peeler 1995 and others). It is reasonable to hypothesize that prey abundance is not a perfect predictor of availability; since we cannot currently measure availability (as opposed to density or abundance), many of our conclusions (for instance on relative prey availability) must remain tentative.

3.1 BREEDING AND REPRODUCTIVE SUCCESS

Several studies have examined relationships between Spotted Owl diet, breeding status, and reproductive success. Some have found a positive correlation between the proportion of large prey consumed and breeding success. For instance in some studies, owls that fledged young may have consumed higher proportions of large prey than those that did not fledge young (Barrows 1985, 1987, Laymon 1988, Thrailkill and Bias 1989, White 1996, also cited in Rosenberg et al. 2003, White 1996, Smith et al. 1999). Unsuccessful nesters consumed more small and medium prey, with small prey consisting of the largest proportion of the diet (White 1996) and their diet was more similar to non-nesters than successful nesters (Smith et al. 1999). "The diets of owls that successfully fledged young differed significantly in terms of prey size from the diet of owls that failed to fledge young (x^2=14.78, df = 2, P<0.001)" (White, 1996:234-235). However, other studies have not found a significant difference between owls that successfully fledged young, and those that did not, in the proportion of large prey consumed (*Ward 1990*, Ward et al. 1998, Forsman et al. 2001, see comments in Smith et al. 1999). In addition, Forsman et al. (2001, 2004) suggested that the higher proportion of large prey in pellets of nesting pairs of spotted owls could be the result of biased delivery of large prey to the female and young by nesting males. Bull et al. (1989) documented this type of bias by observing male great gray owls that were foraging during the day. Such biases are potentially serious and were not considered in many studies of Spotted Owls (*E. Forsman, pers. comm.*).

Smith et al. (1999) calculated using estimates by Ward et al (1998) that energy costs increase by 276% when a male is providing for himself, a female, and one young from egg-laying through fledging. This estimate is similar to those made by *Forsman (Presentation 2004)* (a 266% increase in the number of prey for a pair with two young relative to estimates per owl). The energy cost of producing an egg is small compared to the energy required by a male to provide for itself, the female and young during the nesting period (Ward et al. 1998, Smith et al. 1999). Therefore, consumption of large prey, like woodrats, may influence nest success more than nest initiation (Smith et al. 1999).

Northern Spotted Owls do occasionally forage during the day. Sovern et al. (1994) and Forsman (1976) suggest these foraging events are limited and largely opportunistic. However, Miller (1974) and (Laymon 1988) suggest that those Spotted Owls that successfully fledge young frequently forage during the day (Sovern et al. 1994). Sovern et al. (1994) found that nesting owls were significantly more active during the day than non-nesting individuals; the proportion of time spent roosting vs. active behaviors, which included foraging, socializing, and moving, differed significantly depending on the time of day, with owls becoming more active after 18:00

hours. However, the time spent in active behaviors did not differ between sexes. Nesting owls averaged 1.44 capture attempts per day, while non-nesting individuals averaged 0.24 (Sovern et al. 1994). Capture success rate averaged 22.2%, indicating nesting individuals might be expected to capture 0.32 animals/12-hr day. Chipmunks (*Tamias spp.*) and one unidentified small mammal were the diurnal prey that Spotted Owls targeted during this study. After fledging young, nesting pairs may double that rate (Sovern et al. 1994). Some diurnal prey (average of 3.3±0.2% in Oregon; 8.5% in Washington) may appear in the diet; however, this does not necessarily indicate extensive diurnal movements as most capture attempts were made from the roost tree suggesting opportunistic foraging (Forsman et al. 2001, 2004, Sovern et al. 1994).

Whether it is diet composition, prey availability/abundance, selection, or both (return on foraging investment) that influences reproductive success is unclear (Ward et al. 1998, Smith et al. 1999). Seasonal diet differences and diet shifts following failures suggest selection plays a role (Smith et al. 1999) although such events may be following depletion of preferred prey or shifts in space use (Ward et al. 1998, Carey and Peeler 1995). Ward et al. (1998) showed that Spotted Owls select habitat with large prey, and selectively foraged in sites with greater abundance of large prey (particularly Dusky-footed Woodrats that are usually found in the edge ecotone region between late and early-seral areas in mixed-evergreen forest of northwestern California) as did Carey et al. (1992). Their study assumed that all night locations were foraging locations, which would exclude other typical activities. However, Carey et al (1989) concluded roosting and foraging sites were often synonymous (also see Carey et al 1992). Underestimates of availability of prey could affect estimates of selection, as could underestimates of abundance.

In the study of Ward et al. (1998), no prey species were significantly more abundant at foraging sites of nesting owls who successfully produced young, but the power of the test to detect relative differences was low because abundance varied greatly relative to sampling intensity (lack of power). However, there was a difference in abundances of woodrats in areas selected by breeders and non-breeders. Note that "Ward and Block (1995) found reproductive success of Mexican spotted owls…was not related to the abundance of a single prey species but rather by a suite of the more common prey" (Rosenberg et al 2001). Similarly, Rosenberg et al. (2001) noted that average reproductive performance might not be sensitive to flying squirrel abundance if Northern Spotted Owls switch prey. Spatial variability of primary prey may also influence owl's reproduction (Ward et al. 1998). Relative abundance of woodrats and mice was significantly different among foraging areas within the same reproductive class - white-footed mouse abundance was similar among foraging areas where young owls were not produced compared to areas with young (Ward et al. 1998). Woodrat abundance did vary spatially with reproductive success. Hence, the data on prey effects on breeding and reproductive success are contradictory and no clear conclusions are available.

3.2 IMPORTANCE OF SECONDARY PREY SPECIES ON REPRODUCTION

Characteristics of spotted owl foraging behavior and densities of their prey suggest Spotted Owl populations are limited by prey (Forsman et al. 1984, Thomas et al. 1990, Carey et al. 1992, Rosenberg et al. 2003). As noted above, some studies have found evidence of a positive correlation linking reproductive success and the consumption of large prey (Barrows 1987, Laymon 1988, Thrailkill and Bias 1989, but see White 1996, Forsman et al. 2001, 2004). As Flying Squirrels are present throughout their range, and are a less patchy resource than woodrats, observational studies of reproduction have generally focused on them. Surprisingly, Rosenberg et al. (2003:1720) "…found only a weak relationship between flying squirrel abundance during fall and reproductive success the following spring". The measures that they considered, which included the proportion of nesting pairs, number of young per nesting attempt and overall number of young produced, may not be strongly affected by fall estimates of abundance because of over-winter changes in prey numbers. Prey switching would also reduce sensitivity of reproductive success to Flying Squirrel abundance. "The high spatial variability of prey abundance [such as Flying Squirrels, may influence reproductive success at the territory scale and] likely contributes to the spatial variation of reproductive success of the spotted owl (Ward et al. 1998)…" (Rosenberg et al. 2003:1721). However, lack of correlation with a primary prey species suggests that a different force may be driving reproduction (such as secondary prey, overall prey biomass, weather).

Some prey species may be critical to reproduction despite their limited frequency in the diet of Spotted Owls. For instance, Rosenberg et al. (2003) showed a striking correlation between annual reproductive success of owls and abundance of Deer Mice ($r^2 = 0.68$) despite the small contribution these make to the overall diet (less than 2%). Deer Mice abundance was most closely linked to the number of young per territory "relative to the proportion of pairs that attempted to nest… and the number of young per attempt…" (Rosenberg et al 2003:1720). This could be due to the influence of abundance or perhaps nutrient and energy value (Rosenberg et al. 2003). Alternatively, weather may simply affect both species, which could cause a correlation and not be direct causation (Rosenberg et al. 2003, See weather). Deer Mice in their study represented similar overall biomass as Northern Flying Squirrels, 160±18.8 g/ha and 169±13.9g/ha respectively. However, Deer Mice had higher temporal variability (67.6% of process variation; spatial variation of 12.1%) with more than a 20 fold difference in abundance among years, while Flying Squirrels have greater spatial variability, which was year dependent (37.8%; 24.2% temporal variation) (Rosenberg et al. 2003). Great Gray Owls are known to deliver larger prey to nest and eat smaller food items thereby reducing foraging energy costs (Bull et al. 1989). Spotted Owls may have similar feeding behaviors; therefore, smaller prey items, like *Peromyscus*, may be underestimated in their importance in the diet of Spotted Owls (Forsman et al. 1984, 2001, 2004). Note that *Ward* (*1990*) also noted that mice were more abundant in areas selected for foraging by owls.

There is also evidence in Mexican Spotted Owls that reproductive success responds to a combination of prey instead of a single prey species (Ward and Block 1995). Ward (2001) found in Mexican Spotted Owls that reproductive success was most strongly correlated with abundance of small prey, despite an individual preference for large prey. Seamans and Gutiérrez (1999) also found evidence of an effect of white-footed mouse abundance on Mexican Spotted Owl reproductive success. Blakesley (*pers .obs.)* observed that a peak period of California Spotted Owl reproduction (including the production of triplets) coincided with a *Peromyscus* outbreak possibly due to a large Sugar Pine cone crop the previous fall. In California Spotted Owls in Kings Canyon National Park, *L. Werner* also noticed low reproduction rates in years with low small mammal capture rates in a nearby study area (*pers. comm. 2004*), perhaps indicating low abundance and availability of prey over a broad area. Overall low capture rates of small mammals may be indicative of synchronous fluctuations in the small mammal community, as found by Fryxell et al. (1998). However, without data to verify this, it remains speculation. Recent suggestions have been made that *Peromyscus* and perhaps other species (lagomorphs), which generally make up a small proportion of diet or are a seasonal resource, may influence reproductive success in Northern Spotted Owls (*minutes of March 2004 meeting*).

3.3 SURVIVAL

There are limited data on the influence of prey on Spotted Owl survival. As a predator, prey is essential and, obviously, is the ultimate factor determining survival. Juvenile rabbits and hares may supplement food resources during egg laying, incubation, brooding and early fledging, when the parents still provide for the young (mostly present in the diet March- September). However, juvenile Northern Flying Squirrels are weaned in mid-October to mid-November and may provide a good source of relatively naive prey for juvenile owls during a critical period of time for survival, represented by the dramatic in crease of juvenile Flying Squirrels in the diet from September to early November (Carey 1991, Forsman et al. 1994).

Prey abundance is not generally measured on demographic study areas, and is not considered as a covariate in demographic analysis. The panel believes this is an important area for future investigation. We also recognize that these studies have not been done because of lack of funds rather than a failure of researchers to recognize the importance of these studies. European researchers routinely evaluate prey interactions in owl studies, but there systems are not as complex (low diversity of prey, cyclic rodents are easy to estimate relative abundance) as systems in the Pacific Northwest. Nevertheless, we feel this is a critical information gap that needs to be bridged. Meta-analysis of demographic parameters indicated low female survivorship may drive population change (Anthony et al. 2004). The analysis also indicates that populations at the northern distributional limit have lower survivorship. This may correlate with an increased reliance on a single prey species which is at a lower density compared to other areas in its range, and also to an increase in basic metabolic needs. This is consistent with the hypothesis that food availability or amount of food affects survival. Although this is ultimately true, we do not know if the lower survival of northern populations is related to prey or some other factor because there are no prey data (although see Carey et al. 1992 for demographic effects). Given the sensitivity of lambda to small change in female survivorship, it is unlikely that there will be sufficient statistical power to detect the small, but critical changes that might results from changes in prey availability. Given these complex interactions, it is desirable that the effects of prey on demographic performance, including survival, be examined with a statistically well-designed research program.

4 THE EFFECTS OF NORTHERN SPOTTED OWLS ON PREY POPULATIONS

Spotted Owls have been suggested to depress prey populations (Rosenberg and Anthony 1992, Waters and Zabel 1995, Carey et al. 1992; Carey 2000a, Rosenberg et al 1996). Most of the support for this hypothesis comes from Northern Flying Squirrel studies, perhaps due to the extent to which that species has been studied relative to other prey species, but also perhaps due to the strong linkage between the two species in some regions. Flying Squirrels are the only prey species to account for more than 15% (by number) of the diet throughout the owl's range (*Carey 1993, Forsman Presentation 2004,* Forsman et al. 1984, 2001, 2004).

Only one study has been specifically designed to evaluate the effects of Spotted Owl predation on prey. Flying Squirrel densities before, during and after predation at different intensity levels support the hypothesis that heavy predation reduces population size by 50% with potentially long lasting effects (1-3 years) (Carey et al. 1992). Rosenberg and Anthony (1992), however, estimate only a 25% reduction in density based on the average Spotted Owl home range size of 1000 ha, two squirrels/ha (west slope of the Cascades, Oregon) and the consumption of 500 squirrels per year for one pair of owls (the percentage reduction could be larger in areas of low Flying Squirrel density). *Forsman* (*pers. comm.*) has pointed out that this estimate state to be based on a personal communication from him is in error. Forsman et al. (2004) found that, based on the actual composition of the diet in Oregon, Spotted Owls capture only 208 Flying Squirrels per year when not nesting and 271 per year when they were nesting. This would suggest lower overall prey depletion levels. Nevertheless, at least at local scales, Northern Spotted Owl predation appears to have the potential to depress Flying Squirrel populations.

By contrast, the woodrat literature contains only vague references that predation rates may be high. Substantial numbers of radio-tagged woodrats were killed by predators (both mammalian and raptor) in studies by Sakai and Noon (1993, 1997) in a northern California mixed-conifer mixed-evergreen forest (predators killed 50% of juveniles and 30% of adults (Sakai and Noon 1997)). In Douglas-fir transition forests, Bushy-tailed Woodrats experienced frequent local extinctions with variable prey abundance over time, which may be due to predation (Carey et al. 1992, Carey et al. 1999c, Carey 1991). Predators may be attracted to the clumped populations of Bushy-tailed Woodrats, which is a result of their social behavior (Escherich 1981, Carey et al. 1999c). The fact that woodrats are selectively preyed upon and experience local extinctions provides circumstantial evidence that high predation rates may depress populations for these species too.

5 INTERACTIONS BETWEEN SPOTTED OWLS, PREY AND HABITAT

As indicated above and in Chapter 5 (Habitat Associations), prey availability, numbers, and behavior may play a major role in determining habitat section by Spotted Owls. Habitat type and structure directly influences prey species composition, abundance, and availability. Therefore, the composition of Spotted Owl diet may vary at the scale of individual territories as habitat varies.

Some prey species (e.g. Flying Squirrels, Red-backed Voles) are associated with forest structural complexity (including in old-growth, and in other forest types where this structure is maintained [e.g., old tree retention practices]). Other prey (notably Dusky-footed Woodrats) typically reach higher densities in younger forest, but are bimodal and more abundant in old growth and complex forest than in closed canopy young forests (Carey et al. 1997). Depending on the region and prey, stand structure and management may restrict or enhance prey abundance and availably to Spotted Owls. The ecology, including habitat association, of the primary prey species are described in the appendices.

It has been suggested, based on empirical evidence, that Spotted Owls may select old-growth forest due to higher prey abundance (Forsman et al. 1982, 1984, Carey et al. 1990, Rosenberg and Anthony, 1992). Red-backed Vole abundance is higher in old-growth stands and in stands naturally regenerated from wildfire (such stands contained a large amount of coarse woody debris and snags that were "almost equivalent to old-growth stands" (Gillesberg and Carey 1991, Gilbert and Allwine 1991 and others)). However, studies on Flying Squirrels are more variable. While nearly all studies show higher squirrel densities in older forests, sometimes similar densities can be found in managed or second-growth stands (See Northern Flying Squirrel Appendix for details). Generally, older stands tend to have slightly higher, to much higher densities as stand age increases, but abundance among stands varies with inconsistent results (Carey 1995a, 2000; Rosenberg et al. 1996). Similar Flying Squirrel densities in both stand age-classes suggests that spotted owls avoid second-growth forests or use them in proportion to their occurrence because of low Flying Squirrel (prey) abundance (Forsman et al. 1984, Carey et al. 1990, Solis and Gutiérrez 1990, but see Carey and Peeler 1995).

Note however, that after intense foraging by breeding owls, prey densities in old growth can be reduced by up to 50%, while young forests with old growth legacies may hold high densities of flying squirrels. Both these effects will obscure differences between old growth and young forests (Rosenberg and Anthony 1992, Carey et al. 1992, Carey 1995a,b, 2000, Carey and Harrington 2002).

Differences in forest type also become important; for example Sitka spruce-western hemlock old growth may support fewer Flying Squirrels than Douglas-fir second growth. Douglas-fir dominated old growth may support twice as many Flying Squirrels (or more in the absence of owl predation) than does 40-70 year old second growth without legacies; however 80-100 year old young stands with substantial legacies may actually have the highest Flying Squirrel densities of all (Carey 1995a).

The relatively low use of young stands where woodrats are the primary prey (Sakia and Noon 1993, 1997), even though these young forest types have high woodrat abundance, also suggests that something other than prey abundance *per se* determines habitat selection. However, we note that the conclusions on relative prey abundance in different habitat types must be treated with caution. Empirical evidence (Carey et al. 1992, Rosenberg and Anthony 1992, Waters and Zabel 1995) suggests that Northern Spotted Owls may depress prey populations (see above), in which case local prey abundance may be expected to reflect predation pressure as well as prey-habitat associations. Hence failure to find an association of the abundance of a prey species with its expected preferred habitat is not necessarily strong evidence against such habitat preference (*Carey, pers. comm.*).

As noted above, foraging may be more easily carried out by Spotted Owls in some habitat types. "Radio-telemetry studies indicate that northern spotted owls are seldom located within brush stage clearcuts even though these habitats occur within or adjacent to the home ranges of most radio-tagged birds (*Sisco 1990*, Solis and Gutiérrez 1990, Carey et al. 1992, *C. Zabel, U. S. Forest Service, pers. comm.*)" (as cited by Sakai and Noon 1993:380). Note however Solis and Sisco commented on owls foraging along the edges of such clearcuts and old growth. Young forests have “low vertical diversity of vegetation and high canopy closure with few low structures beneath the canopy that would be suitable as hunting perches”, therefore are “structurally poor for sit-and-wait predators” (Carey et al. 1992:246). “Young second-growth forests often have high tree densities and homogeneous canopies which may impede flight and inhibit the ability of owls to capture prey” (Rosenberg and Anthony, 1992:165). Avoidance of such areas, even when they contain large numbers of a primary prey species (woodrats), is commonly attributed to the unavailability of prey to Spotted Owls (Carey et al. 1992, Rosenberg and Anthony 1992, *Zabel et al. 1993*, Thome et al. 1999 and others). In such areas, the effects of vegetation density, owl wing loading, and habitat use, mean that prey density is a poor predictor of prey availability.

In Southwestern Oregon, Spotted Owls sometimes selectively used young stands (Carey and Peeler 1995). Areas with high woodrat densities may attract Spotted Owls, based on pellets found in sapling/brushy poletimber stands (Carey et al. 1992, also Sakai and Noon 1993). “Because woodrats are arboreal (Linsdale and Tevis 1951), owls may also capture woodrats from trees in sapling/brushy poletimber type stands” (Sakai and Noon 1993:379). Occasional use of such young stands by Spotted Owls may be fostered by specific structure requirements, like remnant patches or available perches to hunt from (*Diller, minutes of March 2004 Meeting*).

In areas with woodrats, Spotted Owls might be expected to preferentially forage stands young enough to contain an abundance of woodrats, yet old enough to allow maneuverability (Thome et al. 1999). Some evidence suggests that 21-40 year-old redwood stands may have these characteristics (Thome et al. 1999). Indeed, territories in northwestern California with higher reproductive success had “lower proportions of the largest basal area class…and 61-80-year age class” and “higher proportions of 21-40-year-old stands” even though “spotted owl locations were characterized by lower proportions of 21-40-year-old stands compared to random locations” (Thome et al. 1999; 56-57). As this study focuses on redwood forests, result may not be applicable to other forest types or regions.

In some other areas, Spotted Owls select foraging areas around talus slopes (Forsman et al. 1984), or in riparian areas (Carey and Peeler 1995, Glenn et al. 2004), probably in response to Bushy-tailed Woodrat abundance. *Ward* (*1990*) showed that Northern Spotted Owls hunted in areas with higher abundance of both woodrats and mice. In the appendix we discuss the suite of factors that effect habitat selection by prey species.

Overall, there seems to be a strong effect of prey distribution on the selection of habitat by Northern Spotted Owl. Indeed, in the Klamath region at least, prey species identity is a better predictor of home-range size than is the proportion of older forest within the range (Zabel et al 1995).

5.1 HABITAT HETEROGENEITY, FRAGMENTATION AND EDGE EFFECTS

Areas where Spotted Owl diets contain large numbers of woodrats [or other non-old-growth species] may benefit from some level of forest heterogeneity. When woodrats were present, Spotted Owl foraging “site selection. . .was more pronounced at the ecotone between late and early seral stages" "where prey were more abundant" (Ward et al. 1998:89). Such results suggest that the spatial configuration and juxtaposition of forest types could have an important effect on prey species.

Lehmkuhl and Ruggiero (1991) estimated that less than 20% of original old-growth forests of the Pacific Northwest remained, with these remnants scattered over a fragmented landscape with successively decreasing patch sizes. They suggested that old-growth patches of 10 ha or less probably function entirely as edge with the loss of "essential old-growth attributes" (Lehmkuhl and Ruggiero 1991:37). However, Ruggiero et al. (1991) found complete biotic communities in small (10-40 ha) patches and field observation suggest many invertebrates and vertebrates with small ranges persist in even smaller patches (*Carey, pers. comm.*). Patches of old growth isolated by clearcuts eventually become legacies in second-growth forests, acting as refugia for species to colonize the second growth and promoting accelerated development of late-seral forest characteristics. There is no doubt that these patches are significant biological legacies, even if in themselves incapable of supporting spotted owls. Such forest fragmentation is regularly equated to habitat fragmentation, although the two terms are not equivalent (Franklin et al. 2002, *A. Franklin presentation 2004*). Fragmentation is often viewed to have negative connotations (reduced habitat cores, increased edge-effects, increased dispersal requirements, etc.)

Little attention has been focused on the effects of fragmentation on small mammal communities (Mills 1995, see review in Paton 1994, Rochele et al 1999) and, therefore, on the effect on predators of these small mammals. Effects associated with fragmentation and edge may include reduced functional size of remnant habitats, which further isolates small populations and increases the risk of extinction through factors of demographic, environmental, and genetic stochasticity and catastrophic events (reviewed by Lehmkuhl and Ruggiero 1991; Mills 1995). Edge effects also include increased susceptibility to edge-induced predation in birds (reviewed by Andrén and Angelstam 1988, Reese and Ratti 1988, Mills 1995) and presumably some small mammals (i.e. old-growth associated species such as Northern Flying Squirrels) (Mills 1995), cascading effects of the elimination of keystone species (see Northern Flying Squirrel section) (Lehmkuhl and Ruggiero 1991), interior and edge species competition (Anderson 1979, Askins and Philbrick 1987, Lehmkuhl and others 1991, Rosenberg and Raphael 1986, Lehmkuhl and Ruggiero 1991), changes in vegetation structure and composition (Lehmkuhl and Ruggiero 1991, reviewed by Saunders et al. 1991, see also Williams-Linera 1990, Mills 1995), and changes in microclimate including light, temperature and moisture that may affect the forest 50 meters to 160 meters from the forest edge (Lovejoy et al. 1986, Chen et al. 1992, Matlack 1993, Young and Mitchell 1994, Mills 1995).

Microclimatic changes at edges may include changes in light, moisture, and temperature which may in turn affect forest structure and prey food availability. Old growth may also act as a climatic buffer reflected by a high water-holding capacity (Franklin et al. 1981), increasing humidity used to maintain green foliage and access to chemically unbound water in the form of dew, rain, or condensation by fog (Meiselman and Doyle 1996, Carey 1991). In addition to the availability of water, increased moisture also tends to increase the abundance of mycorrhizal fungi, a source of food for several prey species including Red-backed Voles and Flying Squirrels (Slankis 1974, Tallmon and Mills 1994, Mills 1995, Carey 1991 and others). Truffles are also nearly absent from clearcuts and remnant edges (Mills 1995) unless coarse woody debris and ericaceous shrubs are retained in the clearcuts (Amaranthus and Perry 1994, Amaranthus et al. 1989, Perry et al. 1989). Edges also have increased quantities of coarse woody debris from fallen trees, blow downs and tree death associated with edge (Lovejoy et al. 1986, Williams-Linera 1990, Laurance 1991, Mills 1995). These fallen trees may not provide a short term benefit to species like Red-backed Voles (which show a preference for logs of advanced decay [Tallmon and Mills 1994, Mills 1995]). However, it is possible that over time, with increased decay, these may eventually prove beneficial.

California (Western) Red-backed Voles are “exceptionally rare in clearcuts” and their abundances were “strongly and negatively affected by clearcutting forests” which may have an effect for 10 to 60 years following clearcutting (Hooven and Black 1976; Taylor et al. 1988, Raphael 1988; Rosenburg et al. 1994, Mills 1995). The average number of unique individuals per trap in unlogged mature-to-old growth (more than 80 years old forests) was significantly greater than in clearcuts (Mills 1995). Overall, fewer individuals were captured in patches 0.6-2.5 ha (remnants) in size when compared to patches greater than 250 ha (control) but “the difference was only marginally significant ($p = 0.1$)” (Mills 1995:399). Remnant forest patches have high interior densities of Red-backed Voles that decrease toward the edge. Interior remnant densities may have six times as many Red-backed Voles compared to remnant edges and have higher densities than the control forests (Mills 1995). These density gradients mirror the effects seen in species confined to islands, due to limited emigration, and may “somewhat counteract” the negative effects of edge (Mills 1995). “…Small islands [or patches] will actually contain higher densities than larger ones… (review by Glicwicz 1980)” (Mills 1995:396). Results from DNA fingerprinting analysis showed that Red-backed Voles in remnants had lower genetic diversity in comparison to voles that were controls (i.e., those found in larger patches) (Mills 1993, 1995). Species associated with late-seral forest may follow a similar pattern to those of the Red-backed Vole.

Rosenberg and Raphael (1986) demonstrated that there was a decreasing frequency of Northern Flying Squirrel occupancy with decreasing stand size (Rosenberg et al 1996). 60-80% of stands that were >23ha were occupied, while there was <10% occupancy in stands <7ha (Rosenberg et al. 1996). As some prey species may go through periodic local extinctions, dispersal distances and barriers to dispersal need to be estimated to understand the likelihood of re-colonization and factors associated with isolation. Barriers to dispersal are plausibly species specific and may include restrictive landscape types, such as clearcuts and early seral habitat (Rosenberg et al. 1996)

In regions where Northern Flying Squirrels and other old-growth associated species are dominant in the diet, Northern Spotted Owls would be expected to show a negative effect of edge habitat (as compared to areas where woodrats predominate) (*Anthony et al. 2002*). Indeed, in fragmented Douglas-fir forests where flying squirrels are the predominant prey, Spotted Owl home ranges were larger compared to areas of “relatively intact forest of mixed-conifer” or areas with woodrats in the diet (Carey 1991, Carey et al. 1992, Ward et al. 1998).

By contrast, in areas where woodrats (or other prey associated with early-seral stages) are dominant in the diet of Northern Spotted Owl, (e.g. in the Roseburg area, Klamath Mountains), reproductive success was correlated with a high amount of edge between known Spotted Owl habitat and other habitat types (*Anthony et al. 2002*, *Anthony et al. 2000,* Franklin et al. 2000). This is consistent with high Dusky-footed Woodrat densities in early-seral habitat, where they have the opportunity to move into and through adjacent habitat types (Sakai and Noon 1993, 1997). Woodrats show no aversion to crossing sharp ecotones into old-growth, where they are more vulnerable to predation by Northern Spotted Owls (Sakai and Noon 1993). As woodrats may be unavailable to Spotted Owls in dense young forest (Forsman et al. 1984, Gutiérrez 1985, Carey et al. 1992, *C. Zabel, U. S. For. Serv. pers. comm.* cited in Sakai and Noon 1993, Rosenberg and Anthony 1992, *Zabel et al. 1993*), young stands may be important source areas for Spotted Owl prey. High availability of prey in edge ecotones may then increase Spotted Owl reproductive success. Radio-tagged woodrats were often killed by predators (both mammals and raptors) with many of the carcasses found in old forest adjacent to younger areas (Sakai and Noon 1993, 1997). Note that other studies show that in conifer/mixed evergreen zones, woodrats are abundant and resident in old growth (Carey et al 1999, Raphael 1988, Rosenberg and Raphael 1986).

Zabel et al. (1995) verified a trend of a negative, linear relationship between home range size during the breeding season and the proportion of woodrats in the diet of Northern Spotted Owls. The proportion of Northern Flying Squirrels in the diet was positively correlated with home range. "Although many of the primary prey species are forest species, some edge habitats may be benefit spotted owls because woodrats, rabbits, snowshoe hares, and pikas are common in non-forest types adjacent to forests" *(Forsman presentation 2004*).

Note that, while ecotones or forest edges may be important to Northern Spotted Owl foraging in some areas of the range, these same areas may also increase risks of Spotted owls from their own predators. See chapter 8 on Demography.

As we have shown, the effects of fragmentation or habitat heterogeneity varies with prey species and with geographic location. Given the additional complexities of multiple types of edges, it is unlikely that we will see any general pattern of fragmentation effects on Spotted Owl foraging or demographic success. For instance, fragmentation of Spotted Owl habitat in 40-48-year-old dense, closed canopy second growth Douglas fir or western hemlock stands without legacies and with little to no understory supports low numbers of woodrats, Flying Squirrels, hares, mice and vole. Clearly fragmentation in this type of habitat would produce the opposite effect as described above. It is therefore quite unlikely that results obtained in one habitat type or one part of the species range could be appropriately extrapolated to other areas, with different prey communities, forest structure, metabolic demands etc.

Given the complex interaction between forest structure, edge, and different prey species, we may expect both temporal and spatial variation in prey responses. For instance, in years of low woodrat abundance the net effect of edges on Spotted Owls might be negative in the southern part of the species' range. We may also expect different effects of heterogeneity at different spatial scales, depending on local prey composition and Spotted Owl territory size. This may be the case where prey populations become locally extinct (due to predation, fire or logging practices) and must be re-colonized from source populations.

6 COMPLEX INTERACTIONS AFFECTING NORTHERN SPOTTED OWLS AND THEIR PREY

Previous sections have shown that interaction between Spotted Owls and their prey may vary strongly, temporally, spatially, etc. It is also to be expected that other factors including weather, the presence of other predators, and forest management, will alter the interaction between Spotted Owls and their prey.

Northern Spotted Owls have been suggested to depress abundance of prey species (Carey et al. 1992). Therefore, it would be expected that some level of interspecific competition between Spotted Owls and other predators, including Barred Owls (see chapter 7), could affect Spotted Owl behavior and demographic parameters. For instance, long-tailed weasels (*Mustela frenata*) killed up to 32% of radio-marked Flying Squirrels in a winter in the Puget Trough (Wilson and Carey 1996, Carey 2000, 2002); other owls (e.g. *Bubo virginianus* and *S. varia*) and mustelids (*Martes americana* and *Martes pennanti*) also consume squirrels in large numbers (Carey 1991, Carey and Curtis 1996, Carey et al. 1996, Carey et al. 1999a, Carey 2000a). High predation rates by multiple predators have the potential of limiting prey populations. *Swingle and Forsman* (*2004*) followed 61 Red Tree Voles for an average of 70 days each. Twenty eight voles were eaten, 15 by weasels, three by owls, and 10 by other or unknown predators; these clearly indicate high levels of predation, which also could indicate competition between weasels and owls. Sakai and Noon (1997) followed 25 Dusky-footed Woodrats over a summer; six were killed by mammals and three by raptors. Spotted Owl behavior seems to track prey population size, avoiding depletion or areas of depletion with activities such as prey switching (Rosenberg et al 1996; Carey and Peeler 1995, also cited in Carey 2000a). "Multiple, abundant prey species allow spotted owls to use small home ranges (Carey et al. 1992) and may dilute predation pressure on any single species (or cause owls and other predators to focus on the most abundant and concentrated prey…)"(Carey et al. 1999c:76). Rosenberg et al. (2003) discuss for the possibility of switching behavior. Note that these are essentially options and hypotheses that are largely untested.

Complex interactions between trophic levels, are plausible, logically consistent, and perhaps important, but impossible to evaluate without a great deal of additional information. These interactions have a significant possibility of affecting diet choice, habitat use, demographic parameters and the application of forest management. Insight into this web of interactions will be time consuming, costly and difficult, but could alter management plans for the Spotted Owl.

7 MANAGEMENT EFFECTS ON FOREST STRUCTURE AND PREY

Sections below are in large part by the work of Carey. See appendix for the full document.

7.1 TIMBER HARVEST

> "Timber harvest (clearcutting, partial cutting, and variable retention harvest systems) is a catastrophic disturbance with both short- and long-term effects on prey. Surprisingly

many forest-floor small mammals respond positively to clearcutting in the short-term (Gunther et al. 1983). This is simply because any disturbance entails release of certain resources that then become available to various life forms, including small mammals. Cone- and seed-laden branches come to the forest floor to be exploited by diverse small mammals. With site preparation, these are often destroyed but colonization by grasses, forbs, and shrubs benefits diverse prey species (dusky-footed woodrats, deer mice, Oregon creeping voles [*Microtus oregoni*]) but the site might well be uninhabitable for a considerable period by the most arboreal rodents—red tree voles, flying squirrels, and Douglas's squirrels. The degree to which legacies are retained during timber harvests is an important determinant of recolonization of the site by all life forms (Perry et al. 1989, Franklin et al. 2000), including the fungi that are the mainstay of the flying squirrel and California red-backed vole diets (*Clethrionomys californicus*) (Amaranthus et al. 1989). These legacies are diverse but include fungal mycelia (indeed intact forest floor microbial communities in patches of intact forest floor), coarse woody debris, intact vascular plants, and fungal and plant propagules. Intentional retention of legacies can accelerate the pace of ecosystem recovery (Franklin et al. 1997)—the rate of change in the new, self-organizing community will be rapid and prey species will be affected differentially. Dusky-footed woodrats are benefited by delayed recruitment of a dominant cohort of conifers and rapid recruitment by evergreen hardwoods; flying squirrels respond oppositely.

Perhaps the biggest consequence of conventional clearcutting comes not during the disturbance itself or the period of rapid reorganization, but later when the conifer canopy closes (the stem-exclusion or competitive exclusion stage, Oliver and Larson 1996, Carey et al. 1999c). Dense, closed-canopy second-growth without legacies can not only be devoid of exploitable prey populations (Carey 1995, Carey and Johnson 1995, Carey and Harrington 2001) but also poorly suited for owl roosting, foraging, or nesting (Carey et al. 1992). This period of low structural diversity can last >100 years (Carey et al. 1999c, Franklin et al. 2002) and can have profound effects on the capacity of the forest to develop biocomplexity in the future (Halpern et al. 1999, Carey 2003a). However, with legacy retention, patchy regeneration of multiple species including hardwoods, and natural disturbances during the periods following either a natural catastrophic disturbance by wind or fire or following partial cuts, the prey base can reach or exceed levels of diversity and abundance found in many old-growth stands and will be used for foraging and roosting by spotted owls (Carey et al. 1992, Rosenberg and Anthony 1992, Carey 1995, Glenn et al. 2004)."

(Carey 2004, see Appendix)

7.2 THINNING

"Thinning can be done in many ways and for many purposes and has differing and diverse consequences on the ecosystem including effects on the prey themselves, the plants that provide them with food and cover, the fungi that provide them with food, and the health and resilience of the forest (Waters et al. 1994; Carey et al. 1996, Colgan et al. 1999; Graham et al. 1999; Carey 2000b, 2001; Thysell and Carey 2000, 2001; Wilson and Carey 2000a, b, 2002b; Carey and Wilson 2001; Sullivan et al. 2001; Muir et al. 2002). All thinning has short-term negative effects on understory plants (mechanical destruction) and below-ground fungi (death of host trees and mechanical destruction). Heavy thinning in the Mixed Conifer/Mixed Evergreen Zone may benefit woodrats and deer mice in the mid-term, but to the detriment of flying squirrels. Conventional thinning in the Western Hemlock Zone may result in very low flying squirrel populations through negative effects on truffle production and arboreal travelways (Colgan et al. 1999, Carey 2000b) and reduced foraging by spotted owls (Meiman et al. 2003) for a long time while increasing numbers of forest-floor rodents (Wilson and Carey 2000). Conventional thinning, however, may result in uniform dense understories unfavorable to both flying squirrels and owl foraging in the midterm. Variable-density thinning, however, hold promise for acceleration of the development of spotted owl habitat and dense prey populations (Carey 1995, 2001, 2003a. Carey et al. 1999a,b; Carey and Wilson 2001; Muir et al. 2002) especially when appropriate attention is paid to decadence (snags, cavity trees, and coarse woody debris) (Bunnell et al. 1999; Carey et al. 1999a, b; Carey 2002). There maybe a short-term impact on truffle production, flying squirrel abundance, and owl foraging, the ecosystem recovers more quickly and begins to develop more quickly and completely than following conventional thinning. Variable-density thinning has all the positive effects of conventional thinning, such and increased growth of trees, crown differentiation, development of understory, and increased flowering and fruiting of understory plants (Harrington et al. 2002, Wender et al. 2004) that provide important ancillary foods to spotted owl prey (Carey 2000a) without the same extent of negative mechanical impacts, loss of canopy connectivity, loss of spatial heterogeneity, loss of woody plant diversity (variable-density thinning stresses multipspecies management)." (Carey 2004, see Appendix)

Note that E. *Forsman* (*pers. comm.*) has expressed concern that regular thinning of young stands may make those stands unsuitable for Tree Voles. While there is no research that clearly documents the effects of thinning on Tree Voles, anecdotal evidence suggests thinning eliminates Tree Voles. Currently this relationship is not well documented.

7.3 FIRE SUPPRESSION

"Fires play different roles in different ecosystems (Franklin et al. 2002). Some forests and their fauna are well-adapted to fire—understory may be highly flammable, but quick to recover, and overstory trees may be quite fire resistant. This is true of the mixed-conifer forest of southwestern Oregon and northern California, where the old-growth is even more patchy and coarse-grained than the forests to the north, with the forest incorporating various evergreen hardwoods and hard-leaved shrubs especially supportive of dense woodrat populations. Forest to the north in western Oregon and Washington have increasing fire return intervals up through British Columbia where millennia might pass without catastrophic fire on some sites. Wind can be an important catastrophic disturbance in coastal forest, but intermediate disturbances due to wind, ice, snow, and disease may prove to be more important in forest developmental processes. East of the Cascades, forest historically appeared to have shorter, but spatially highly variable fire return intervals, often with frequent fires of low to moderate intensity. There, fire suppression has altered the ecology of the forests with fire-adapted understories of grasses, forbs, and low shrubs being replaced by flammable ladder fuels that may threaten catastrophic destruction of the forest when fire does occur. But eastside forests are diverse and conditions in dry site ponderosa pine (*Pinus ponderosa*) are too often generalized to other types. Furthermore, grazing and silviculture has compounded the changes in eastside forests (Graham et al. 1999). Franklin et al. (2002) point out the patterns in eastside forest are often misunderstood, with patches within late-seral forests interpreted as independent stands instead of part of the forest mosaic. The traditional forestry view of stands as homogeneous units of vegetation and the human tendency to reduce variability to one or two dimensions portend many management mistake eastside. Researchers in interior forests have found that approaches to managing forest for diversity and support of top avian predators, like the goshawk (*Accipiter gentilis*) (Reynolds et al. 1992) entail much the same approach adopted by researchers seeking to solve the spotted owl/spotted owl prey base dilemma in Westside forests (Carey et al. 1992, 1999a, b, 2003a,b). The same will likely prove true in management of spotted owls and spotted owl prey eastside—spatial heterogeneity (patchiness) may prove to be the key to restoration of forest health and low intensity fire regimes while retaining patches of complex forests that benefit owls and their prey.” (Carey, see Appendix)

8 UNCERTAINTY

Though the overall quality of the currently available data is good, there are large gaps in the understanding of prey species ecology and their interactions with their environment, other small mammals, and predators. The lack of long term abundance estimates limits our ability to determine how abundance and availability changes over time and how these abundances affect reproductive success and survival in both territorial and “floater” owl populations. How the “floater” population interacts and competes for food with the breeding population and their foraging patterns are largely unknown. Although interactions between prey and owls are hypothesized to determine home range size, reproductive success, and limits to distribution, the details of such relationships are unknown. Results of present studies are habitat and species specific and have limited applicability throughout other parts of the range of the Northern Spotted Owl. The question of what is driving the system and what role intra- and interspecies competition plays is still uncertain.

One of the premises that run throughout the literature is to equate abundance with availability. The accuracy of this assumption is unknown and unlikely to be resolved as the question of how to measure true prey availability is probably unattainable.

Another major uncertainty concerns prey ecology and owl demography. A majority of the research effort has focused on flying squirrels and to a lesser extent woodrats. However, only a weak relationship between reproductive success and flying squirrel abundance has been shown. It is plausible that the answers lie in complex interactions of several prey species, and suggestions have been brought forward that perhaps the secondary prey may provide the essential nutrients and energy for reproduction. Prey species may also fluctuate in parallel affecting reproduction and survival (Bloxton 2002, Fryxell et al. 1998). For now, these are just hypotheses that need to be examined. Currently, species other than Flying Squirrels and woodrats have received relatively little attention.

Little is also known about the factors that affect prey abundance, although it is known that their numbers fluctuate widely. How Spotted Owl diet changes in response to individual species fluctuations has not been assessed. As mentioned above, weather has been shown to affect prey litter size, sexual composition, and possibly mortality and reproductive success. Weather may also interact with other factors in a synergistic manner amplifying the effects on Spotted Owls. Interacting factors, such as weather and habitat heterogeneity, are likely to affect different prey species differently; the resulting effects on owls are likely to be complex and remain unknown.

9 SUMMARY AND CONCLUSIONS

In summary, Northern Spotted Owls feed mainly on forest small mammals, particularly arboreal and semi-arboreal species. The average prey size (74-116g) is relatively large compared to their body size. Though it has been suggested that there is a positive correlation between large prey and reproductive success, this relationship remains uncertain as there are conflicting results. There are also some results suggesting effects of secondary prey. Northern Flying Squirrels and woodrats comprise a bulk of the diet, but secondary species may be importation for survival and reproduction. Deer Mice, Red Tree Voles, Red-backed Voles, and two species of lagomorphs are considered locally and/or seasonally importation in the diet. Diet varies with the distribution and abundance of prey as well as with the type of habitat. Diet also varies locally, seasonally, and annually. Whether demographic variability in Northern Spotted Owls is affected by prey abundance, prey distribution or total prey biomass is unknown. Factors affecting the distribution and abundance of prey will vary with species, food source, season, biotic community (i.e., forest type and seral stage), geographic location, and sympatric species of competitors and predators. Weather may influence both owl and prey species directly and/or indirectly, though little data are available regarding its effect on prey. Interactions between Spotted Owls, prey and habitat are complex. Fragmentation or habitat heterogeneity affects prey species differently and is habitat and prey base specific. While habitat heterogeneity may benefit the owl in areas were woodrats are the primary prey, it has been shown to increase owl home range size in areas were Flying Squirrels dominate the diet. The extent to which these generalizations may be applied throughout the range of the owl is untested, and it is likely inappropriate to extrapolate the results from one area to another. The effects of fragmentation (both positive and negative) vary with prey species ecology and with temporal variation in abundance of species in the ecosystem. Further complexities include interactions amongst prey species, between predator and prey, and amongst predators that vary temporally, spatially, and with forest management. Overall there are large gaps in the information necessary to explain how prey species, weather, habitat, and forest management interact to affect Spotted Owl demography.

The basic conclusions set out in the 1990 listing of the Northern Spotted Owl are generally confirmed with recent information. The association of Spotted Owls with Northern Flying Squirrels and woodrats, their dominant prey items, is upheld, as are geographic differences in the importance of these prey types. Diet composition has remained relatively consistent, with annual and territorial variation as seen in previous studies.

However, within these broad patterns, important new information has been brought forth. Prey species differ in their response to forest structure and conditions. It is clear that under some circumstances, habitat heterogeneity and presence of edge may be favorable for Spotted Owls by potentially increasing prey abundance and availability. The extent to which these result may be extrapolated is unknown at this time.

There is some evidence that suggests that secondary prey species influence Spotted Owls. However, this is speculative, and future research is needed to quantity their importance. Similarly, complex interactions between vegetation, prey species, Spotted Owls, other predators and weather are predicted to affect overall Spotted Owl population trends, but are not well understood at this point.

10 INFORMATION NEEDS

Information on some prey species and on complex interactions among the habitat-prey-predator communities is largely lacking despite the general acknowledgement that understanding prey ecology is essential when studying and managing a predator. The following is a brief list of information needs, which if these needs were met would be useful for future Status Reviews.

- Long-term, year round demographic studies of prey species, including abundance, ecology, limiting factors, weather effects, dispersal distances and local extinction characteristics, etc.
- Long-term seasonal diet variation in owls
- Diet and reproductive performance of owls at high elevation
- Individual territory and stand scale diet variation and their correlation to reproductive output of owls
- Foraging patterns and diet variation in the juvenile and “floater” population
- Weather effects on owl, owl behavior, and prey abundance at the territory scale
- Weather effects on prey species and Spotted Owls
- The effects of prey on demographic performance
- Influence of prey abundance and type during winter on subsequent Spotted Owl survival and reproduction
- Secondary prey species abundance and ecology
- Evaluating whether predator can limit or depress prey abundance
- Interspecific competition among prey species

- Methods for increasing prey abundance and owl foraging in 2nd growth forests

Though Spotted Owl diets are well documented at broad regional scales, diet variation at the individual territory and stand scale are less well understood. Forsman et al. (2001) did compare diets at the territory scale, however, only 17 territories had sufficient sample size for the comparison and the sample size was too small to determine causes for individual prey use. Notably, "Ward et al. (1998) evaluated the relationship of Northern Spotted Owl reproduction with the abundance of prey at the level of the individual territory and found that because of the high spatial variability of prey abundance, they could not reliably estimate the abundance of prey at the scale of the individual owl" (Rosenberg et al. 2003). However, understanding diet variation at these scales will enhance our ability to directly correlate diet with reproductive success and survival. Along with general breeding season diet, non-breeding/winter diet and foraging patterns possibly determine nest initiation and survival. If Northern Spotted Owls are displaced to higher elevations by Barred Owl invasion, changes in diet and reproductive success may be needed to understand changes in demographic parameters, management strategies, extinction rates, and viable population estimates.

Currently, there are no long term, year-round demographic studies available on prey. This limits our ability to comprehend the influence of prey, both primary and secondary species, on owl demographics. We have no answers to questions like: What causes large prey fluctuations and how do they affect the Spotted Owl? Are there predictable patterns for different species? How do prey dynamics correspond with fluctuations in spotted owl reproduction? Do Spotted Owls depress prey? How do "floater" and juveniles use food resources and do the affect the breeding population? These questions are probably only answerable through long term monitoring and experiments like the Forest Ecosystem Study deliberately designed to test such hypotheses (Carey et al. 1999d). Long-term prey studies on owl demographic study areas could significantly increase our understanding of the interactions of the predator and its prey, leading to a substantial potential for changes in management plans. If management plans for prey species are to be developed to benefit owl populations, prey ecology needs to be examined. Factors limiting species abundance, such as weather, forest management effects, interspecies competition, dispersal distances and local extinction characteristics, will alter prey availability of the owl.

Currently, it is undetermined if weather affects owls directly, indirectly or both. It is plausible that weather may cause both owl and prey mortality and may affect the owl hunting efficiency. Different prey species may also react differently to various weather conditions. Investigations of the effect of weather on owls and a wide diversity of prey species at a territorial scale over broad regions should clarify these interactions and may explain some of the variation in owl reproductive success and survival. To this end, studies on climate change on weather and on metabolic demands may be useful.

Little attention has been focused on species other than Northern Flying Squirrels and to some extent woodrats, although some research in recent years has begun to focus on Red Tree Voles. It has long been thought that secondary prey species, a combination of prey species, or total prey biomass may affect owl reproductive success and survival. Secondary species may provide essential nutrients and energy required for reproduction.

The ultimate question is ‘how do you manage a predator, like the Spotted Owl, without understanding and managing the species on which it depends?’ Habitat management may be sufficient, but at this point, we have a relatively poor understanding of the interactions between habitat, prey, and Spotted Owls. Ultimately, the question will boil down to: How does one manage for biocomplexity that provides multiple ecological services from spotted owl prey to spotted owls themselves to healthy, resilient forests.

11 TABLES

Table 4.1: Percent composition of prey items †

	C Humboldt County CA 850m-1340m	I South Coast Range OR	A South-western OR 1350m-1750m	J Southwest Interior OR	E Elliot Coast Range OR	S Central Oregon Coast Range	H Central Coast Range, OR	F Blue River and McKenzie Ranger Districts OR*	L Central Cascades OR	M East Cascades OR	D North coast OR Coast Range	G North Coast Range OR	K North Cascades OR	B North-western WA- not Olympics 244m-1800m (forest area)	O Western Cascades WA	P Eastern Cascades WA	N Olympic Peninsula WA	Q Sub-province N: Western Olympic Peninsula WA ** P<0.001	R Sub-province N: Eastern Olympic Peninsula WA ** P<0.001
Northern Flying Squirrel *Glaucomys sabrinus*	10.1	36	49.6	28.2	32.1	43.9	49.5	45.7	34.7	41.1	45.9	48.4	52.1	50.7	29.3	40.7	54.3	63.3**	45.2**
Bushy-tailed woodrat *Neotoma cinerea*			11.6		17.3			5.1			5.6			4.4	1.3	8.7	5.3	1.1**	9.6**
Dusky-footed woodrat *Neotoma fuscipes*	38.5																		
Woodrats		18.2		27.8		6.3	7.1		9.6	5.1		11.8	2.3						
Red tree vole *Arborimus longicaudus*	8.8	18.2		2.6			12.7	6.7	5.1			4.9							
Phenacomys intermedius															3.7	0.8	0.2		
Red-Backed Voles *Clethrionomys spp.*	2.1	2.8	7	6.8			2.2	12.8	10.7	12			26.9	6.8	10.3	6.4	5.8	1.2**	10.3**
Deer Mice and Mice	6.8	6.2	3.9	4.9	10.4	10.9	10.5	4.9	6.4	4	15.9	17.3		20.6	15.2	6.5	11.3	15.6**	7.0**
Leporidae spp. – Rabbits and Hares		4.6		2.6	3.4	2.5	3.6	5.7	4.7	4.3	1	0.8		3	1.9	3.6	6.3	4.1	5.5
Microtus spp	10.7		20.9		17.2	13.3					3.5			0.7	5.7	1.9	1.7	0.9	2.5
Misc. Mammals	12.1	8	4.7	17.1	13.1	16.8	8.5	9.5	18.5	14.1	22.3	11.7	4.8	10	24.1	16.4	8.3	7.1	10
Unidentified bird	4.6	3.6	1.6	5.7	6.1	4.8	3.9		4.1	3.9	3	3.8	13.9	2.8	6	4.4	6.4	6.4	5.3
Insect	7.6	2.4	0.8	4.3	0.5	1.5	2.1		3.1	15.4	1.8	1		1	2.5	10.6	0.4		
Miscellaneous				0.1			0.1		0.1	0.1		0.5		1			0.1	0.3	0.6

A Cutler and Hays, 1991 sampling dates: April-August, 1988 129 prey items (82 pellets), 4 territories
B 579 Hamer et al. 2001 sampling dates: mostly April-August 1986-1989 265 prey items, 28 territories
C Ward et al. 1997 sampling dates: March-September 1987-1988 495 prey item, 8 pairs, 1 single (9 territories)
D *Anthony et al. 2000*: 1992-1999 206 pellets
E *Anthony et al. 2000*: 1992-1999 318 pellets
F Rosenberg et al. 2003: 1987-1996, excluding 1993
*excluded, only spp >= 5% biomass in any given year.
G-M: *Forsman Presentation 2004*: 1970-2001
N-R: Forsman et al. 2001: 1983-96, after lumping territories with <20 prey N=64territories, O=12 territories, P=26 territories, Q,R=32 territories each.
S: Anthony et al. 1998: 1990-1995
†: Prey species greatly simplified from individual study reports. Standard errors, when reported, have been removed and species lists have compressed by added species totals together.

Table 4.2: Percent biomass of prey items †

	C Humboldt county, CA 850m-1340m	I South Coast Range, OR	A Southwestern OR 1350m-1750m	J Southwest Interior, OR	E Elliot Coast Range, OR	S Central Oregon Coast Range	H Central Coast Range, OR	F Blue River and McKenzie Ranger Districts, OR*	L Central Cascades, OR	M East Cascades, OR	D North coast, OR Coast Range	G North Coast Range, OR	K North Cascades, OR	B Northwestern WA-not Olympics 244m-1800m (forest area)	O Western Cascades, WA	P Eastern Cascades, WA	N Olympic Peninsula, WA
Northern Flying Squirrel *Glaucomys sabrinus*	9.3	38.6	53.5	30.1	30.2	46.1	58.2	48.8	45.7	56.3	57.5	52.4	74.5	58.1	45.3	52.5	58.6
Bushy-tailed woodrat *Neotoma cinerea*			28.9		35.7			10.5			13.5			11.6	4.5	18.1	9.8
Dusky-footed woodrat *Neotoma fuscipes*	70.9																
Woodrats		37.1		48.7		14.5	16.1		20.7	12.4		25.9	5				
Microtus spp	2.9		9.6		3.6	3.1					1			0.1	2.6	0.5	0.4
Red tree vole *Arborimus longicaudus*	1.7	4.2		0.6			3.8	3.7	2.3			1					
Phenacomys intermedius															2	0.6	0.1
Red-backed Voles *Clethrionomys spp*	0.4	0.6	1.5	1.3			0.5	5.5	2.7	3.5			8.2	1.6	3.6	2.2	1.2
Deer Mice and Mice	1.3	1.2	0.8	1	2.1	2.3	2.5	1.6	1.5	0.9	4.5	3.9		4.5	4.9	1.9	2.5
Leporidae Spp - Rabbits and Hares		11.6		5.9	13.9	12	9.9	10.7	12.5	12.7	4	2.2		13.4	8.9	9.4	16.3
Misc Mammals	11.5	4	4.8	8.8	11	17.9	5	9.6	11.7	10.9	17.7	10.4	1.7	9.3	22.7	10.6	6.2
Miscellaneous																	<0.05
Unidentified bird	2	2.8	1	3.5	3.5	4	3.9		2.8	2.4	1.8	4.3	10.7	1.4	5.5	3.5	4.8
Insect	0.1	TR	<0.1	0.1			0.1		0.1	0.9		0.1	0	S0.05	<0.05	0.7	<0.05

A Cutler and Hays, 1991 sampling dates: April-August, 1988

B Hamer et al. 2001 sampling dates: mostly April-August 1986-1989 265 prey items, 28 territories

C Ward et al. 1997 sampling dates: March-September 1987-1988 495 prey item, 8 pairs, 1 single (9 territories)

D *Anthony et al. 2000*: 1992-1999 206 pellets

E *Anthony et al. 2000*: 1992-1999 318 pellets

F Rosenberg et al. 2003: 1987-1996, excluding 1993

*excluded, only spp >= 5% biomass in any given year.

G-M: *Forsman Presentation 2004*

N-R: Forsman et al. 2001: after lumping territories with <20 prey N=64territories, O=12 territories, P=26 territories, Q,R=32 territories each.

S: Anthony et al. 1998: 1990-1995

†: Prey species greatly simplified from individual study reports. Standard errors, when reported, have been removed and species lists have compressed by added species totals together.

SCIENTIFIC EVALUATION OF THE STATUS OF THE NORTHERN SPOTTED OWL

CHAPTER FIVE

Habitat Associations

Drafting Author:
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1 INTRODUCTION

Habitat for Spotted Owls includes characteristics of vegetation, climate, geography, prey, predators, competitors, and interactions between these factors. Prey, predators and competitors of Spotted Owl are covered in other chapters of this report. This chapter focuses on the vegetational, climatic, and geographic aspects of Spotted Owl habitat. Research has emphasized vegetation composition of Spotted Owl habitat, at least in part because timber harvest and other management activities that affect vegetation can be modified by humans, whereas climate and geography cannot. The emphasis in this chapter on forest and landscape attributes reflects the historic research emphasis. Within sections of this chapter, findings are generally organized by geographic province (see figure in introductory chapter), from north to south and west to east. Few studies of habitat use by juvenile Northern Spotted Owls have occurred since 1990, and all studies of owls that did not use radio-telemetry were conducted in March-August. Consequently, unless otherwise noted, habitat associations discussed in this chapter apply to territorial Spotted Owls during spring and summer.

More studies of habitat relationships have been conducted on the Spotted Owl than any other raptor in the world (Lõhmus 2003). Habitat use by Northern Spotted Owls has been evaluated by a variety of methods and at several spatial scales for more than two decades (Gutiérrez et al. 1995; Franklin and Gutiérrez 2002). In general, studies completed by 1990 showed that Northern Spotted Owls consistently used old-growth forests, forests of mixed mature and old-growth, or, especially in the Redwood region, mature forest with structural characteristics similar to old-growth stands, for foraging, roosting and nesting in proportions greater than expected based on availability. Thomas et al. (1990:164) characterized Northern Spotted Owl habitat as follows:

> "Structural components that distinguish superior Spotted Owl habitat from less suitable habitat in Washington, Oregon, and northwestern California include: a multilayered, multispecies canopy dominated by large (>30 inches in d.b.h.) conifer overstory trees, and an understory of shade-tolerant conifers or hardwoods; a moderate to high (60 to 80%) canopy closure; substantial decadence in the form of large, live coniferous trees with deformities—such as cavities, broken tops, and dwarf mistletoe infections; numerous large snags; ground-cover characterized by large accumulations of logs and other woody debris; and a canopy that is open enough to allow owls to fly within and beneath it."

Johnson (1980) provided a framework for discussing orders of habitat selection: first-order selection is the physical or geographical range of a species, second-order selection determines the home range of an individual, third-order selection involves the use of habitat components within the home range, and fourth –order selection is choice of, for example, prey items within an individual habitat component. In this hierarchy, higher orders of selection are conditional upon lower orders. For example, selection of forest stand types by a Spotted Owl within its home range is constrained by selection of the home range. Following Johnson's (1980) framework, research reviewed in this section examined second- and third- order selection.

Establishing the spatial extent of an owl's home range and relative use within the home range (second-order selection) requires use of radio-telemetry. In several studies, composition of owl home ranges or core areas established using radio-telemetry was compared to composition of a larger forested landscape. Because the intensity and high cost of radio-telemetry studies limited sample sizes, many recent landscape level studies on Spotted Owls have approximated home range or core area composition (second-order selection) using Geographic Information technology and extensive Spotted Owl location data collected during demographic studies and other owl surveys. In these studies, circles centered on Spotted Owl nest or roost locations were drawn on vegetation maps to approximate home range or core areas. Corresponding circles were located randomly within forested landscapes, and comparisons were then made between the composition and, sometimes, spatial configuration of habitat (including fragmentation) with owl sites. Recently, several studies have modeled demographic responses of owls (survival, recruitment, and reproductive rates) as a function of habitat available to owls.

Third-order selection by Spotted Owls has been evaluated at a variety of spatial scales, from gross categorization of forest stands to detailed measurements of forest structure. Stand condition is a general classification based on species composition, tree age or size, canopy closure, fire regime, soil, climate and/or topographic characteristics. Researchers have defined stand conditions differently among studies, but, in general, an effort was made to distinguish stands characterized by large, old trees from those characterized by smaller-sized, younger trees. Alternatively, several studies classified stands according to physiognomic stages of stand development (Buchanan et al 1995:302, after Oliver 1981):

> "The stand initiation stage is the establishment of the regenerating stand by an even-aged cohort of trees and may last > 40 years. During stem exclusion, the second stage, the initial cohort occupies all available growing space and prevents other trees from invading the stand. This is followed by the understory reinitiation stage, where shade-tolerant (or moisture-limited) tree species begin to develop ≥ one strata in the understory. Forests of the old-growth stage are characterized by uneven-aged cohorts that result from perturbations of various scale and intensity."

At a finer spatial scale, forest structure (canopy cover, tree diameter distribution, snag density, coarse woody debris, etc.) was quantified from detailed measurements at nest, roost, and random locations. At this scale, most studies measured habitat association by comparing characteristics of areas used by owls with areas available within the home range, within the same stand, or at random locations.

In the following, we review what we have learned about Northern Spotted Owl habitat associations since 1990. In particular, we ask which aspects of our previous understanding are confirmed by recent research and which aspects have changed or clarified. We pay particular attention to similarities and differences in findings among provinces.

2 HOME RANGES AND CORE AREAS

2.1 HOME RANGE AND CORE AREA SIZE

Home range sizes of Northern Spotted Owls have been estimated on five study areas in Washington, Oregon and California since 1990 (Table 5.1). Home range sizes were estimated by fitting owls with backpack or tail-mounted radio transmitters, determining owl locations by triangulation on the radio signal, and calculating the area traversed by the owls based on the distribution of the triangulated owl locations. The simplest and most consistently applied analytical method for calculating Spotted Owl home range size was to estimate the Minimum Convex Polygon (MCP), the area of the smallest polygon containing all of an owl's radio locations. The MCP may include portions of a landscape not used by an owl, and therefore may be more appropriately considered the area traversed rather than the area used by an owl (Carey et al. 1992). Other methods of estimating home range size include calculation of MCP using a subset (e.g. 95%) of the spatial extent of locations (95% MCP), modified minimum convex polygon (MMCP) or various smoothing methods, including kernel estimators. Kernel estimators use probabilistic models to estimate the relative use of areas traveled by an animal. A utilization distribution, which is a probability density function that indicates the likelihood of an animal occurring at each point within the range, quantifies relative use. Home range size is then reported typically as the area containing that portion of the utilization distribution where the animal is likely to be found 95% of the time (Kernohan et al. 2001). Kernel estimates are less sensitive to sample size and outliers than MCP estimates (Kernohan et al. 2001).

Home range area for Northern Spotted Owl pairs varied by physiographic province and forest type and among individual owls within a study area (Table 5.1). MCP home range estimates reported from 1990 to present were similar to those tabulated by Thomas et al. (1990:194).

A home range core area was defined as the area within a home range that receives disproportionately high use (Bingham and Noon 1997), and may be estimated empirically using kernel methods. Core area sizes were extremely variable among owls but similar at two study areas in the Oregon Coast Range, averaging 94 ha (SE = 14.9; n = 24; range = 5 to 273) even though MCP home range size (more sensitive to sample size; see above) differed by study area (Glenn et al. 2004).

The influence of landscape attributes on home range size has been inferred by comparing differences in forest age, amounts of mature and old-growth forest, forest fragmentation, tree species composition and distribution of major prey species with differences in home range area. Carey et al. (1992) found that the area traversed by owls (100% MCP home range) was 85% larger in more heavily fragmented Douglas fir forest in the Oregon Coast Range and 237% larger in more heavily fragmented mixed conifer forest in the Klamath Province relative to less fragmented areas of the same forest types/geographical areas (Table 5.1). However, the amount of old forest within home ranges was similar among study areas in the Carey et al. (1992) study.

Glenn et al. (2004) compared home range sizes in two study areas in the Oregon Coast Range. The Elliot State Forest study area (ESF) contained a mix of old, mature and pole size conifer, and the North Coast Range study area (NCR) contained mostly forest < 80 yrs old. Both study areas consisted of approximately 23-25% hardwood forest, predominantly in riparian areas. Home ranges were larger at NCR than ESF whereas core area size was similar among study areas (Table 5.1). Variation in home range size was best explained by models containing the proportion of mature/old forest within the home range (41% of variation explained), with smaller home ranges having greater proportions of mature/old conifer forest. There was very little mature/old forest at NCR. On average, owl locations at both study areas were closer to edges between hardwood forest and other cover types and farther from forest-nonforest edges than random points, but the authors noted this was not true for all individuals.

In contrast to these findings, in study areas dominated by late-successional forest in the southern Oregon Coast Range and California Klamath Province, home range size of Spotted Owls was not correlated with the proportion of the home range in old-growth forest (Zabel et al. 1995). Rather, the proportion of the diet containing woodrats explained 41% of the variation in Spotted Owl home range size. Home ranges were smaller where woodrats dominated the diet ($r^2 = 0.64$, $n = 15$) and larger where flying squirrels dominated ($r^2 = 0.56$, $n = 15$). Within one study area where woodrat density was estimated, home range size was negatively correlated with woodrat abundance ($r^2 = 0.41$, $n = 12$; Zabel et al. 1995).

The response of one Spotted Owl to timber harvest was evaluated in a detailed study in the Oregon Coast Range (NCR study area, above; Meiman et al. 2003). This male owl's breeding season home range and core area sizes were similar pre- and post-harvest but its nonbreeding season home range and core area sizes were larger after harvest. The owl's core area of use shifted away from the thinned stand following harvest. Inferences from this study were limited because it included only one individual owl.

2.2 HOME RANGE AND CORE AREA COMPOSITION

Many researchers have compared stand conditions surrounding owl locations to random locations by mapping circles of various radii around owl nests or roosts, and then comparing forest conditions within the circles. In nearly all cases, the amount of mature and old-growth forest was greater within circles containing owls than random locations, ranging from 30–78% at owl sites and 6-63% at random sites (Table 5.2; see also Swindle et al. 1999).

One study in the Eastern Cascades of Washington found results contrary to this general trend (*Irwin et al. in press*). *Irwin et al.* (*in press*) found more mature and old-growth forest (> 64 cm dbh) in random locations than owl locations and more forest 20-64 cm dbh in owl locations than random locations. Furthermore, owl locations were positively associated with proximity to riparian habitat and negatively associated with trees 13-19 cm dbh and with elevation. *Irwin et al.* (*in press*) hypothesized that development of dense understories of shade tolerant trees 13-19 cm dbh, which resulted from fire suppression since 1910, may have led to abandonment of 45 owl territories in mesic forests of their study area.

Within commercial forest in the California Redwood Zone, 200 ha circles centered on owl nests contained forest > 60 yrs old in similar proportion to that found within 200 ha circles centered randomly on forest not used for nesting (nest circles mean = 42%, SE = 6%; random circles mean = 41%, SE = 6%; Folliard et al. 2000). However, the area at nest sites composed of forest

31-45 yrs old (mean = 46%, SE = 8%) and 45-60 yrs old (mean = 55%, SE = 8%) was greater than unused sites (31-45 yr old forest mean = 29%, SE = 6%; 45-60 yr old forest mean = 34%, SE = 7%), whereas the area of forest 8-30 yrs old was lower at nest than unused sites (nest site mean = 24%, SE = 5%; unused site mean = 53%, SE = 9%; Folliard et al. 2000).

In a study area (BLM Arcata Resource Area [ARA]) characterized by small, isolated patches of old growth forest surrounded by areas of extensive timber harvest in the California Klamath Province, Gutiérrez et al. (1998) compared landscape composition within 200 ha plots surrounding Spotted Owl nest and roost sites (n = 29) with landscape locations unused by Spotted Owls (n = 15). Owl use sites contained 32% mature and old-growth forest (SE = 4) compared to 22% at unused sites (SE = 3). Habitat dominated by brush (< 25% canopy cover, woody plants < 15.2 cm dbh) comprised 24% of owl use areas (SE = 1) and 40% of unused areas (SE = 18). Cover type heterogeneity, measured by Simpson's heterogeneity index, was lower at used than unused areas (used = 0.60, SE = 0.02; unused = 0.65, SE = 0.03). Landscape characteristics of owl use sites in the ARA were also compared to an equal number of owl use sites in another study dominated by larger more contiguous areas of old forest (the Willow Creek Study area [WCSA] of Franklin et al. 2000 and Hunter et al. 1995). The WCSA owl sites contained more mature and old-growth forest (WCSA mean = 50%, SE = 3), more pole and medium conifer (WCSA mean = 14%, SE = 1%; ARA mean = 7%, SE = 2%), and less brush (WCSA mean = 10%, SE = 2%) than ARA.

In some studies, landscape composition was evaluated within nested circles. In general, differences between owl locations and random sites diminished as circle size increased (Hunter et al. 1995, Ripple et al. 1997, Meyer et al. 1998, Swindle et al. 1999, *Perkins 2000*). Amount of mature and old-growth forest was higher in owl sites than random landscape locations even within annuli created by concentric circles up to 3.4 km radius in one study in Oregon (Meyer et al. 1998) and up to 0.6 km radius in another study in Oregon (Swindle et al. 1999). Differences in outer rings indicated that differences between larger circles were not simply artifacts of differences in nested smaller circles in this population (Meyer et al. 1998).

In general, across studies, hardwood and younger conifer forest types were not greater within owl circles than random circles with the following exception: greater amounts of hardwood forest were found in owl than random sites beyond the smallest (0.8 km radius) circles in the Klamath Province of Oregon (Meyer et al. 1998).

In the Oregon Coast Range Spotted Owls were negatively associated with 0-40 and 41-70 yr old stands at three of four spatial scales evaluated (50, 100, and 600 ha), positively associated with 101-200 yr old stands at 200 ha scale and positively associated with > 200 yr old stands at all scales based on stepwise logistic regression for 82 owl and 82 random sites (*Zabel et al. 2001*).

2.3 REPRODUCTION, RECRUITMENT AND ADULT MORTALITY

Hicks et al. (2003) measured productivity, subadult recruitment and adult turnover rates at 100 Spotted Owl sites spanning the Washington Cascade Range over a 10 yr period. Owl nest sites were grouped into five vegetation zones, from west to east: western hemlock, silver fir, interior western hemlock, grand fir, and interior Douglas fir. Physical and geographic parameters (precipitation, elevation and longitude) were weakly correlated only with productivity (regressions P > 0.05 and $r^2 < 0.05$). The number of young fledged per territory differed by vegetation zone, decreasing from east to west. Three young were fledged in 15% of nesting attempts in the Interior Douglas fir (easternmost) zone, 3% of attempts in the grand fir zone, and never in the three westernmost zones. Owls in the three westernmost zones had lower adult turnover rates and lower subadult recruitment rates than owls in the two easternmost zones. Because this study was not based on mark-recapture methods, turnover and recruitment were confounded with detectability. However, trends found in this study were confirmed by estimates of survival and fecundity in a meta-analysis using mark-recapture data (see Demography Chapter).

Irwin et al. (*in press*) compared Spotted Owl reproductive rates among Fire Management Analysis Zones (FMAZ), which were based on vegetation associations, natural fire regimes, and other factors (see section 4.2). Similar to the findings of Hicks et al. (2003), the highest Spotted Owl reproductive rates were in Ponderosa pine/Douglas fir forests and grand fir mixed coniferous forest, and the lowest reproductive rates were in western hemlock and subalpine forests of the Eastern Cascades, Washington. *Irwin et al.* (*in press*) also compared reproductive output of Spotted Owls inside Late-Successional Reserves (LSR) with owls outside LSRs. Assignment of an owl to inside or outside and LSR was based on whether the majority of a 200 ha circle surrounding the owl site center was comprised of LSR or not. Mean productivity was 0.60 young/yr (SE = 0.04) in LSRs and 0.72 young/yr (SE = 0.06) outside LSRs. *Irwin et al.* (*in press*) did not present the location of LSRs among FMAZ in their study; therefore we can not evaluate the degree to which differences in owl productivity among FMAZ and between LSR/non-LSR may be confounded.

An index to Spotted Owl reproductive rates in the Klamath Province, Oregon, increased with increasing proportion of mature and old-growth forest in the landscape around nest sites (Ripple et al. 1997). The reproductive index standardized the number of young fledged at a site to the average number of young fledged in the same years, to account for missing data from some sites in some years, given the annual variation in the number of young fledged throughout the study area (Ripple et al. 1997).

Within commercial forest in the California Redwood Zone, Spotted Owl sites with the highest reproductive success (n = 25) had greater proportions of 21-40 year-old stands within a 398 ha circle surrounding the site center than sites with lower reproductive success (n = 26). Reproductive success was measured as the proportion of years when ≥ 1 juvenile owl fledged. However, Spotted Owl site centers had lower proportions of 21-40 year-old stands than random locations (Thome et al. 1999). Thome et al. (1999) hypothesized that Spotted Owls may have benefited from higher woodrat availability in the 21-40 year-old stands. Thome et al. (2000) also found for the same Spotted Owl sites that those with at least one turnover in four annual intervals (n = 30) had lower proportions of 21-40 year-old stands (mean = 0.23, SE = 0.05) than those without turnovers (n = 21, mean 21-40 year- old stands = 0.36, SE = 0.06). Fifty percent of the new recruits were subadults (1 or 2 years old). Because female Spotted Owls generally do not breed until at least 3 years old (see Demography chapter), turnover rates and reproductive rates were confounded in this study.

Neither *Irwin et al.* (*in press*), Ripple et al. (1997), nor Thome et al. (1999) measured survival rates in relation to the same independent variables with which they measured reproductive rates, so it is unknown whether the factors positively associated with owl reproduction were also positively associated with owl survival.

2.4 FOREST FRAGMENTATION AND LANDSCAPE CONFIGURATION

Franklin and Gutiérrez (2002) conducted a meta-analysis of the effects of forest fragmentation and heterogeneity on all three subspecies of Spotted Owls. In this meta-analysis, Northern Spotted Owls were represented by seven studies in the Olympic Peninsula, Washington, Coast Range, Klamath Province, Eastern and Western Cascades of Oregon, and Klamath Province of California (Lehmkuhl & Raphael 1993, Ripple et al. 1991, *Johnson 1992*, Meyer et al. 1998, Ripple et al. 1997, Hunter et al. 1995, *Morganti 1993*). Meta-analysis confirmed that sites occupied by Northern Spotted Owls contained greater amounts of mature and old forest than randomly located sites in forested landscapes (see section 2.2; Table 5.2). Comparisons of fragmentation and heterogeneity were limited because dissimilar metrics were used in individual studies. However, six metrics were common to two to three studies, and the following three showed consistent relationships to owl occupancy across studies: mean patch area of mature and old-growth forest, amount of patch interior of mature and old-growth forest, and a fragmentation index (GISfrag of Ripple et al. 1991). Magnitude of effects for these three metrics were similar between the Western Cascades and Klamath Provinces, which suggested that owl site occupancy was positively associated with old forest patch area and size of patch interior and negatively associated with the fragmentation index.

Other measures of fragmentation varied between owl and random sites for individual study areas. On the Olympic Peninsula, in addition to greater amount of owl habitat and larger mean patch area, owl sites (n = 78) had lower patch density and isolation indices than random sites (n = 100; Lehmkuhl and Raphael 1993). Within 3258 ha circles, percent owl habitat was 46% for owl sites and 34% for random locations. Nest patches were larger than the largest old conifer patches in random circles in the Klamath Province, Oregon (Ripple et al. 1997).

Subsequent to the meta-analysis of Franklin and Gutiérrez (2002), *Perkins* (*2000*) found Simpson's Evenness Index was higher within 112 ha surrounding nest than random non-nest locations, indicating a more even distribution of cover types around nest than non-nest locations in the Oregon Coast Range. Additionally, percent old growth and young stands with remnant large-diameter trees were greater around nest locations and discriminated between nest and non-nest locations. *Perkins* (*2000*) also found differences between old growth stands used for nesting and old growth stands not used for nesting were best explained by the ratio of core:edge of the stand and complexity of the stand shape, both of which were higher at nest stands than non-nest stands.

In the California Redwood Zone, 200 ha circles centered on owl nests (n = 60) contained more edge (juxtaposition of different cover types or age class of the same cover type) and were lower on slopes than 200 ha circles centered randomly on forest not used for nesting (n = 60; Folliard et al. 2000). Dispersing juvenile owls in the Coast Range, Klamath Province and Western Cascades, Oregon, showed no differences in use of forests with low, medium, or high levels of fragmentation, based on the numerical value of a fragmentation index calculated within 1.6 km radius circles (Miller et al. 1997).

Keithley and Motroni (*2000*) compared vegetation composition and configuration within 200 ha circles among > 300 Spotted Owl sites (exact number not specified) and 55 randomly selected non-owl sites throughout the northern Coastal province in California. Vegetation was classified as: "preferred owl habitat" (conifer stands with ≥ 61 cm quadratic mean diameter [qmd] and ≥ 70% canopy cover, and hardwood stands with ≥ 76 cm qmd and ≥ 70% canopy cover); "marginal habitat" (conifer stands with ≥ 61 cm qmd and < 70% canopy cover, conifer stands with < 61 cm qmd, hardwood stands with ≥ 76 cm qmd and < 70% canopy cover, and hardwood stands with < 76 cm qmd); "woodrat habitat" (conifer stands with < 61 cm qmd and 10-50% canopy cover and hardwood stands with < 76 cm qmd and 10-50% canopy cover); grass and shrub; non-forest (urban, barren and water). Spotted Owl sites were further classified according to land management (private, public managed, public reserve). Spotted owl sites of all three land management categories contained more preferred owl habitat, more marginal habitat, more woodrat habitat and a higher mean Shape Index (Shape Index increases as patch shapes become more irregular) than non-owl sites (ANOVA multiple means test $P < 0.05$). Mean fractal dimension, perimeter to area ration and Shannon Evenness Index were similar among Spotted Owl sites and non-owl sites (*Keithley and Motroni 2000*).

Zabel et al. (2003) built models to predict Spotted Owl site occupancy in the Klamath Province in California. They found that models which included habitat edge and core area variables as well as non-linear relationships between occupancy and roosting and foraging habitat performed better (based on correct classification of independent data sets) than models based only on linear relationships to roosting and foraging habitat. Among 200, 550 and 900 ha scales, models performed best at 200 ha, although the authors note that this may be due to a larger sample size for the smaller scale.

Zabel and Pagliughi (*2003*) tested the model of Zabel et al. (2003) on portions of the Six Rivers and Mendocino National Forests and found that the model performed poorly in predicting Spotted Owl presence and absence; only 48% of points were correctly classified. Failure of the model to perform well was likely due, at least in part, to the fact that habitat data used in the model were from 200 ha buffers around call point locations rather than owl roost or nest locations.

2.5 SURVIVAL, REPRODUCTION AND SITE OCCUPANCY IN RELATION TO FOREST FRAGMENTATION AND LANDSCAPE CONFIGURATION

Ripple et al. (1997) found that an index to reproductive rates (see above) at 20 owl sites in the Klamath Province, Oregon, increased with increasing proportion of old conifer forest in the landscape ($r = 0.64$, $P = 0.03$). Old conifer forest included open (40 to 59%) and closed (≥ 60%) canopy stands dominated by conifers ≥ 50 cm dbh.

Thrailkill et al. (*1998*) modeled territory occupancy, nest success and turnover on individual owl territories ($n = 64$) as a function of the amounts of various habitat types within circles of five different radii (1.1–3.4 km). Territory occupancy and nest success were negatively related to the amount of clearcut area surrounding owl site centers across spatial scales. Turnover rate was negatively related to the amount of suitable habitat within the smallest circles and positively related to the amount of clearcut area within 1.6 and 1.9 km radius circles.

Meyer et al. (1998) examined reproductive success as a function of landscape characteristics, including fragmentation, at 50 Spotted Owl sites in the Oregon Coast Range, Klamath Province, and Western Cascades. Reproduction was not related to any landscape measures in the Coast Range nor Cascades, but in the Klamath Province was positively correlated with increased fractal dimension, increased number of old-growth patches, and increased amount of hardwood forest within 2.4-km-radius circles centered on owl nests (or centers of activity if no nest was known; adjusted $R^2 = 0.56$).

Four studies modeled the effects of weather variables and landscape characteristics on temporal and spatial variation of Northern Spotted Owl survival and reproductive rates (Franklin et al. 2000, *Olson et al. 2004*, *Anthony et al. 2002a*, *Anthony et al. 2002b*). Methods are described in the Demography chapter (section 2.1), as are analyses pertaining to weather (section 2.2). The following results pertaining to habitat are a reiteration of those in the Demography chapter (section 2.1). Franklin et al. (2000) and *Olson et al.* (*2004*) also estimated habitat fitness potential (λ_H) of individual owl sites using modified Leslie projection matrix methods. Habitat fitness potential was interpreted as follows: $\lambda_H = 1$ indicates that owls in a territory are replacing themselves, $\lambda_H < 1$ indicates that owls in a territory are not replacing themselves, and $\lambda_H > 1$ indicates that owls in a territory are more than replacing themselves.

In the California Klamath Province, survival was positively and non-linearly associated with the amount of interior older forest (> 100 m from an edge), the amount of edge between older forest and other vegetation types, and showed a quadratic (convex) relationship to the distance between patches of older forest (Franklin et al. 2000). Reproductive output was negatively and non-linearly associated with the amount of interior older forest, had a quadratic (concave) relationship to the number of older forest patches, and was positively associated with the amount of edge between older forest and other vegetation types. Thus, there appeared to be a trade-off between the benefits to survival conferred by interior older forest and benefits to reproduction conferred by less interior older forest and more convoluted edge between the two habitat categories. Estimates of λ_H ranged from 0.438 to 1.178. Based on 95% confidences intervals, 69% of owl territories had estimates of $\lambda_H > 1$, indicating owls at these territories more than replaced themselves. Franklin et al. (2000) suggested that habitat quality may determine the magnitude of λ (population trend) and recruitment may determine variation around λ. In addition, owls in territories of higher habitat quality (i.e., $\lambda_H > 1$) had greater survival during inclement weather than those in poorer quality habitat.

In the central Oregon Coast Range, survival had a quadratic (convex) relationship to the amount of mid- and late-seral forest within 1500 m of owl site centers (707 ha circles; *Olson et al. 2004*). The best model explained only 16% of the variation in the data. Of the variation explained by the model, habitat accounted for 85%. Reproductive output was positively related to the amount of edge between mid- and late-seral forests and other habitat classes. The best model explained 84% of the total variability; however, the habitat variable accounted for only 3% of the variation explained by the model. A mixture of older forests with younger forests and nonforested areas appeared to benefit owl life history traits. Estimates of λ_H ranged from 0.74 to 1.15 (mean = 1.05, variance = 0.005), with 95% confidence intervals around λ_H for all but one territory overlapping 1, indicating a potentially stationery population based on habitat pattern (*Olson et al. 2004*).

In the western Cascades, owl survival had a quadratic (concave) relationship to the amount of non-habitat within 1500 m of owl site centers. The best model of survival explained 58% of total variance, and habitat accounted for 32% of the variance explained by the model. Owl productivity showed a negative linear relationship to the largest patch size of old conifer (> 50 cm dbh) forest within 1500 m of owl site centers (*Anthony et al. 2002a*). The best model explained 77% of the variation in owl productivity; however, 99.6% of this variation was accounted for by owl age, 0.4% by weather, and a negligible amount by habitat.

In the southern Cascades, two nested circles (167 and 1565 ha) and the ring between the circles (1388 ha) were used to characterize habitat at owl sites (*Anthony et al. 2002b*). The best model of owl survival indicated that survival increased non-linearly with the amount of mature and old growth forest within 167 ha around site centers and had a quadratic (convex) relationship to the amount of non-habitat in the 1388 ha ring. These two habitat covariates explained 54% of the spatial variation in survival; temporal variation was essentially zero (*Anthony et al. 2002b*). Owl productivity was positively related to the proportion of mature and old-growth forest within 600 m of owl site centers. However, the best model accounted for 25% of the total variance in reproductive output and the habitat variable only accounted for 7% of the model variance. Seventy-four percent of the model variance was explained by a biannual pattern in reproduction ("even-odd year effect") and the experience of male owls on a territory (*Anthony et al. 2002b*).

2.6 FIRE EFFECTS

In 1994, the Hatchery Complex wildfires burned 17,603 ha in the Wenatchee National Forest, eastern Cascades, Washington, affecting activity centers of six Northern Spotted Owl sites (*Gaines et al. 1997*). Spotted Owl habitat within 2.9 km radii of the activity centers was reduced by 8–45% (mean 31%) due to direct effects of the fire and by (cumulatively) 10-85% (mean = 55%) due to delayed mortality of fire-damaged trees and insect caused tree mortality. Spotted Owl habitat was defined as having ≥ 60% canopy closure, numerous snags, and ≥ 2 canopy layers, and was measured from field-verified aerial photo interpretation before the fire, immediately post-fire, and one year post-fire (*Gaines et al. 1997*). Spotted Owl habitat loss was greater on mid-upper slopes (especially south-facing) than within riparian areas or on benches (*Gaines et al. 1997*). Direct mortality of Spotted Owls was assumed to have occurred at one site. Data were too sparse for reliable comparisons of site occupancy or reproductive output between sites affected by the fires and other sites on the Wenatchee National Forest.

Two wildfires burned in the Yakama Indian Reservation, eastern Cascades, Washington, in 1994, affecting home ranges of two radio-tagged Spotted Owls (*King et al. 1997*). Although the amount of home ranges burned was not quantified, owls were observed using areas that received low and medium intensity burning. No direct mortality of Spotted Owls was observed even though thick smoke covered several owl site centers for a week.

2.7 SUMMARY OF HOME RANGES AND CORE AREAS

Home range size of Spotted Owls appeared to be influenced by a variety of factors, including proportion of mature and old growth forest within the home range, forest fragmentation, and dominant prey species. Despite variation in methods used, all studies outside the Eastern Cascades and Redwood zone showed that Spotted Owl core areas contained greater proportions of mature/old forest than random or non-use areas. In the Eastern Cascades, this trend was reversed; further research should examine putative causes of these regional differences and whether the differences in use of mature/old forest are related to regional differences in population trend (see Demography chapter).

Studies consistently showed that mature/old forest patch area was an important predictor of forest occupancy by Spotted Owls. While a fragmentation index was negatively associated with site occupancy in some studies, a trade-off between large patches of mature/old forest and juxtaposition of land cover types appeared to benefit Spotted Owls in other studies. We recommend that additional studies with long-term survival and reproductive data conduct analyses similar to those of Franklin et al. (2000) and *Olson et al.* (*2004*). Such studies may elucidate the geographical extent to which the trade-offs between interior patch area of mature/old forest and edge with other cover types occurs.

3 STAND CONDITION

3.1 JUVENILE DISPERSAL

Only one study after 1990 reported on habitat use by dispersing juvenile Northern Spotted Owls; it was conducted in the Oregon Coast Range, Klamath Province and Western Cascades (Miller et al. 1997). Old-growth and mature forest were combined in analyses and defined as forest dominated by trees > 53 cm dbh, generally 100% canopy closure, at least two height classes of trees, and decayed living trees, snags and downed woody material. Other cover types defined were closed sapling-pole-sawtimber stands (2.5 to 53 cm dbh and > 60% canopy closure), open sapling-pole stands (2.5 to 53 cm dbh and < 60% closure) and clearcuts. Used and available habitat were measured within 1.6 km radius circles surrounding owl locations. Dispersal was divided into two phases: transience and colonization. Transience was defined as “a period of extensive movement from one area to another” and colonization as “the period when an animal attempts to become established in a new area” (Miller et al. 1997:143). Available habitat was defined by the area with a 1.6 km radius of roosts because the mean straight-line dispersal distance of juvenile owls during the transience phase of dispersal was 1.6 km. Mature and old-growth forest was used slightly more than expected based on availability during the transience phase (n = 21 owls) and nearly twice its availability during the colonization phase (n = 18 owls). Closed pole-sapling-sawtimber habitat type was used roughly in proportion to availability in both phases; open sapling and clearcuts were used less than expected based on availability during colonization.

3.2 FORAGING AND ROOSTING

In all studies that used radio-telemetry to establish forest stand types used by Spotted Owls for foraging and roosting it was assumed that nighttime locations represented foraging behavior and daytime locations represented roosting behavior.

In the Western Cascades of Washington, Spotted Owls used mature/old forest (dominated by trees > 50 cm dbh with > 60% canopy closure) more often than expected for roosting during the non-breeding season (n = 175 roosts) and used young forest (trees 20-50 cm dbh with > 60% canopy closure) less often than expected based on availability (Herter et al. 2002).

In the Oregon Coast Range and Klamath Provinces, old-growth forest was the only forest type used for foraging and roosting in greater proportion than its availability at the landscape scale (Carey et al. 1992). At a finer scale, however, owls used portions of young forests for foraging in greater proportion than its availability, especially where woodrats were present (Carey and Peeler 1995). The latter analysis was based on frequency of use by owls within approximately 20 ha landscape units classified according to cover type and topography.

In the Western Cascades of Oregon, 23% of foraging locations (n = 38) obtained using radio telemetry were in late seral/old-growth stands (≥ 80 yrs old), even though these stands comprised only 10% random locations (n = 50; Irwin et al. 2000). Similarly, 13% of foraging locations and 38% of random locations were in stands <40 yrs old. Most of the study area was harvested 60 years previous to the study or regenerated after fires 100 yrs previously. Consequently, "nearly all stands sampled contained more than one large (> 80 cm dbh) tree/ha" and foraging stands had more large snags (> 50 cm dbh) than random stands (Irwin et al. 2000:179).

In Redwood National and State Parks, California, the use of old-growth stands for roosting (83% of roosts) was greater than expected based on availability (41% of random stands) and use of second-growth stands (6% of roosts) was less than expected based on availability (51% of random stands; n = 37 roosts, n = 37 random locations; *Tanner 1999*). Use of partially harvested stands (11% of roosts) was similar to random locations (8% of random stands; *Tanner 1999*).

3.3 NESTING

In mixed conifer forest of the Eastern Cascades, Washington, 27% of nest sites were in old-growth forests, 57% were in the understory reinitiation phase of stand development, and 17% were in the stem exclusion phase (Buchanan et al. 1995). Buchanan et al. (1995) did not evaluate the proportion of the greater landscape in the different stages of stand development. In a study of 20 nests in the Klamath Province, Oregon, all were found in old conifer forest (Ripple et al. 1997). In the Western Cascades, Oregon, 50% of Spotted Owl nests (n = 44) were in late seral/old-growth stands (≥ 80 yrs old) and none were found in stands < 40 yrs old although 10% and 38% of random locations (n = 50), respectively, were in these stand ages (Irwin et al. 2000; see section 3.2 for description of study area).

In commercial redwood forest of California, 54% of nests were found in stands 31-60 yrs old, 30% in stands 61-80 yrs old, 17% in stands > 80 yrs old (Folliard et al. 2000). Mean percent of these forest age classes in 60 sites centered randomly on forest not used for nesting were 31, 14, and 7%, respectively. Sixty-four percent of Spotted Owl pairs nested in stands with residual, older trees present.

3.4 SUMMARY OF STAND CONDITION

Spotted owls consistently used mature/old forest disproportionately for natal dispersal, foraging, roosting and nesting compared to other cover types available.

4 STAND STRUCTURE

4.1 FORAGING AND ROOSTING

Within Olympic National Park, Mills et al. (1993) compared nine characteristics of Spotted Owl roost or nest (n = 32) and non-response (n = 230) sites in old-growth forest. Variables measured were: community type, vertical canopy layering, cover of lowest canopy layer, number of trees > 80 cm dbh on a 0.1 ha plot, distance between trees, average snag dbh, distance between snags, percent cover of vascular plants, percent cover of logs. Stepwise logistic regression correctly classified 90% of stands on the western side of the park and 79% of stands on the eastern side. Only two of the variables measured were consistently important in regression models. Spotted owls tended to roost in stands with greater vertical canopy layering and greater snag diameter.

North et al. (1999) measured forest structural variables at Spotted Owl foraging locations obtained from radio-telemetry of 11 owls in the Olympic Peninsula and Western Cascades, Washington. Measurements were taken at four plots within each of 43 stands representing low (n = 13), medium (n = 12), and high use (n = 18) for foraging. Six stand attributes differed by and were positively related to owl use intensity: density of trees ≥ 80 cm dbh, snag basal area, snag volume, intact snag volume, foliage volume, and tree height class diversity.

Buchanan et al. (1999) used data from an intensive Spotted Owl study using radio-telemetry on the western Olympic Peninsula to choose 16 foraging and roosting locations that were not in old-growth habitat and 16 random locations from within MCP home ranges. They then separated roosting and foraging locations into those with single detections and those with multiple detections. They measured tree and snag density by diameter class, canopy cover, cover of downed wood, and shrubs within three 0.8-ha plots at each location. Locations with a single visit were similar to random locations whereas locations with multiple visits had greater snag density > 50 cm dbh and higher canopy closure. Buchanan et al. (1999) recommend that younger forests managed for Spotted Owls on the Western Olympic Peninsula should contain ≥ 10 snags/ ha that are > 50 cm dbh.

Vegetation structure was measured at Spotted Owl roosts (n = 146) located using radio-telemetry during the non-breeding season in the Western Cascades, Washington (Herter et al. 2002). Spotted owls roosted in areas lower in elevation, with larger tree dbh, fewer trees/ha, greater canopy cover, less shrub cover, and less down wood than found at random locations (n = 60).

Stepwise logistic regression selected the number of trees/ha, shrub cover, and volume of down wood for discriminating between roost and random stands.

King (*1993*) compared vegetation characteristics between 219 owl use sites (86% roosting locations combined with 14% foraging locations) and 209 random sites in the Eastern Cascades, Washington, on managed forest in the Yakama Indian Reservation. Nearly all stands in the study area had been selectively harvested prior to the study (uneven age management). Owls used sites with higher canopy closure, higher basal areas of medium-sized fir trees (27.5-52.4 cm dbh), higher slopes, taller mature-sized trees (52.5-89.9 cm dbh), and lower shrub height, grass cover, bare ground, and herb cover. Canopy cover was by far the most important discriminator between owl and random sites. *Pidgeon* (*1995*) conducted a study similar to that of *King* (*1993*) on the unmanaged portion of the Yakama Indian Reservation, comparing 163 owl use sites (88% roosting locations combined with 12% foraging locations) with 138 random loctations. Ground cover of litter, canopy cover, basal area of large conifers, and log volume were the best discriminators between used and random locations and were higher at random locations.

In Redwood National and State Parks, California, roost sites of Spotted Owls were at lower elevations, had more canopy layers, a higher density of old growth trees and more small woody debris (1-30 cm diameter) than random sites (n = 37 roosts, n = 37 random locations; *Tanner 1999*).

At the southern end of its range in Marin County, CA, roost sites of Northern Spotted Owls differed from random locations by having greater variation in tree diameters, greater number of potential nest trees, higher percent slope, and more large woody debris (*Chow 2001*). Potential nest trees were defined as trees with either a cavity > 48 cm along the tree axis, a broken top > 53 cm diameter with live branches over it, or an existing platform nest > 60 cm diameter.

Ting (*1998*) compared the ambient temperature at spotted owls roost locations with temperatures at random locations within the same stand and random locations within adjacent stands of younger forest on the Willow Creek Study Area (WCSA), Klamath Province, California. Temperatures at roosts were lower than at random sites in adjacent younger stands; temperatures at random locations within roost stands were intermediate between roost and younger stand locations. *Ting* (*1998*) also compared temperature profiles within mature/old growth and younger forest at both WCSA and Redwood National Park (RNP) in coastal California. Both age classes of forest stands were similar in RNP and were cooler than stands on the WCSA. Mature/old growth stands were cooler than younger stands at WCSA.

4.2 NESTING

Hershey et al. (1998) compared stand structure of nest sites (n = 105) and paired random sites in four Provinces (Olympic Peninsula, Washington, and Coast Range, Klamath and Western Cascades, Oregon). Random sites were restricted to stands dominated by trees > 50 cm dbh. Evidence of fire was present at 86% of nest sites and 76% of random sites. The total density and basal area of live trees were higher at nest than random sites, mostly due to greater densities and basal area of trees < 23 cm dbh. Variation in tree diameters between nest and random sites was similar. Density and basal area of broken-top trees and volume of down logs in decay classes 4 & 5 (most decadent) were higher at nest than random sites.

On the eastern slope of the Cascades, Washington, on the Wenatchee National Forest, Buchanan et al. (1995) compared habitat characteristics at 62 nest sites with those at 62 paired random sites within the same forest stands. Nests were in mixed conifer forests within grand fir, Douglas fir and western hemlock forest associations. Nest sites had lower canopies of dominant/codominant and intermediate trees, more Douglas fir trees 35-60 cm dbh, more ponderosa pine trees 61-84 cm dbh, greater live tree basal area, greater basal area of decadent snags, and less basal area of more intact snags. Volume of coarse woody debris and percent canopy closure were similar between nest sites and random sites within nest stands. Evidence of past fire was visible at 92% of nest sites. These data were reanalyzed by Buchanan and Irwin (1998) by stratifying nests within five Fire Management Analysis Zones (FMAZ). FMAZ were designated by the Wenatchee National Forest based on vegetation associations, topography, precipitation, frequency of lightning strikes, and estimates of fuel loading and fire frequency. In addition to differences in tree species among zones, trees were smaller and younger and had higher canopy closure in more xeric zones.

Buchanan (*1996*) also characterized vegetation around spotted owl nests in the Klickitat region of the eastern slope of the Cascades, Washington. In contrast to the study on the Wenatchee National Forest to the north (Buchanan et al. 1995; previous paragraph), terrain in the Klickitat region was less steep and > 50% of the 31 nest sites examined had experienced partial logging, primarily by pre-commercial thinning (*Buchanan 1996*). Nest trees in the Klickitat region were larger and older than trees in the Wenatchee National Forest, but occurred in stands dominated by younger trees (*Buchanan 1996*). Evidence of past fire was visible at 71% of nest sites. *Buchanan* (*1996*) found few structural differences between nest sites and paired random sites within the same stands (e.g., total basal area and height of live trees, total canopy closure, snag density, volume of downed wood) except that the number of canopy layers was greater at nest plots (median = 2.0) than random plots (median = 1.8; $z = 2.20$, $P = 0.028$). Total basal area of live trees and number of canopy layers were greater at sites on federal than non-federal (state and private) lands.

In the Oregon Coast Range, density of snags < 53 cm dbh, number of horizontal vegetation layers and density of broad-leaved trees were higher at Spotted Owl nest (n = 51) than random (n = 50) sites whereas density of live conifers 53–86 cm dbh and density of snags 53–86 cm dbh were lower at nest than random sites (*Thrailkill et al. 1998*). Random sites were located in stand types used by Spotted Owls for nesting within the study area (*Thrailkill et al. 1998*).

Irwin et al. (2000) compared vegetation structure among nesting (n = 44), foraging (n = 38) and random (n = 50) stands within home ranges of 12 pairs of Spotted Owls in the Western Cascades, Oregon. Random sites were restricted to habitat types used by owls. Stands sampled for foraging were all from owl pairs that nested at least once and received disproportionate use (4% of telemetry locations in 1% of adaptive kernel home range; all were within 60% adaptive kernel core area). Zero nests, 13% of foraging and 38% of random locations were in stands < 40 yrs old. Foraging and nesting stands had significantly greater number of large (> 50 cm dbh) snags than random stands. Volume of large and small woody debris was greater at foraging than nesting and random stands. Herbaceous and shrubby understory vegetation < 0.5 m tall was less at foraging than nesting and random locations for most stand age classes. All stands used by owls had canopy cover > 80% (estimated using a spherical densiometer).

Pious (*1994*) measured vegetation and physiographic characteristics in 52 nest and 22 roost stands in commercial forest of the California Coast Range (both Redwood and Douglas fir zones). Although no statistical comparisons were made and random sites were not measured, total canopy closure in nest and roost stands was similar (nest mean = 83%, SE = 1.7, median = 86; roost mean = 85%, SE = 1.0, median = 86). Mean conifer tree age was 73 years (SE = 12.0, median = 63, n = 41) in nest stands and 63 years (SE = 5.1, median = 69, n = 14) in roost stands.

LaHaye and Gutiérrez (1999) measured stand structure at 44 Spotted Owl nests and 44 paired random sites within the same stands in the Coast Range and Klamath Provinces of California. Among 17 variables compared, basal area of trees > 90 cm dbh, basal area of hardwoods 41-60 cm dbh, and basal area of Douglas-fir snags were different between nests and random points, and were greater at the nest site for all three variables.

On the Klamath National Forest, in the California Klamath and Cascade provinces, stand structure was measured at 29 Spotted Owl nests and 27 paired random sites within the same stands (*White 1996*). No differences were found in any variable measured (e.g., tree and snag basal area by diameter class, log volume, shrub cover, canopy cover, ground cover) except diameter of the tree at the plot centers.

On commercial timberlands in the California Klamath and Cascade provinces, stand structure was measured at 12 Spotted Owl nests, two nests immediately adjacent to the timberland, and two Spotted Owl roost sites (*Farber and Crans 2000*). Mean canopy closure within one ha plots was 67% (range 48–80) using a sighting tube. In other stands, mean canopy closure was 16 to 23% lower using a sighting tube than using densiometers (*Farber and Crans 2000*). Quadratic mean diameter of trees > 12 cm dbh within one ha surrounding nest trees averaged 31 cm (SE = 2). The number of large snags (> 28 cm dbh)/ha and pieces of large woody debris (> 28 cm diameter)/ha were highly variable among plots (mean = 32 snags, SE = 8; mean pieces of large woody debris = 181, SE = 18). These data were compared to data from 18 non-randomly selected commercially thinned stands. Mean canopy closure in thinned stands was 46% using a sighting tube. Quadratic mean diameter of trees > 12 cm dbh in thinned stands was 33 cm (SE = 1, range 23–42).

4.3 SUMMARY OF STAND STRUCTURE

Forest stand structural attributes positively associated with foraging, roosting and nesting included vertical canopy layering, tree height or diameter diversity, canopy volume, canopy closure, snag diameter, snag basal area or volume, tree diameter and log volume. These attributes correspond to those identified by Thomas et al. (1990) as important components of Northern Spotted Owl habitat. Notably, positive relationships were found with the aforementioned attributes whether the samples of owl and random locations were within old growth forest, non-old growth forest, National Parks, public land, private land, or an Indian Reservation. Even in the Eastern Cascades and Redwood zone, where owl core areas contained lower or equivalent proportion of old forest compared to random locations, large trees (often residuals older than the surrounding stand) were important components of Spotted Owl nest locations (Buchanan et al. 1995, *Irwin et al. in press*, *Lowell Diller, pers. comm*.).

5 NEST TREES

On the Olympic peninsula, tree species used for nesting included western hemlock, Douglas fir, western red cedar, Pacific silver fir, and grand fir (Forsman and Giese 1997). Seventy-eight percent of 116 nests were in live trees and 22% in snags. Fifty-three percent of nests were in side cavities (the most common nest type in the western side of the study area, at 71%), 37% were in top cavities (the most common nest type in the eastern side, at 51%) and 10% were in external platforms. The majority of top cavity nests in live trees were in trees with secondary tops growing above the cavity. On average, external platform nests were in smaller trees (mean dbh = 89 cm, SE = 15.7) than cavity nests (mean dbh = 142 cm, SE = 6.2). External platforms were in old stick nests built by common ravens or goshawks (n = 5), debris platforms on deformed limbs caused by dwarf mistletoe infections (n = 3) and debris accumulations at locations where trees had split into multiple tops (n = 3). The mean dbh of all nest trees was 137 cm (SE = 5.9, range = 30-379 cm), while the mean dbh of nest trees in the west was 158 cm (SE = 6.0), and in the east was 107 cm (SE = 6.3). Location of nests was similar to random locations in slope aspect and position on slope, but more nests than expected were on steeper slopes. Seventy-one percent of nests were in forests dominated by trees ≥ 100 cm dbh with multi-layered canopies; 19% were in forests dominated by trees 50-99 cm dbh with multi-layered canopies; 8% were in forests with a mosaic of small (13-49 cm dbh) and large (≥ 50 cm dbh) trees; 2% were in relatively even-aged forests of trees with dbh 50-99 cm.

Hershey et al. (1998) measured characteristics of 105 nest trees in four Provinces (Olympic Peninsula, Washington and Coast Range, Klamath and Western Cascades, Oregon). Eighty-eight percent of nest trees in Oregon were Douglas fir. In the Olympic Peninsula, nest trees were well distributed among Douglas fir, western hemlock and western red cedar. In the four provinces, 73-97% of nests were in live trees. Side cavities comprised 3-15% of nests in the Coast Range, Klamath, and Western Cascades and 67% of nests on the Olympic Peninsula. Top cavities made up 55-87% of nests in the Coast Range, Klamath and Western Cascades and 27% in the Olympic Peninsula. External platforms accounted for 41% of nests in the Klamath Province and 7% in the remaining three provinces. In the Klamath Province, more nests than random sites were on the lower third of slopes; in the other provinces, most nest and random sites were on the middle third of slopes. Mean dbh of all nest trees was 139 cm (SE = 5.2); dbh of trees with cavity nests (mean = 144 cm; SE = 5.6 cm) was greater than trees with platform nests (mean = 120 cm; SE = 15.4).

In the northern portion of the eastern Cascades, Washington, 92% of 85 nest trees were in Douglas fir (Buchanan et al. 1993). Use of Douglas fir trees was higher than expected based on tree species composition of nest stands. Eighty-eight percent of nest trees were live and 12% were snags. Eleven percent of nests were in side cavities, 6% in top cavities, 80% in external platforms, and 4% on live branches adjacent to the trunk. Among platform nests, 31% were on mistletoe brooms, 51% were in stick nests on top of mistletoe brooms, and 12% were stick nests. Stick nests were apparently made by goshawks. Median age of nest trees was 137 yr (range 66-

700). Nest tree age was greater than the age of randomly selected trees. Nest trees on south-facing slopes were older (median age 165 yr) and larger in diameter (dbh mean = 76, SE = 5) than those on north-facing slopes (median age 127, dbh mean = 58, SE = 3). Trees with external platform nests were smaller than those with top or side cavity nests. The disproportionate use of Douglas firs for nesting was attributed to the prevalence of mistletoe infections in this species (Buchanan et al. 1993). For this same data set, nest trees in xeric zones tended to be on north-facing slopes whereas nest trees were more evenly distributed among slope aspects in other zones (Buchanan and Irwin 1998).

In the southern portion of the eastern Cascades, Washington, 81% of 31 nest trees were in Douglas fir, 13% in ponderosa pine, 3% in Grand fir and 3% in black cottonwood (*Buchanan 1996*). Use of Douglas fir trees was higher than expected based on tree species composition of nest stands. Twenty-three percent of nests were in cavities, 65% in external platforms, and 13% on live branches. Among platform nests, 35% were on mistletoe brooms, 40% were in goshawk nests and 25% were on broken tops of trees. Median age of nest trees was 250 yr (range 66-980). Nest tree age was greater than the age of randomly selected trees (*Buchanan 1996*).

In the Eugene BLM District, Oregon Coast Range, 89% of 53 nest trees were in Douglas fir, 6% in western red cedar, 4% in bigleaf maple and 2% in western hemlock (*Thrailkill et al. 1998*). Eighty percent of nests were in living trees with broken tops, usually with secondary live tops. Mean nest tree dbh was 146 cm (range 93-213; *Thrailkill et al. 1998*).

In commercial forestland in the Western Cascades, Oregon, 65% of nest trees (n = 44) were >120 years old and 73% were > 80 cm dbh; these trees were legacies from previous stands subjected to either timber harvest or fire (see above; Irwin et al. 2000). Seventeen nests were in cavities, 22 in external platforms, and five were unknown. Nest trees in young/mid-seral (< 80 yrs old) stands were often much older than majority of trees in the stand (Irwin et al. 2000).

Two studies described nest trees on commercial forest in the California Coast Range. In forest owned by Louisiana-Pacific Corporation, nests (n = 97) occurred in redwood (73%), Douglas fir (14%), tanoak (8%), grand fir (3%), western hemlock (1%) and golden chinquapin (1%; *Pious 1994*). Sixteen percent of nests were in side cavities, 14% in top cavities and 65% were in stick platforms. Mean nest tree dbh = 106 cm (SE = 69, range 26-378; *Pious 1994*). On Simpson Timber Company Land, 53% of 60 Spotted Owl nests were in tree deformities (broken tops, platforms, or cavities) and 47% of nests were external platforms (mostly squirrel or vole nests; Folliard et al. 2000). Seventy-three percent of nest trees were residual trees (older than the surrounding stand).

Three studies described nest trees in National and State Parks and other reserved land of the California Coastal province. Eleven nests were found in Humboldt and Del Norte Counties; 10 nests were in redwood trees and one was in a Douglas fir; three were in cavities and eight were in external platforms (*Tanner 1999*). Mean dbh of nest trees was 257 cm. In Marin County, among 28 Spotted Owl nests in redwood, Bishop pine, hardwood, Douglas fir, and mixed forest types, 89% were in conifers (Douglas fir, redwood and Bishop pine) and 11% in hardwoods (California bay and tanoak; *Chow 2001*). Only one nest (4% of total) was in a side cavity, 25% of nests were in top cavities, and 71% were in external platforms. Mean conifer nest tree dbh was 113 cm while mean hardwood nest tree dbh was 48 cm. In another study in Marin County, 42% of 120 nests were in redwoods, 38% in Douglas fir, 8% in bishop pine, 7% in California bay, 3% in tanoak, and 2% in coast live oak (*Fehring et al. 2003*). Among the 120 nest trees, those containing platform nests (88%) were smaller in diameter (mean = 92 cm; SE = 42) than those containing cavity nests (12%; mean = 126 cm; SE = 54; P = 0.001; *Fehring et al. 2003*).

Of 69 nests in the California Coast Range and Klamath Provinces measured by LaHaye and Gutiérrez (1999), 83% were in Douglas fir, 9% in redwood, and < 2% each in Bishop pine, tan oak, canyon live oak, black oak, chinquapin, and white fir. Twenty percent of nests were in side cavities, 60% in top cavities, and 20% in platforms. Nest tree dbh was similar among trees containing different nest types (side cavity mean was 157 cm, SE = 3 while top cavity mean was 138 cm, SE = 1, and platform mean was 119 cm, SE = 3).

On the Klamath National Forest, in the California Klamath and Cascade provinces, 41% of 29 nests were in cavities and 59% on platforms, with cavity nests occurring predominantly in Douglas fir forest and platform nests found mainly in mixed conifer forest (*White 1996*). Differences in nest type used were attributed to past timber harvest; however, timber harvest was confounded with forest type (mixed conifer forests had been more heavily harvested in this study area). Eighty-six percent of the 29 nests were in Douglas fir trees (*White 1996*).

In the California Cascade and Klamath provinces, 14 of Spotted Owl nests on private and timber company lands were external platforms; 12 were in mistletoe brooms and two were in raptor nests (*Farber and Crans 2000*). The nest tree data were combined with data from two roost trees in the following results. Mean tree diameter was 59 cm (SE = 3, range 17–34); mean tree age was 110 yr (SE = 7, range 59–184). These nest and roost trees were larger than the quadratic mean diameter of other trees (> 12 cm) in the surrounding one ha (mean = 31 cm, SE = 2).

Nest types and primary nest tree species used by Northern Spotted Owl are summarized in Table 5.3. Platform nests were more prevalent in the Eastern Cascades and California Coast Range than in other provinces, and were found in commercial forests more often than public lands of the Western Cascades, Oregon. Trees containing platform nests were generally smaller than trees containing cavity nests. Differences in nest types was not attributable solely to tree species; Douglas fir was a common nest tree species throughout the range of the Northern Spotted Owl, providing top cavities in mesic regions and mistletoe platform nests in more xeric regions.

Marshall et al. (2003) noted that approximately 90% of known Spotted Owl nests on the Applegate Ranger District of the Rogue River National Forest (Klamath province, Oregon) were in dwarf mistletoe brooms in Douglas fir trees. They compared the number of mistletoe brooms within plots surrounding 35 randomly selected nests and “nonnest” plots within 11 of the 35 nest stands. Based on a classification system that incorporated the number and type of mistletoe brooms, nest plots had more mistletoe infection and more intense infection than nonnest plots. Furthermore, 51% of Spotted Owl nests were located in mistletoe brooms that originated from the tree bole even though 8% of brooms originated from the bole. In contrast, only 20% of nests were in brooms that originated on branches even though 75% of brooms originated from branches.

6 SUMMARY

Information about Northern Spotted Owl habitat associations on private land was sparse at the time of the 1990 status review. Since then, many studies on private land have been completed and made available for public review. These studies help to broaden the scope of our knowledge throughout the subspecies' range. We also commend researchers for taking advantage of long-term Spotted Owl demographic data sets to investigate habitat associations. We encourage further exploitation of these data to measure demographic responses to habitat configuration.

Much of the information reviewed in this chapter confirmed the definition of suitable owl habitat of Thomas et al. (1990; see chapter Introduction). In the redwood zone of coastal California, Spotted Owls used younger stands for nesting than elsewhere in the range of the Northern Spotted Owl, although in the majority of young redwood stands used for nesting, residual (older) trees were present. Furthermore, as was noted in Thomas et al. (1990), structural attributes of young redwood stands are similar to attributes that accrue only in very old forests in most of the owl's range.

MCP home range estimates reported from 1990 to present were similar to those found previous to 1990. New studies (post-1990) showed that home range size was influenced by the degree of forest fragmentation and proportion of home range in mature and old forest, with increased home range size found in more fragmented landscapes and in home ranges containing a smaller proportion of mature and old forest. Primary prey species consumed by Spotted Owls was also related to home range size, with larger home ranges occurring where flying squirrels dominated the diet and smaller home ranges where woodrats dominated the diet.

In most cases, the amount of mature and old-growth forest in home ranges and core areas was greater around owl site centers than around random landscape locations, with exceptions found in the Eastern Cascades, Washington, and commercial redwood forest, California. In the Klamath province, hardwood forests were found in greater amounts at owl than random locations. When evaluated at several scales using the same data sets, differences between owl locations and random landscape locations generally diminished as distance from the owl site center (usually a roost or nest location) increased.

In the Eastern Cascades of Washington, Spotted Owls locations (200 ha) had less old-growth forest and more forest 20-64 cm dbh than random locations. Spotted owls in this study area had the lowest estimated apparent survival probability and one of the highest reproductive rates among 14 study areas throughout the range of the Northern Spotted Owl (Anthony et al. 2004; see Demography chapter, WEN study area). Further research may be warranted on whether results of fire suppression and consequent development of shade tolerant understories of pole-sized trees negatively affect spotted owl populations in this province.

Dispersing juvenile owls used mature and old-growth stands more than expected based on availability, especially during the colonization phase. Mature and old-growth stands were consistently used by territorial Spotted Owls for foraging and roosting more often than expected based on availability. At foraging and roosting sites, one or more of the following attributes tended to be greater than at random locations: canopy diversity, canopy closure, snag diameter, snag volume, dbh of large trees, amount of large woody debris.

Stand ages used for nesting by Spotted Owls varied by province and study area, with 17-100% of nests occurring in old forest among studies. At nesting sites, one or more of the following tended to be greater than at random locations: tree basal area, density of broken-top trees, number or basal area of decadent snags, volume of decadent logs.

Across provinces, the majority of Spotted Owl nests were in live trees. Cavity nests predominated in the Olympic Peninsula, Oregon Coast Range, public forest in the western Oregon Cascades. External platform nests were more prevalent in the Klamath province and commercial forests of the western Oregon Cascades and comprised the majority of nests in the eastern Cascades of Washington and both commercial and public forest in the California Coast Range. Trees containing platform nests tended to be smaller in diameter than those containing cavity nests.

Little was known about the effects of forest fragmentation on Northern Spotted Owls in 1990. Subsequent research has shown that whereas owl locations used for nesting and roosting tend to be centered in larger patches of old forest than in the available landscape, forest fragmentation is not necessarily equivalent to habitat fragmentation, at least in some portions of the Northern Spotted Owl's range (Franklin et al. 2002). Ecotones within owl home ranges may benefit Spotted Owls by providing increased prey abundance and/or availability but still need to be balanced with the presence of interior older forest (*A. Franklin, pers. comm.*).

A meta-analysis showed that owl site occupancy was positively associated with mean patch area of old forest and negatively associated with forest fragmentation, whereas studies in the redwood zone suggested diversity of cover types was higher at owl nest sites than locations not used for nesting. The degree of forest fragmentation did not appear to influence use of stands by dispersing juvenile owls.

Effects of forest fragmentation and heterogeneity on Spotted Owl survival and reproduction varied among studies. When considering both survival and reproduction, owls appeared to benefit from a mixture of mature/old forest and other cover types in the California Klamath province and from a mixture of older forests with younger forest and non-forested areas in the Oregon Coast Range. It is also noteworthy that landscape composition of stand ages was not a good predictor of reproductive output in two studies in the Oregon Cascades.

Studies on forest fragmentation and heterogeneity have provided insight into the most profound change in our understanding of habitat associations of the Northern Spotted Owl. Home ranges composed entirely of pristine old forest may not be optimal for spotted owls in the Klamath province and Oregon Coast Range, although large patches of older forest within the home range do appear to be necessary to maintain a stable population. We caution that these findings should not be extended to other areas of the subspecies' range.

7 TABLES

Table 5.1. Mean annual home range and core area sizes of Northern Spotted Owls. Data presented were estimated using 100% Minimum Convex Polygon method (MCP; all studies), and various alternate methods (some studies).

			MCP Home Range (ha)		Alternate Method					
						Home Range (ha)		Core Area (ha)		
Province and forest type	n		Mean	SE	Method	Mean	SE	Mean	SE	Source
WA Eastern Cascades	5	owls	3669	876	--	--	--	--	--	King 1993
OR Coast Range										
Mixed conifer, fragmented	5	pairs	1675	352	MMCP[a]	1154	235	--	--	Carey et al. 1992
Douglas fir	5	pairs	1569	463	MMCP[a]	1018	160	--	--	Carey et al. 1992
Douglas fir, fragmented	4	pairs	2908	595	MMCP[a]	1721	413	--	--	Carey et al. 1992
OR Coast Range										
Elliott State Forest	15	owls	1108	137	95% Fixed Kernel	842	115	87[b]	6	Glenn et al. 2004
Northern Coast Range	9	owls	2214	357	95% Fixed Kernel	1344	247	100[b]	5	Glenn et al. 2004
OR Klamath										
Mixed conifer	3	pairs	533	58	MMCP[a]	472	43	--	--	Carey et al. 1992
Mixed conifer, fragmented	6	pairs	1796	261	MMCP[a]	1208	272	--	--	Carey et al. 1992
OR Western Cascades	6	pairs	3066	1080	Adaptive Kernel	--	--	417[c]	129	*Miller et al. 1992* Irwin et al. 2000
CA Coastal redwood/Douglas fir	9	owls	786	145	95% Adaptive Kernel	685	112	98[d]	22	Pious 1995

[a] Modified Minimum Convex Polygon.
[b] Core area defined by greater than average observation location density for a given owl.
[c] Core area arbitrarily defined as 60% adaptive kernel contour.
[d] Core area arbitrarily defined as 50% adaptive kernel contour.

Table 5.2. Percentage of mature and old-growth forest (mean and SE) within circles around Northern Spotted Owl activity centers and random points or complete landscape areas.

	circle size	Owl location			Random location			Criteria for random location	Source
Province & forest type	(ha)	n	%	SE	n	%	SE		
WA Olympic Peninsula	3253	59	53	--	100	34	--	Within Olympic National Forest	Lehmkuhl and Raphael 1993
WA Cascades	314	74			1			Total 3000 km^2 study area	Hicks et al. 2003
Western Hemlock			42	11		12			
Silver Fir			44	17		20			
Interior W. Hemlock			42	14		49			
Grand fir			53	17		18			
Interior Douglas fir			44	21		18			
WA Eastern Cascades[a]	200		48			36		Within 23,832 km^2 study area	Irwin et al. in press
FMAZ 1		30	10	5	21	30	8		
FMAZ 2		56	13	4	16	22	7		
FMAZ 3		57	8	3	42	20	4		
FMAZ 4		62	6	3	18	19	5		
FMAZ 5		22	5	5	28	16	5		
OR Coast Range	200	19	36	--	19	14	--	BLM lands surveyed for owls	Meyer et al. 1998
OR Coast Range	112	41	32	3	41	11	2	No nest found on surveyed area; at least 1260 m from nest sites	*Perkins 2000*
OR Klamath	200	21	30	--	21	6	--	BLM lands surveyed for owls	Meyer et al. 1998
OR Klamath	118	20	45	26	20	14	20	Contained ≥ 40% forest cover	Ripple et al. 1997
OR Western Cascades	200	10	27	--	10	12	--	BLM lands surveyed for owls	Meyer et al. 1998
OR Western Cascades	260	30	78	12	30	63	20	Within Willamette National Forest	Ripple et al. 1991
OR Western Cascades	500	103	60	2	70	53	2	Centered on National Forest Land	Johnson 1992
CA Klamath	200	33	47	--	50	36	--	Within 292 km^2 area, < 1351 m elev	Hunter et al. 1995

Footnotes:
a FMAZ = Fire Management Analysis Zone.

Table 5.3. Percent of Northern Spotted Owl nest types.

Province	Primary nest tree species	n	Nest type – Percent of Total Side cavity	Top Cavity	All Cavity	Platform	Source
WA Olympic Peninsula	western hemlock, Douglas fir, western red cedar	116	53	37	90	10	Forsman and Giese 1997
WA Olympic Peninsula	western hemlock, Douglas fir, western red cedar	15	67	27	93	7	Hershey et al. 1998
WA E. Cascades (north)	Douglas fir	85	11	6	17	84	Buchanan et al. 1993
WA E. Cascades (south)	Douglas fir	31	--	--	23	77	Buchanan 1996
OR Coast Range	Douglas fir	30	7	87	93	7	Hershey et al. 1998
OR Coast Range	Douglas fir	53	37	61	98	2	Thrailkill et al. 1998 [a]
OR Coast Range							
North Coast	w. hemlock, Douglas fir	12	92	8	100	0	Anthony et al. 2000
Elliott State Forest	Douglas fir, w. red cedar	22	36	9	45	55	Anthony et al. 2000
OR Klamath	Douglas fir	29	3	55	58	41	Hershey et al. 1998
OR Western Cascades	Douglas fir	27	15	78	93	7	Hershey et al. 1998
OR Western Cascades	Douglas fir	39	--	--	44	56	Irwin et al. 2000
CA Coastal	redwood, Douglas fir	97	16	14	30	65	Pious 1994
CA Coastal	redwood, Douglas fir	60	--	--	53	47	Folliard et al. 2000
CA Coastal	redwood	11	--	--	27	73	*Tanner 1999*
CA Coastal	Douglas fir, redwood, bishop pine	28	4	25	29	71	*Chow 2001*
CA Coastal	redwood, Douglas fir, bishop pine	120	--	--	12	88	Fehring et al. 2003
CA Coastal & Klamath	Douglas fir, redwood	69	20	60	80	20	LaHaye and Gutiérrez 1999
CA Klamath & Cascades	Douglas fir	29	--	--	41	59	White 1996
CA Klamath & Cascades	Douglas fir, sugar pine	14	--	--	0	100	Farber and Crans 2000

Footnotes:
a Some of the nests in this sample may have been included in Hershey et al. (1998).

SCIENTIFIC EVALUATION OF THE STATUS OF THE NORTHERN SPOTTED OWL

CHAPTER SIX

Habitat Trends

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SUMMARY

We evaluated current estimates of Northern Spotted Owl habitat trends on Federal lands. We evaluated two sources of suitable habitat (nesting, roosting, and foraging) loss; loss due to timber harvest and loss due to natural disturbance. We also commented on the validity of the conclusions that could be drawn from the available information, and then made an assessment of these habitat changes as potential threats to Northern Spotted Owl conservation. We included an evaluation of the current methods used to determine habitat trends with the intention of fostering improvement of future analysis of habitat changes. We were unable to evaluate habitat trends for non-Federal lands because of the lack of data or access to the data and the ability to verify and conduct quality control on the data.

THREAT ASSESSMENT

The threat of Northern Spotted Owl habitat loss from timber harvest on Federally-managed public lands (hereafter "Federal lands") has clearly been substantially reduced since 1990. Logging of Northern Spotted Owl habitat on Federal lands has been lower than originally anticipated by the Fish and Wildlife Service (USFWS) in 1990, at the time of listing of the owl, and by the Northwest Forest Plan in 1994. While there are risks that some existing suitable habitat could be lost or degraded by natural disturbance anywhere within the range of the Northern Spotted Owl, these risks appear consistent with historical patterns. However, threats from catastrophic habitat loss have increased on the east side of the Cascade Range and some locations within the Klamath region. The trend of forest development in these areas will continue to increase the risk of habitat loss. Because more years of fire suppression have occurred during the time the owl has been listed there has been a concomitant increase in the accumulation of fuels in these forests, which makes these forests more susceptible to stand replacement fires, pests and pathogens. This significant threat will remain for some time. In some areas, managing the threat of habitat loss by wildfire should be a habitat management priority. In addition, it has been hypothesized that succession toward shade-tolerant understory trees on the east slope of the Cascade Range may reduce owl occupancy (presumably because of reduced prey abundance and/or access *(Irwin and Thomas 2002).* If true, this would represent another growing threat resulting from lack of tree density control, which is a consequence of fire suppression.

On non-Federal lands there is evidence that some degree of habitat loss exists, however, it is incompletely documented and will remain a source of conjecture without more complete information. Lack of coordinated conservation measures to assure the continued existence of habitat on non-Federal lands was cited as a risk at the time of listing, and this risk continues. However, the emergence or existence of State Forest Practice Rules and Habitat Conservation Plans have reduced this risk because management of State and private lands are better coordinated with Federal habitat management than at the time of listing.

HABITAT TRENDS ESTIMATES

FEDERAL LANDS

The Northern Spotted Owl habitat trend analysis conducted by the USFWS (USDI 2004) indicated an overall decline of approximately 2.11% in the amount of suitable habitat due to range-wide management activities from 1994 to 2003. The majority of management-related habitat loss was in Oregon. Habitat loss due to natural events totaled 224,041 acres, which equated to a 3.03% decline in available habitat range-wide over this period. Overall, habitat loss range-wide due to all factors has resulted in a total decline of 5.14% between 1994 and 2003 (0.57% per year). Annual rates of habitat loss due to management activities were less than 25% of rates projected at the time of listing. Between 1994 and 2004, it was estimated that there would be an 8% increase in available habitat range-wide, resulting from succession of younger forests into suitable habitat.

NON-FEDERAL LANDS

As noted above, data are insufficient to determine the rate of change on non-Federal lands since 1990. However, there have been two major changes on non-Federal lands concerning suitable habitat protection since the owl was listed; increased state regulation and the emergence of Habitat Conservation Plans (HCPs). In general, HCPs represent a significant positive development in terms of reduced habitat risk over State Forest Practices Rules alone. In concert with the Northwest Forest Plan (NWFP), HCPs offer the opportunity to develop landscape scale approaches to Northern Spotted Owl habitat conservation rather than focusing on individual owl sites. However, poor documentation of initial baselines for most HCPs precludes estimates of habitat trends. We believe the development of HCPs is a positive step in owl conservation because they offer opportunities to increase cooperation between private landowners and government agencies and to seek creative ways to manage habitat in working forests.

EVALUATION OF DATA ON HABITAT TRENDS

It is our conclusion that the habitat losses calculated by the USFWS (USDI 2004) are conservative but reasonable approximations of habitat change. Unfortunately, limited data is available to assess habitat loss on a range-wide basis for Northern Spotted Owls. We recognize that the data and approach used by the USFWS is the best available. However we provide the following evaluation to encourage improvement in future habitat assessment efforts.

In general, the methodologies used by the USFWS to assess trends in suitable habitat are limited by data quality. The reliability of the data from a specific source is difficult to interpret because statistical bias is poorly controlled (i.e. dependence on data from external sources with the ability to conduct quality control, duplicated accounting for the same affect, and subjective corrections to data), and, to a lesser extent, the inclusion of debatable assumptions (such as the inclusion of exchange lands and recently developed habitat). Despite these shortcomings, there are currently no other viable alternatives to estimate habitat change on Federal lands. Given the sources of bias, we believe these data overestimate habitat losses, but we cannot determine the magnitude of the bias. The risk associated with these estimates being wrong is low, given all indications that the habitat loss has been low.

Habitat removal due to management activities is probably estimated with the greatest accuracy because individual projects that affect Northern Spotted Owl habitat are subject to intensive habitat surveys. Estimates of habitat changes ensuing from natural disturbance events are probably less accurate, due to reduced intensity of surveys and analytical review.

We remain poorly informed concerning habitat trends on non-Federal lands. The USFWS examined information submitted by private entities as well as information contained in Habitat Conservation Plans and associated reports to determine if the information was not sufficient to calculate a rate of change on non-Federal lands. The USFWS determined there was insufficient documentation of the habitat baseline and lack of information about habitat change to allow the estimation of habitat trends on non-Federal lands. The panel recognizes that this information is usually maintained by private landowners and may be proprietary. Future habitat trends analysis of all forested lands within the range of Northern Spotted Owl using remote sensing could provide valuable insight to the continued role of non-Federal lands in supporting conservation of owl habitat.

SOURCES OF UNCERTAINTY FOR HABITAT TRENDS

HABITAT BASELINE ON FEDERAL LANDS

Any assessment of habitat change requires a reference condition for the habitat of interest to provide a basis for comparison at various intervals over time. A regional compilation of baseline habitat to measure change was not available until 1994, with the completion of the Northwest Forest Plan. We recognize that the decade-old Forest Plan habitat assessment, as an accurate portrayal of Northern Spotted Owl habitat, has many shortcomings. The strength of the Forest Plan suitable habitat baseline lies in its consistency across the entire range of the Northern Spotted Owl. The Forest Plan baseline was considered suitable for broad-scale analyses such as comparison of management alternatives. The USFWS was placed in a situation where it had to choose between using an outdated baseline with known weakness or waiting for a new baseline to be completed. We agree with the USFWS's decision that the Forest Plan baseline provides the best available common denominator for calculations of range-wide rates of habitat change.

LAND ACQUISITIONS ON FEDERAL LANDS

Lands containing suitable habitat were acquired by Federal agencies but not counted in the habitat trends data. The lack of inclusion of acquired land by the existing habitat trends estimates has resulted in an overestimation of habitat loss on lands managed under the Northwest Forest Plan for owl conservation, but correctly depicts a non-net change on a landscape basis. About 19,500 acres of habitat were acquired by Federal agencies from 1994 through 2003 through land acquisitions. These lands were not added to the habitat baseline or suitable habitat estimates conducted by the USFWS (USDI 2004). The development of habitat baselines that track changes regardless of ownership to account for this source of variation when estimating amount of suitable habitat will be very important for the determination of habitat trends in the future.

COLLECTION OF AND ADJUSTMENTS TO CONSULTATION DATA

In general, the basic data derived from the Federal consultation process (Biological Assessments, Section 7 Consultations etc.) generally overestimated impacts to Northern Spotted Owl habitat. Individual consulting agencies used and managed consultation data differently, with different application of terms, different scales at which data were collected, and different data management practices. There was possibly a double counting of effects within a data set.

Recognizing these confounding effects in the data, adjustments to these data made by the USFWS from the consultation process were made to help control known sources of bias in the primary data that were used to determine habitat impacts. The USFWS, who conducted the trends analysis, believes the actual effects described in the consultations are usually less than those originally estimated, because harvest area size is usually reduced from that initially proposed for consultation, and there are delays in project implementation. These effect add another source of potential unknown bias to the estimates of management-based losses. We were unable to fully quantify the extent of overestimated effects.

Interpretations from the available habitat trends data base are also limited because the information is not spatially referenced. Calculations of habitat fragmentation were not possible from the available habitat trends data. Implications of habitat loss of individual Northern Spotted Owl demographic areas can not be determined with these data.

NATURAL HABITAT DISTURBANCE

The 1990 listing document anticipated habitat trends by management only, thus anticipated habitat losses due to natural disturbance events were not calculated. Because there was no baseline or basis for comparison of losses from natural disturbance, we were unable to make comparisons. Estimates of natural disturbance effects on suitable habitat are difficult to assess accurately. The difficulty of tracking widely dispersed natural disturbance effects and interpreting the impact will likely remain the primary source of this uncertainty. Interpretations of natural disturbance effects are likely to differ between agencies and staff in different provinces. It would seem reasonable and prudent for agencies to develop a single consistent, robust procedure for evaluating or characterizing natural disturbance events.

There appear to be considerable inaccuracies in estimates of habitat impact by fire. Assessments made soon after a fire may misrepresent the eventual habitat effects. It is often difficult to determine how much habitat was removed by fire, particularly regarding whether habitat affected by moderate intensity fire was sufficiently altered to be unusable by Spotted Owls. An area that has been burned does not always equate to habitat loss (Bond et al. 2002). Wildfires accounted for 75 percent of the natural disturbance loss of habitat estimated for the period between 1994 and 2003. Fifty percent of the loss from natural disturbances reported can be attributed to the Biscuit fire.

On the east side of the Cascade Range and Klamath region, past forest management practices, including fire suppression, selective logging, and unmanaged overstocked plantations, have resulted in changes in tree species composition that make areas more susceptible to large-scale insect outbreaks. Wildfire risk and management will be a continuing source of threat to existing Late Successional Reserves. Sudden Oak Death is a relatively new and unknown threat to habitat in the southern part of the Northern Spotted Owl range.

HABITAT DEVELOPMENT

The development of suitable Northern Spotted Owl habitat is a vital part of the long-term habitat management approach of the Northwest Forest Plan. Losses of habitat typically occur in a tangible time frame, such as with harvesting or catastrophic fire, while habitat development does not. Management activities designed to accelerate development of new habitat are becoming an important part of forest management. Retention of legacy (snags and course woody debris) in current areas of timber harvest will shorten the time necessary for those areas to achieve the habitat complexity deemed to be suitable Northern Spotted Owl habitat. There is a need for land managers to develop the ability to track development of habitat and validation of that habitat for its suitability to owls. Estimates of habitat development should be included in future habitat trend analyses.

FUTURE INFORMATION NEEDS

A Range-wide, spatially explicit database would make it possible to effectively track changes in forest condition from individual management activities and natural disturbance.

More information is needed on changes on non-Federal land to provide a more complete picture of habitat change within the range of the Northern Spotted Owl.

An improved ability to differentiate types of disturbance would be valuable. Assessments of fire and insect damage are particularly problematic in terms of defining the effect on owl habitat. There appear to be considerable inaccuracies in estimates of habitat impact by fire. Improved confidence in remote sensing methodologies to describe habitat condition would be very valuable, such as Light Detection and Ranging (LIDAR). Increased emphasis on non-clearcut harvest methods may limit traditional remote sensing disturbance detection.

An improved confidence in our ability to track and validate the suitability of newly developed habitat would be very valuable.

More information on the actual impacts of Sudden Oak Death on Northern Spotted Owl habitat would be valuable.

1 INTRODUCTION

When the Northern Spotted Owl was listed as a threatened species throughout its range in 1990 (*USDI 1990*), one primary concern was the widespread loss of habitat. Estimates of loss of old-growth forests since the late 1800s throughout the Pacific Northwest indicated the majority of old-growth forests had been removed. At the same time, predicted rates of habitat removal on Federal lands in 1990 suggested that insufficient suitable habitat would persist outside of existing reserved areas to support a viable population of Northern Spotted Owls. Based upon these factors, the U. S. Fish and Wildlife Service (USFWS) determined that the Northern Spotted Owl was likely to become endangered within the foreseeable future throughout all or a significant portion of its range, which contributed to its listing as a threatened species.

The amount of existing Spotted Owl habitat and its distribution have often been at the center of the Northern Spotted Owl conservation debate. Our objective in this section is to evaluate the estimates of changes in Northern Spotted Owl habitat that have occurred since the owl's listing, and to assess any changes in risk to Northern Spotted Owl habitat.

This chapter provides an evaluation of the relevant information on the distribution and trends in Northern Spotted Owl habitat, the validity of the conclusions drawn from such information, and other information relative to assessment of the habitat changes as a potential threat to Northern Spotted Owl populations. Our assessment was accomplished by examining the literature with a focus on current estimates of the amount of range-wide suitable habitat. The most comprehensive examination of habitat trends was provided by the USFWS for use in this review. The USFWS accepted responsibility for collating and summarizing the information provided in response to public comment and maintained in its databases for the use by SEI. The report (*USDI 2004*) is an update of the first comprehensive attempt by the USFWS to examine changes in habitat (*USDI 2001*) of Northern Spotted Owls since listing in 1990. Throughout this report, we refer to the USFWS reports to provide a description of methods data on habitat trends and a context for interpreting and evaluating the habitat trends results and ultimately, together with other relevant literature, to support our conclusions about changes in threat to the Northern Spotted Owl. Although some parts of this report are based on material contained in the USFWS reports, any conclusions are our own.

Our approach was to:

Provide context for evaluating habitat change as it influences Northern Spotted Owl conservation.
Describe current efforts to evaluate Northern Spotted Owl habitat trends and conditions, and to evaluate the accuracy of those estimates.

Provide an evaluation of risk relative to changes in the extent of Northern Spotted Owl habitat, its condition, and its distribution.

2 CONTEXT FOR EVALUATING NORTHERN SPOTTED OWL HABITAT CHANGE SINCE ITS LISTING

2.1 HISTORIC RANGE OF VARIATION IN HABITAT

Regional estimates of historical old forest variability can provide context for current habitat trends estimates. Historical variability in the amount of old forest (referred to by various authors by different names, but all related to structurally complex forests) in the range of the Northern Spotted Owl has been the subject of keen interest. In western Washington and Oregon, historical disturbance regimes were characterized by large, infrequent fires (Henderson et al. 1989, Wimberley et al. 2000). Calculations of pre-logging old growth in western Washington and Oregon are relatively consistent. Franklin and Spies (1991) suggested between 60 and 70 percent of the landscape was old growth. Booth (1991) estimated approximately 62% of western Washington and Oregon were in forests greater than 200 years of age. Ripple et al. (2000) estimated that in the central Oregon coast range 63% of the pre-logging forest landscape was old growth. Rasmussen and Ripple (1998) estimated 72% of the pre-logging landscape in southern Oregon Coast Range was comprised of the large conifer size class. Similarly, *Teensma et al. (1991)* reported that 62% of the forests in the Oregon Coast Range in 1850 was over 100 years old. Harrington (2003) has provided documentation of the early surveys utilized by many of these estimates. Several of these estimates were aided by Forest Resources surveys from the 1930s. *Zybach (1996)* used a wide variety of historical accounts and timber records to conclude that historically (because of the fire frequency), only about forests of the Columbia Gorge 5 to 15% forest in at least 200 years of age. Range-wide estimates of historic conifer forest > 150 years in Table 6.1 were estimated by the Conservation Biology Institute *(James Strittholt, pers. comm.)*. The Puget Lowland Forests and Central Pacific Coastal Forests are two areas that have experienced the largest changes in old forest area and presumably suitable owl habitat.

Wimberley et al. (2000) simulated long-term historical variability in the amount of old growth forest and late successional forests in the Oregon Coast Range. Based on an age-class-demographic simulations and assumptions about the fire regime, they estimated that old growth forests covered between 25 and 75% of the province over the 3,000 year simulation. At the scale of late successional reserves (40,000 ha) old growth percentages varied from 0 to 100%. Contemporary estimates of current old-growth (5%) and late successional forest (11%) in the Oregon Coast Range were lower than expected under the simulated historical fire regimes; however, the authors noted that considerable uncertainty surrounds their estimates.

In the past, estimates of remaining old growth on specific landscapes have been widely divergent (i.e. Haynes 1986 and Morrison 1988). In describing the sometimes widely divergent results from early remote sensing studies, Jiang et al. (2004: 321) stated:

> "differences in the underlying data sources (dates of acquisition, resolution, and ancillary data support) represent other sources of divergence among the studies. Consequently, despite the wealth of data available, a reasonably accurate and timely spatial database for late seral conifer forests for the entire PNW region for conservation planning purposes was not available."

Current estimates of the amount and spatial distribution of contemporary old growth forests benefit from modern data analysis methods and sophisticated error checking.

Jiang at al. (2004) found approximately 11.6 million ha (~19%) of the PNW was classified as old conifer forest (>150 years). Another 11.8 million ha (~19%) was classified as mature conifer forest (50-150 years). Thus, over 23.4 million ha (~38%) of the PNW was late seral conifer forest (old and mature conifer cover classes). The extent of late seral forests varied greatly between the eight ecoregions. The Central and southern Cascades and Klamath-Siskiyou ecoregions contained the highest amount of late seral forest in the region.

2.2 RATES OF NSO HABITAT CHANGE PRE-1990

Long-term habitat trend information for land managed by the Forest Service presented in the listing document was originally supplied and verified by the Forest Service, Pacific Northwest Region (*USDI 1990, Appendix F*). Changes in amount of Spotted Owl habitat was estimated from estimates of the average annual volume of timber harvested during each decade from the 1950s to the present. Because harvest volume was relatively constant from 1960 through 1990, authors of the 1990 status review assumed that rate of habitat decline was also constant during this period.

Several studies within the range of the Northern Spotted Owl have used remote sensing time series as a tool for examining the dynamics of landscape change. Due to the resolution of remote sensing data, the major focus most studies of this landscape change analysis has been on large forest disturbances, primarily clearcut logging and catastrophic fire. There are several examples illustrating differences in forest cover change rates between public and private lands (Table 6.2). Cohen et al. (2002) published landscape-wide estimates of forestland harvest rates for Western Oregon. Although not specific to suitable habitat, these estimates provide insight into harvesting trends over nearly the last quarter century. Cohen et al. (2002) found that across ownerships the stand replacement disturbance was lowest in the early 1970s (0.5% per year) and that rate increased to over 1.2% per year throughout the mid 1980s. By the first half of the 1990s the rate had declined to 0.7% per year. Harvest rates on public lands (state and Federal) were consistently below this average.

Cohen et al. (2002) also found that the harvest rates on private industrial lands were consistently about twice the average rate of harvest on public land throughout the 23 year sample period. In the late 1980s and early 1990s the harvest rate was estimated at 2.4% per year for private industrial land. An increase in private non-industrial lands owner's harvest rates started in the 1970s when the rate was 0.2% per year and continued to increase to the early 1990s when the rate was similar to that of the private industrial lands. There was a steep decline in harvest rates between the late 1980s and the early 1990s on State and Federal and private industrial forest lands.

Natural disturbance has also been documented using remote sensing time series. Staus et al. (2002) found that between 1972 and 1992 forest disturbance inside existing protected areas in the Klamath-Siskiyou Ecoregion was 0.2% per year.

2.3 CONTEXT FOR ASSESSING CHANGES TO NORTHERN SPOTTED OWL HABITAT

The 1994 biological opinion on the Northwest Forest Plan predicted continued losses of suitable habitat as the result of management. The 2001 habitat trends reports (*USDI 2001*:23) states:

> "Based on the analysis and modeling done in 1994 for the ROD (Record of Decision) (*USDA/USDI 1994a* and *b*), the USFWS's 1994 biological opinion on the Forest Plan concluded that the planned decadal timber harvest rate of owl habitat (about 20,000 acres per year or approximately 2.5 percent of all suitable owl habitat per decade) would be consistent with expectations for the conservation of the owl (*USDA/USDI 1994a*). Although this rate of harvest is not a biological threshold for this species, an assessment of the cumulative total impact from past consultation in relation to this decadal rate provides an opportunity for drawing conclusions about then trends in change to owl habitat in relation to implementation of the Forest Plan."

The assessment of impacts habitat trends over time to Northern Spotted Owl conservation requires a valid comparison with reported effects on owls relative to baseline data. There are two key sources of baseline data that can be used to predict the status of Northern Spotted Owls: 1) demographic analyses and 2) overall change in suitable habitat. The USFWS (and other agencies) rely on these data to evaluate owl status. The status and trend (effectiveness) monitoring plan for the owl integrates results of demographic studies with those from habitat studies to estimate whether owl populations will respond as predicted to given changes in habitat quantity and quality. The USFWS assumed that tracking and evaluating changes to owl habitat provides the basis for assessing the success of conservation efforts in relation to effects on owl populations.

In the 2001 report the USFWS (*USFWS 2001*:*8*) stated that:

> "Previous owl survey efforts don't provide a valid baseline since they do not represent population size nor are effects to specific sites tracked over time. There is insufficient information on owl densities in different habitat types or on different ownerships for determining population size. Numbers of owl individuals or pairs, without link to habitat estimates, don't offer a basis for tracking changes to the owls' status on other than local areas. The demographic study provides range wide estimates of population trends and are critical in assessing the overall conservation effect. Range-wide meta-analyses of demographic data tracks owls across a variety of ownerships and ecological conditions, the results provide trend information that extends beyond just Forest Plan implementation, and incorporates effects of other natural and human-made factors."

When reporting potential impacts to owls from specific projects (Section 7 consultation), agencies have reported numbers of known owl locations (or activity centers) in project areas. Changes in numbers of owls have not played a role in any of the major planning efforts, and most of the data from previous survey reports of owl locations are now outdated and of little use in addressing population questions. However, if the surveys were adequate then they represent a condition at a point in time. If at a later date surveys over the same area showed a decline in owl territories, it suggests something might have happened, particularly if this were matched to other surveys in an adaptive management (quasi experiment) context. Lint et al. (1999) noted that more useful information about species trends was gained through a demographic and habitat-based monitoring effort than by surveys alone.

2.3.1 ANTICIPATED HABITAT LOSS FROM MANAGEMENT ACTIVITIES

The USFWS (*USDI 2004*) compared the estimated habitat losses to those that were expected in 1990. As stated in *(USDI 2004:16*):

> "The 1990 listing document states the following regarding management-based habitat trends on Federal lands: 'In Oregon and Washington, about 64,000 acres of old-growth and mature forests suitable for Northern Spotted Owls have been logged on the National Forests each year over the past nine years; this represents a decline in non-reserved owl habitat on Forest Service land of about 2.3 percent per year and a reduction of about 1.5 percent per year in the total amount of owl habitat on National Forests in Oregon and Washington (Thomas et al. 1990). The anticipated harvest rates for old-growth and mature forests for the next 10 years are about 39,400 acres/year, or roughly 1.4 percent of the non reserved old-growth and mature forests on Forest Service lands annually in Oregon and Washington. About 1 percent (4,700 acres) of the suitable habitat on Forest Service lands in California will be harvest each year (Thomas et al. 1990).'(*USDI 1990 p.26188*)
>
> 'On an annual basis, the Bureau of Land Management awards contracts to harvest 32,940 acres, of which 22,800 acres are clear-cut and 10,140 acres are partially cut. Of the acreage cut, approximately 66 percent of the harvest is in forests over 200 years old (*Nietro, pers. comm.*). On Bureau of Land Management lands in Oregon, an average cutting rate of 23,400 acres/year is expected to continue. This would eliminate all Northern Spotted Owl habitat on non-protected Bureau lands, except for the Medford District, within the next 26 years (*USDI 1990*). At current logging rates all remaining suitable habitat will be eliminated in 12 (Eugene District) to 52 (Medford District) years (*USDI 1990*).' (*USDI 1990* p. 26193)
>
> 'This loss of old-growth and mature habitat continues, with projected losses on Federal lands of about 3 percent per year on Bureau of Land Management and 1 percent per year (about 40,000 acres) on Forest Service land (*USDI 1990*).' (*USDI 1990 : 26152, 26160, 26163, 26184*)"

3 ESTIMATES OF SUITABLE HABITAT TRENDS

3.1 CHANGES IN HABITAT AMOUNT ON FEDERAL LANDS

The USFWS (*USDI 2004*) estimated trends in suitable habitat acreage on Federal lands for the nine year period between 1994-2003. The 2004 (*USDI 2004*) assessment incorporated the habitat trends calculated in 2001 (*USDI 2001*). The first comprehensive attempt by the USFWS to examine changes in critical habitat (*USDI 2001*) and take of Northern Spotted Owls since listing in 1990, the latest report (*USDI 2004*) updated those values. Both reports used the same approach of assessing individual project scale impacts and summarizing results on a province scale. The USFWS was dependent on a partnership with the US Forest Service and the Bureau of Land Management to supply the basic data the USFWS used to create the habitat trends reports. The USFWS did not have the resources to produce an independent estimate of habitat change and remains dependent on a shared responsibility with the management agencies. The 2004 report (*USDI 2004*) superceded the 2001 report (*USDI 2001*). The 2004 report benefited from previous experience in having increased clarity and a keener focus *(Karl Halupka, pers. comm.)*. The USFWS used the same metric (annual rates of habitat change) for habitat change as the 1990-listing document. The panel has no information in which to assess the habitat trends between 1990 and 1994.

3.1.1 OBJECTIVES

As stated in the 2004 report (*USDI 2004: 30*):

> "The objectives of this report were to 1) calculate rates of habitat change on federal lands that have occurred due to management actions, natural events, and habitat development since the Northern Spotted Owl was listed; and 2) compare these rates to rates that occurred before listing and that were anticipated to occur after listing."

3.1.2 METHODS

Both the 2001 and the 2004 assessments used data that were gathered to make assessments of habitat change used Section 7 consultations, Biological Opinions, and Biological Assessments to determine possible impacts to habitat. These estimates were compared to the Forest Plan baseline as well as the changes in habitat there were anticipated at the time of listing. Section 7 consultations between the USFWS and other Federal agencies to assess project impacts are required under the Endangered Species Act. USFWS has focused its analysis of project-related effects on the Northern Spotted Owl to the land use allocations established under the Forest Plan for the purpose of owl conservation.

3.1.3 CONSULTATION DATA BASE

The USFWS maintains the primary data from their own consultation records (management-related loss) needed to evaluate changes to habitat. This database was created for the 2001 estimate of habitat change. Because consultations and other habitat impact assessments were derived from planned activities, assistance from the Forest Service and BLM was required to update their consultation data. The best available information provided by the land management agencies (FS and BLM) was used on the changes that actually occurred following individual project implementation. Updates primarily consisted of adjustments to the consultation database for habitat acres that were not harvested or otherwise removed, although they were originally planned for removal during consultation. Federal land management agencies were asked to provide additional information on activities and natural events of 100 acres or more in size that may have impacted suitable habitat.

3.1.4 RESULTS OF THE USFWS HABITAT CHANGE ASSESSMENT

The USFWS report (*USDI 2004*) presents rates of habitat loss attributed to management activities and natural events (e.g., fire, insects, disease, etc.) on Federal lands across the range of the Northern Spotted Owl and by individual physiographic province. The USFWS (*USDI 2004*) provides rates of habitat loss spatially and by agency as reported in the 1990 listing document for comparison purposes. Differences in how habitat is estimated and defined can confound estimates of actual change to habitat across the landscape. The USFWS focused on calculating rates as the percent change in habitat availability over time to standardize measures of change in spite of differences in starting baselines. Estimates of habitat that has developed through vegetative succession and growth (referred to by some as "ingrowth") were discussed in the report but not included in the synthesis.

The results were summarized as follows from the 2004 report (*USDI 2004:11*), See Appendices for supporting tables from (*USDI 2004:20*).

> "Our results indicated an approximate 2.11 percent decline in the amount of available habitat due to management activities range-wide. The majority of management-related loss was concentrated in Oregon, although the California Cascades province suffered a relatively high rate of loss as well. Habitat loss due to natural events totaled 224,041 acres, equating to a 3.03 percent decline in available habitat range-wide from 1994 to 2002. Between 1994 and 2004, project methods estimated that there would be an 8 percent increase in habitat available rangewide due to ingrowth/successional processes. Overall, habitat loss rangewide due to all factors has resulted in a total decline of 5.14 percent between 1994 and 2003 (0.57 percent per year).
>
> Annual rates of habitat loss due to management activities from 1994 to 2003 are less than 25 percent of rates projected at the time of listing and 15 percent of rates reported up to the time of listing."

3.2 CHANGES IN HABITAT AMOUNT ON NON-FEDERAL LANDS

The USFWS (*USDI 2004*) report does not consider habitat change on non-Federal lands. The USFWS examined information in their files that was submitted by private entities on their Habitat Conservation Plans and associated reports to determine if the information was sufficient to calculate a rate of change on non-Federal lands. They concluded (*USDI 2004*:6) that:

> "Such a calculation requires an estimate of the amount of Northern Spotted Owl habitat at some past time (usually the start of the Habitat Conservation Plan) and either a current habitat estimate or the amount of habitat removed/added since the original habitat estimate. Habitat values must be based on approximately the same definition or description to allow calculation and comparison of rates. Unfortunately, in almost all cases, we lacked some of the necessary information. The information typically lacked a starting estimate of habitat, reported harvest in terms of total forest acres that included

non-habitat, or included significant amounts of habitat acquisition that could not be accounted for in the baseline."

The Panel found no additional sources of information to make any meaningful statements about habitat trends on non-Federal lands. The same methodological and access problems that limited the USFWS in their 2004 estimates (*USDI 2004*), also limited the panel. Most timber harvest records are in terms of volume and are of little value in interpreting habitat removal (for example *American Resource Council, 2004*). Remote sensing studies are generally out of date ending in the early 1990s (see Table 6.2). Cohen et al (2002) reported harvest rate by ownership group for five periods between 1972 and 1995 and by three Oregon coast range provinces. Inference as to change in suitable habitat would require significant assumptions concerning the percent of habitat that made up the harvests, and the amount of natural disturbance. Estimates of habitat change from HCPs often are either simulated (i.e. *Farber 2003*) and may lack verification or lack a reliable baseline for comparison and have known shortcomings in estimation of habitat change despite, in the case of the Washington State Department of Natural Resources, high quality stand inventories (*WA DNR 2004a*). In a recent workshop in British Columbia, no information was presented on habitat trends (*Zimmerman et al. 2004*). Efforts are currently ongoing to attempt to estimate habitat change on non-Federal lands in Washington State (*Joe Buchanan, pers. comm.*) The panel recognizes that this information on potential harvest of habitat is usually maintained by private land owners and is proprietary and that would have little access to the information for conducting this habitat trend analysis.

4 EVALUATION OF SUITABLE HABITAT TRENDS AND THE RISKS TO OWL HABITAT

Limited empirical data is available to assess habitat loss on a range-wide basis for Northern Spotted owls. *Thomas et al.* (*1990*) compiled estimates of the amount of spotted owl habitat on most public lands, but were unable to estimate amount of habitat on private lands and from several state and tribal landscapes. Since then, several estimates of current suitable habitat and projected rates of change have become available only for Federally managed lands. Those habitat trends estimates that are available were prepared by the Services (*USDI 2004*).

The following section discusses the accuracy of habitat assessments, the sources of bias, and the assumptions made in the USFWS's analysis of suitable habitat trends (*USDI 2004*). Our interpretations are made with respect to the strengths and limitations of the existing level of resolution of habitat change. We also assess our confidence in these estimates.

4.1 EVALUATION OF METHODOLOGIES USED TO DETECT CHANGE

We conclude that the habitat losses presented in (*USDI 2004*) are conservative, but are reasonable approximations of habitat change. In general, the methodologies used by the USFWS to assess trends in suitable habitat are limited by data quality, and the reliability of specific applications is difficult to interpret because there was a poorly controlled bias inherent in the methodology and data acquisition process that was available. Despite these shortcomings there are no other viable alternatives to estimate habitat change on Federal lands. Given the sources of bias, we believe these estimates of habitat loss overestimate losses, although the magnitude of the inaccuracy cannot be determined. However, the risk associated with these estimates being wrong is low, given that all information indicates that habitat loss has been low.

The following section discusses sources of uncertainty concerning methodologies, data, assumptions, and their implications for estimating habitat trends. This section is organized by topic: data from consultations and their adjustments and natural events, the baseline from which change was estimated, the calculation method, assumption about land transfers, and habitat development.

4.2 BASELINE HABITAT FROM WHICH HABITAT CHANGE IS ESTIMATED

4.2.1 CREATION OF THE NORTHWEST FOREST PLAN BASELINE.

When the Northern Spotted Owl was listed in 1990, a regional compilation of habitat was not available. This habitat compilation was not completed until 1994, with the completion of the NWFP. In order to develop a regional map of existing Northern Spotted Owl habitat, two types of information were needed: (1) the distribution of vegetative cover types, and (2) identification of the cover types that provide habitat for Northern Spotted Owls.

At the time FEMAT was convened, there was no single source of vegetation information across the range of the Northern Spotted Owl. A new vegetation map showing seral classes was created by FEMAT reclassifying and merging information from different federal ownerships (*FEMAT 1993*, Appendix VIII A). Satellite imagery was used to define general stand conditions while suitable habitat definitions provided by local biologists were used to develop a classification believed to represent nesting, roosting, and foraging habitat (suitable habitat). The methods for compiling and checking the FEMAT baseline using geographic information system technology was a substantive advance over the manual methods used in previous regional assessments, such as the Interagency Scientific Committee report (*Thomas et al. 1990*).

4.2.2 USE OF THE FOREST PLAN BASELINE

In both assessments used to estimate Northern Spotted Owl habitat trends, the *USFWS (USDI 2001*, *2004*) used the Forest Plan baseline. They required a reference condition for habitat, against which to evaluate changes in suitable habitat acreage over time. They ideally sought a habitat baseline with particular characteristics. The USFWS stated (*USDI 2004*:2) that:

> "We sought a habitat baseline with particular characteristics. The habitat baseline needed to be: range-wide in scale; developed with a consistent methodology across that range; consistently applied over a number of years to allow for change over time to be evaluated; and recognized and accepted as a reasonable approach to this complex problem by the agencies responsible for managing Federal lands."

The USFWS's 2001 (*USDI 2004:3*) rational for selection of the Forest Plan baseline is summarized as follows: They stated:

> "The habitat baseline developed for the Northwest Forest Plan (Forest Plan) was used as a reference condition because it has all of these characteristics. It is a spatially unified database that covers 57 million acres of the Spotted owl's range in the Pacific Northwest. Temporally the Forest Plan baseline (1994), spans a time period close to a decade, thus allowing for a reasonable calculation of a rate of change over time and is comparable in length to that evaluated in 1990 at the time the Spotted owl was listed.
>
> The Forest Plan habitat baseline was formally adopted by the land management agencies in 1994 with the signing of the Record of Decision for Amendment to Forest Service and BLM Planning Documents within the Range of the Northern Spotted Owl. This database includes Spotted owl baseline habitat values for all administrative units within the Forest Plan boundaries and serves as the habitat baseline for this report."

4.2.3 ALTERNATIVE BASELINES CONSIDERED

In 2004 the USFWS revisited the use of the Forest Land Baseline. It was generally recognized that the decade old habitat assessment may have many shortcomings in terms of an accurate portrayal of habitat used by Northern Spotted Owls. Since the 1994 Forest Plan baseline was developed, there have been several efforts to create alternate, more accurate, descriptions of baseline conditions. The USFWS (*USDI 2004*) explored a number of other habitat baselines that were products of these efforts to evaluate whether they might better to calculate current rates of habitat change across the range of the Northern Spotted Owl. These baselines included various local habitat baselines, the California Baseline, and the Interagency Vegetation Mapping Project. The Interagency Vegetation Mapping Project represents the new generation of habitat assessment, but was not ready for use by the USFWS and us. It was the determination of the USFWS that local habitat baselines generally did not meet the above-mentioned criteria. The USFWS (*USDI 2004*) examined other habitat baselines as a reference for conditions against which to evaluate changes in habitat over time across the range of the Northern Spotted Owl (see Appendices for a summary and evaluation of these other baselines.)

4.3 EVALUATION OF BASELINE INFORMATION

The strength of the Forest Plan suitable habitat baseline lies in its consistency across the entire range of the Northern Spotted Owl. It was developed with the best methods available at the time and attempts to portray habitat believed, by local biologists, to be used by owls. The Forest Plan baseline was considered suitable for broad-scale analyses such as comparison of management alternatives in FEIS (*USDI 1993, 2004*). *Mickey (2004)* has criticized the claims that the Northwest Forest Plan baseline is based on too general a data set to accurately represent habitat used by spotted owls, and that the consistency of the methodologies are difficult to determine.

Due to variation in GIS and maintenance of baseline data at multiple scales, estimates of suitable owl habitat have varied among administrative units since 1994. Since only nine years have passed since implementation of the Record of Decision, the USFWS used estimates from the

FSEIS (*USDA/USDI 1994a* and *b*) as the basis for estimating change over time. The point accuracy of the Forest Plan Baseline was not intended to be sufficient for project-scale assessments. In a recent analysis comparing Northern Spotted Owl location data with the Northwest forest plan baseline (*USDI 2004*, see Appendices), the data suggests that the vast majority of owl sites were within or near designated suitable habitat. However, there was fairly low confidence among owl biologists that the Forest Plan Baseline accurately describes suitable owl habitat *(Martin Raphael, pers. comm.)*.

Since establishment of this baseline in 1994, most changes to the Forest Plan baseline have been measured at the project scale using habitat information available only to the local administrative units conducting the assessments. These administrative units maintain a local baseline of habitat customized to their local situation and information. These local habitat baselines have not been consolidated at the regional or range-wide level and do not have consistent approaches or definitions. Solis (1995) noted in reference to the Northwest Forest Plan that detailed descriptions of suitable habitat were lacking and inventories to accurately describe the quantity, quality and distribution of habitat were also missing.

Our interpretation is that local habitat baselines do not allow effects of habitat to be aggregated across the range of the Northern Spotted Owl. At the scale of individual projects, agencies (BLM, USFS, USFWS) assess effects to habitat using the best available information (the local baselines). We now know that these local baselines can differ substantially from the Forest Plan baseline.

The extent of possible overlap between the local baselines and the Forest Plan Baseline is not clear. Although the accuracy can not be totally reconciled, *USDI 2004* (Appendix 4 and 10) reports considerable overlap when comparing Northern Spotted Owl location data with suitable habitat maps for Washington, Oregon, and California. This is important evidence that, although the accuracy of the Northwest Forest Plan baseline may not be validated, the risk in using the baseline for range-wide estimates is reasonable. It is possible that the local and Forest Plan baselines account for different acreages; if true, this represents a source of uncontrolled bias. If this local habitat baseline includes, under its definition of habitat, areas or conditions not considered habitat in the Forest Plan baseline, the reported acres of habitat removed may overestimate the effects of the project relative to the Forest Plan baseline. Conversely, if the local habitat baseline does not include all areas defined as habitat in the Forest Plan baseline, effects are underestimated relative to the Forest Plan baseline. The USFWS has stated the project effects that compiled overestimate effects relative to the Forest Plan baseline *(USDI 2004:16*). The level and direction of differences between local baselines by the Forest Plan baseline varies widely by area.

Our assessment is that there are flaws in the Forest Plan baseline, but there is no viable alternative. It would be very difficult to aggregate local baselines, which are believed to better reflect the key components of suitable habitat, into a new baseline. The Interagency Vegetation Mapping Project has the potential to update the vegetation classification range-wide and be validated with local definitions that have been field verified.

The USFWS had to choose between using an outdated baseline with known weakness or waiting for a new baseline to be completed. Using local habitat definitions from a region-wide assessment was not practical. The argument for using the Forest Plan baseline was reasonable given the range-wide scale required. Determining the inaccuracies inherent in using an alternative baseline to the Forest Plan baseline were beyond our capabilities to evaluate. We did not know if bias in the Forest Plan baseline had consistent consequences range-wide. However, given the small changes in suitable habitat observed between 1994 and 2002, the relative risk of using available habitat trend assessment information for Federal lands was low.

The Interagency Vegetation Mapping Project, once complete and validated, will provide a new reference condition, and thus may be useful for evaluating trends in habitat change in the future. It will contain the local accuracy constraints as does the current Forest Plan baseline. However, there must be both methodological and validation consistency in order to achieve a consistent baseline. The Interagency Vegetation Mapping Project will also provide a baseline for all habitats within the range of the Northern Spotted Owl. We believe that the appropriate scale to interpret habitat change should remain at the province.

4.4 ASSUMPTIONS CONCERNING CHANGES IN FEDERAL LAND OWNERSHIP

Another source that contributes to the overestimation of habitat loss was the treatment of land exchanges. About 19,500 acres of habitat were acquired by Federal agencies from 1994 to 2003 through land transfers and exchanges (*USDI 2004* Appendix 5). The USFWS did not consider habitat additions to the Federal land base as a change in habitat condition. These additions were not included in the Forest Plan baseline or in calculations of habitat trends. We believe it was reasonable for the USFWS to maintain a common baseline for this assessment because often the land use allocation was not known and details of habitat status were from mixed sources and not verifiable (*Karl Halupka, pers. comm.*). Changing the baseline through time influences the relative contribution of specific habitat losses or gains through time.

In the long term, failure to include land transfers will result in underestimation of habitat managed under the Forest Plan. In the East Cascades province the habitat acquisitions were about 80% of the acreage that was lost (8,613 acquired, 10,788 lost). In the West Cascades province land that was acquired replaced about 35% of the acreage lost (4,025 acquired, 11,389 assumed lost).

The lack of inclusion of these lands represents an important footnote in the interpretation of these habitat change rates. Future analysis based on the Interagency Vegetation Mapping Project will cross ownerships and provide a better bases to address changes in ownership in the context of distribution of habitat.

4.5 CONSULTATIONS USED IN HABITAT CHANGE CALCULATIONS

As previously stated, the most recent analysis of habitat trends by the USFWS (*USDI 2004*) is an update of the 2001 report (*USDI 2001*). The 2004 report incorporated all the refinements of the information from the 2002 report as well as updated information. In assembling data for the 2001 habitat assessment (*USDI 2001:6*), the authors of the assessment noted that it was apparent to the USFWS that individual consulting agencies used and managed consultation data differently. These differences included the use of terms and/or definitions of terms, the interpretation of impacts to owls, the different scales at which data are collected, how data are managed, and double counting of effects data.

In both 2001 and 2004 (*USDI 2001, 2004*), the majority of data available for habitat assessments were associated with implementation of the Forest Plan as individual projects or plans on local scales. Because of inherent GIS errors associated with digitizing, use of different mapping sources, use of different terms, and use of different organizational levels, the USFWS recognized that the consultation data base did not lend itself to sophisticated statistical analysis.

Instead, the USFWS viewed these data as useful to evaluate general tendencies or trends and identify issues warranting further consideration (*USDI 2004:16*). We agree with this view; as such, all acreage change figures are rounded to the nearest one thousand, and should be viewed as approximations only. Although the USFWS estimates are approximations, our conclusion is that these trend assessments provide reasonable estimations about the general status of Northern Spotted Owl habitat on Federal lands.

4.5.1 ADJUSTMENTS TO IMPACTS IN PRIMARY DATA

A simple cumulative total of consultation acres cannot be directly compared to the total estimate of owl habitat over the Forest Plan area to accurately calculate actual impacts to owls. Adjustments were made to help control known sources of bias in the primary consultation data that were used to determine habitat impacts. To support the evaluation, the USFWS (*USDI 2001*), along with the Forest Service and BLM, investigated the accuracy of 35 biological opinions to identify whether the figures reported in the opinions accurately represented potential effects to owls. Of the 298 consultations examined for the assessment, 35 opinions represented the majority (about 70%) of the acres under the purview of the Forest Plan. The results of this examination were used to remove sources of double counting, reconcile terms, and adjust the cumulative database and total effects downward approximately 40% to represent a more realistic estimate of expected impacts to owls (*USDI 2001* Table 6.4-1). However, since adjustment data were used only from opinions where there were acre differences greater than 1,000 acres (8 of 35 opinions reviewed out of 298 Forest Plan opinions in total), these revised effect estimates still slightly over-represent potential effects to owl habitat (*USDI 2001*).

The sources of data (project level consultations) for habitat change were believed to have consistently overestimated actual habitat loss (*Danielle Chi, pers. comm.*). It was assumed that counting of unimplemented projects over-represented the actual anticipated effects to Northern Spotted Owl habitat. Improved tracking of projects was in place for the 2004 estimates to help reduce much of the source of error from unimplemented projects.

Consultations (Section 7) assess the potential effects of the worst case alternative, but often other alternatives are selected *(Karl Halupka, pers. comm.).* The USFWS believes the actual effects are usually less than those originally predicted, adding another source of potential unknown bias (very likely overestimate of actual habitat acres harvested) to the estimates of management-based losses *(Karl Halupka and Danielle Chi, pers. comm.).* The 2004 (*USDI 2004*) assessment is an improvement in that it focused on suitable habitat only, while avoiding quantification of harassment. In 2001 (*USDI 2001*), double counting of effects to the same acres and activity centers may be the largest source of overestimation. Therefore , the USFWS is unable to fully quantify the extent of overestimated effects.

4.5.2 EVALUATION OF CALCULATIONS OF HABITAT CHANGE FOR FEDERAL LANDS

We agree with the USFWS's decision that the Forest Plan baseline provides the best available common denominator for calculations of range-wide rates of habitat change. Calculating rates of habitat removal from the Forest Plan baseline was intended to provide an index of habitat removal that should be generally applicable under other broad habitat definitions and their associated baseline levels. The 1990 listing document presented information about habitat trends separated by management agency and state. Anticipated habitat loss due to natural disturbance events was not calculated in 1990. Having no baseline or basis for comparison eliminated the possibility for making this comparison.

Calculating average rates across years smoothes the effects of adjustments to project scope provided by the land management agencies. The USFWS's methods for tracking effects would inflate inter-annual variation. Averaging reduces this potential bias, because treatment effects from a project or natural disturbance are assigned to a single year, though in reality they likely occur over a longer period.

The USFWS calculated separate rates of change for habitat removal (resulting from management activities and different types of natural disturbance) and for habitat development. We agree with the USFWS that estimates of habitat removal due to management activities is probably estimated with the greatest accuracy because individual projects that affect Northern Spotted Owl habitat are subject to intensive habitat surveys. Estimates of habitat changes ensuing from natural disturbance events are probably less accurate due to reduced intensity of surveys and analytical review. Timber harvests included all forestry activities in the USFWS's consultation database, so these calculations probably will slightly overestimate timber harvest impacts.

4.6 HABITAT CHANGE AS A RESULT OF MANAGEMENT

The rate of habitat loss on all federal lands managed for the Northern Spotted Owl has been less than anticipated at the time of listing and under the NWFP. Riparian areas and other designations have resulted in about 15% more land being managed for late-successional forest objectives (*USDI 2004*).

We concluded the reasons for the lower loss of habitat on Federal lands include the following:

The anticipated harvest levels on Federal lands has been lower than anticipated.

The changing approach to harvesting has left more structural legacy (residual trees and coarse woody debris), which fosters the development of habitat complexity.

The harvest of old growth forests has been lower than anticipated.

Lower levels and less intense harvest has resulted in less loss of existing late-successional forest.

The area in riparian management zones was significantly underestimated in original FEMAT assessments.

4.7 NATURAL STAND DISTURBANCE EVENTS

Estimates of natural disturbance effects (fire, insect damage etc.) on suitable habitat are difficult to assess accurately. The difficulty in tracking these widely dispersed effects and interpreting the impacts will likely remain the primarily source of uncertainty in impact assessment. The acreages of habitat appear to be large (*USDI 2004* Table 6.3 and 6.5, Appendices), but are consistent with historical variation.

4.7.1 INCONSISTENT INTERPRETATION OF IMPACT INFORMATION

The majority of changes to suitable Northern Spotted Owl habitat probably are captured in the USFWS's 2004 (*USDI 2004*) assessment despite likely inconsistencies in agency interpretation. Apparently, the USFWS was still developing a tracking strategy for natural disturbances at the time the assessment was written. Data used for the habitat trend assessment was generated in response to requests to Federal land management agencies (Forest Service, BLM, and National Park Service) to provide estimates of habitat lost from all natural events affecting over 100 acres of habitat.

Interpretations of natural disturbance effects are likely to differ between agencies and staff from different provinces. Confounding estimates of habitat removal by fire and assessments made soon after the event may misrepresent the total habitat effects. In particular, the impact of moderate intensity fire on habitat suitability is difficult to assess. *Bond (2003)* assessed the habitat condition after the Star fire in the Sierra Nevada and found a considerable discrepancy between the condition and suitability assumed by the Forest Service and what was verified in the field. Many of the areas that were assumed not to be suitable because of fire damage still met the specification that were known to support California Spotted Owls in the area. *Bevis et al.* (*1997*) also reported continued owl use of lightly burned sites in the eastern Cascades, however, overall owl use shifted away from more heavily burned areas. High intensity fires resulted in a loss of habitat suitability. *Anthony et al*. (*2002*) found continued occupancy of forests impacted by the Quartz Creek fire on the Rogue River National Forest in Oregon. Bond et al. (2002) observed Spotted Owls for fires in California, Arizona and New Mexico and found that moderate and light severity wildfires in those areas had short-term impact on owl survival, site fidelity, and reproductive success. Estimating the influence of fire on habitat has the danger of either overestimating or underestimating the eventual (i.e., long-term) effect. Delayed tree mortality, especially after moderate intensity wildfire or by secondary insect activity in injured trees, could expand post-fire mortality (Gaines et al. 1997).

In conducting their habitat trend analysis, the USFWS did not specify how to characterize disturbance effects on habitat to natural disturbance, and noted evidence of inconsistency of treatment in their request for information about natural disturbance. The report (*USDI 2004:8*) states "Consequently, different administrative units may have used different criteria for determining how much habitat was removed by an event, particularly regarding whether habitat affected by moderate intensity fire was sufficiently damaged to be unusable by Spotted owls."

4.7.2 FIRE EFFECTS

Wildfires accounted for 75 percent of the natural disturbance loss of habitat in the nine years between 1994 and 2003. New approaches to wildfire detection, prevention, and suppression were successful in reducing the extent of wildfires until the 1960s. During that period fire frequencies declined and fuel loadings increased (Agee 1994). Area burned by wildfires in the Interior Columbia Basin has steadily increased from the 1970s to the present. Currently the extent of wildfires in the Interior Columbia Basin is approaching the historical levels of the early 1900s (*USDA / USDI 2000*).

Hessburg et al. (1994) described the historical and current roles of insects and pathogens in eastern Oregon and Washington. They concluded that a century of fire protection has promoted a steady shift away from open ponderosa pine and western larch forests toward denser late-seral fir forests. The harvesting of high valued seral overstory trees accelerated conversion to insect and pathogen susceptible late successional forests. Douglas fir and grand fir are highly susceptible to root pathogens, bark beetles, defoliators, and dwarf mistletoe. Excluding fire from the grand fir and Douglas fir forests has been the single greatest detriment to diversity of eastside forests, and the primary factor in current susceptibility to major pathogens and insects.

Management can promote forest structures that are consistent with those that would have resulted from the historical fire regimes. Agee and Edmonds (*USDI 1992*, Appendix F:419) recommend active management that affords longer term protection of habitat. MacCracken et al. (1996) describe the forest health/spotted owl dilemma in the eastern Cascades as either 1) basically do nothing and hope for the best or 2) restore some semblance of historical range of variability in disturbance. There are often considerable administrative and economic barriers to forest restoration. The Washington State Department of Natural Resources *(WA DNR 2004b)* recently amended their HCP to promote Northern Spotted Owl habitat restoration in eastern Cascades. On the Yakima Indian reservation, King et al. (1997) describes how recent management trends can be reversed by shifting forests from late seral, fire tolerant, pathogen and insect susceptible forests by developing a seral dominated forest matrix. There are similar threats to the long-term maintenance of Northern Spotted Owls habitat exist on the Okanogan and Wenatchee National Forests in Washington state (*Paul Flanagan, pers. comm.*)

The Gotchen Late-successional Reserve in the eastern cascades of Washington provides an interesting case study for LSR susceptibility. Mendez-Treneman (2002) describes a LSR on the trajectory of substantial continued tree mortality, increased fuel loading and increased risk of stand replacement fire. Spruce budworm has been defoliating portions of the LSR since 1994 (*Willhite 1999*). After several years of defoliation by spruce budworms, grand fir mortality increased with mortality varying from individual pockets of 6-12 trees to the majority of the stand (Mendez-Treneman 2002). *Willhite (1999)* detailed the extent of defoliation and examined the possible suppression of the Spruce budworm populations on the Gotchen with a biological insecticide (*Bacillus thuringiensis* (*Bt*)). Mendez-Treneman (2002) examines the possibility of active management to maintain owl habitat and reduce risks associated with crown fire and mortality from the spruce budworm. No loss of habitat as a result of insect or pest activity was reported for this province in the 2004 USFWS report on habitat (*USDI 2004 Table 6.3*).

The changes in the mixed conifer community that have resulted in habitat conducive to the Northern Spotted Owl, have also resulted in a shift toward greater instability (Maffei and Tandy 2002). Much of the newly developed Spotted Owl habitat may be relatively short-lived as habitat because replacement Douglas-fir and ponderosa pine nest trees are unlikely to develop given the successional pathway (Lehmkuhl et al. 1994). Maffei and Tandy (2002) estimate that 70 percent of the Spotted Owl suitable habitat has been lost as a result of combined effects of western spruce budworm, root disease, bark beetles in the McCache LSR in the eastern Oregon Cascades.

The Forest Plan acknowledges the potential for the loss of owls and habitat from catastrophic events such as wildfire, particularly in East Cascades Provinces and the Klamath Province. Fires can have significant impacts on owl habitat and forest health in general and are of particular concern when they affect large portions of LSRs or multiple LSRs. Fifty percent of the habitat loss from natural disturbances reported in by the USFWS (*USDI 2004:Table 6.3 and Appendix 9),* can be attributed to the Biscuit fire. Treatments to reduce risk in and around LSRs are typically designed to protect owl habitat over the long term by reducing the likelihood of catastrophic effects; in the short term however, prescribed fire could adversely affect nesting owls directly or indirectly by affecting their prey (Carey et al. 1992, Zabel et al. 1995, North et al. 1999, *Wirtz et. al. 1988*). Bond (2002), however found no such short-term affect on owls.

The extent and intensity of natural disturbance events is highly variable (Wimberley et al. 2000). The nine years of record (*USDI 2004*) in the available assessment is simply a snapshot in time allowing no conclusion about natural disturbance trends. Long term changes in fire regime have been studied. Taylor and Skinner (2002) found in the Klamath Mountains that the fire return intervals at the watershed level are currently less frequent than they were historically. Their hypothesis is that fire suppression has altered the historic fire regime of 20 years to the current estimate of 238 years. Wildfire risk and management will be a continuing source of threat to existing LSRs.

4.7.3 PESTS AND DISEASE

Forest management practices including fire suppression, selective logging, and unmanaged overstocked plantations have resulted in changes in tree species composition that make areas more susceptible to large-scale insect outbreaks (Agee and Edmonds *USDI 1992*, Hessburg et al. 1994, Lehmkuhl et al. 1994). A spruce budworm outbreak in the eastern Washington Cascades started in 1998 and has caused widespread tree defoliation. There is evidence of competitive stress on large old ponderosa pine and Douglas-fir trees in eastside forests making these trees susceptible to fir-engraver beetles and western pine beetles (*Paul Flanagan, pers. comm.*). It was surprising that no habitat loss was documented in the 2004 (*USDI 2004*) assessment of changes in suitable habitat in eastern Washington. These types of impacts were anticipated and considered in the development of the Forest Plan (*USDA/USDI 1994a and b*).

Lehmkuhl et al. (1994) documented changes in vegetation cover, landscape attributes and the range of historical variability in eastern Oregon and Washington. They documented that forests became more dense in vertical and horizontal canopy structure as understory cover increased with regeneration of mostly shade-tolerant species. The distribution of forest age class and structure changed with smaller area in early seral and old forest stages and greater area in multiple canopy young and mature stands. The percentage of visible dead trees increased.

4.7.4 POTENTIAL IMPACTS OF SUDDEN OAK DEATH

Sudden Oak Death (SOD) has the potential to be locally important in some parts for the range of the Northern Spotted Owl. SOD infects many important tree species within the range of the NSO including Douglas-fir, coast redwood, tanoak, Pacific madrone, Canyon live oak, and California black oak. Tanoak, Pacific madrone, and Canyon live oak are important hardwood components in the mixed-evergreen forests characteristic of the Klamath-Siskiyou region of southwestern Oregon and northwestern California. The virulence of the disease in tanoak and Canyon live oak has already been noted. Although the literature does not yet cite golden chinkapin (*Castanopsis chrysophylla*) as a host for SOD, it may be susceptible because it is closely related to oaks. Douglas-fir is unquestionably the most important conifer within the range of the NSO; the eventual effect of SOD on Douglas-fir and coast redwood are currently unknown although branch mortality has been noted on both species as well as mortality on redwood sprouts. Significant mortality of any of these species would certainly modify existing NSO habitat, and could cause local extinction of some species such as tanoak, the species that appears most vulnerable to SOD (See Appendices for an overview of the disease).

The current effect of SOD and its possible duration are unknown. Modifications to Northern Spotted Owl habitat from SOD would be in the form of: (1) altered forest structure and composition, with potential impacts on thermal cover and vertical structure, hunting perches, and ground cover density; (2) elimination of potential nest trees; and (3) changes in prey base because of loss of food and cover for prey.

Altered forest structure due to SOD is most probable in the case of the mixed-evergreen forests that are characteristic of much of the Northern Spotted Owl habitat in the Klamath-Siskiyou region. These forests are characterized by a mixed forest of evergreen conifers (Douglas-fir, western hemlock, sugar pine, incense-cedar, and Port-Orford-cedar) and evergreen hardwoods (tanoak, Pacific madrone, golden chinkapin) (Franklin and Dyrness 1973). Douglas-fir and tanoak are the most common constituent species with Douglas-fir emerging above a lower canopy of tanoak and other evergreen hardwoods. Evergreen shrubs, such as Pacific rhododendron and salal along with hardwood saplings characterize the understory.

The evergreen hardwood trees and shrubs, which are the group currently projected to be most impacted by SOD, are important in supporting the prey base for NSO. For example, tanoak, Canyon live oak, and golden chinkapin periodically produce large crops of acorns (mast) and Pacific madrone produces large crops of fruit that are important food resources for small mammals. They also provide nest sites for arboreal species, such as the Northern Flying Squirrel, as well as for any other species that utilize tree cavities.

Elimination of the evergreen hardwood tree over- and mid-story would also result in significant modification of the microclimate within the stands, which could last for a significant period. This level of mortality has been observed in some heavily infected stands in which tanoak was dominant or co-dominant. Replacement of the lost evergreen hardwood component by conifers, such as Douglas-fir, could take decades or even centuries on some of these sites. Depending upon the relative proportion of evergreen hardwoods and conifers, increases in radiation and temperature and reductions in relative humidity could range from slight to very significant, including effective elimination of forest influence on the site.

Loss of the evergreen hardwood dominant and co-dominant trees would directly affect Northern Spotted Owls by eliminating potential nest trees and thermal cover. Evergreen hardwoods are currently used as nest trees. For example, in the California Coast Range 8% of the nest trees were tanoak and 1% were golden chinkapin (Pious 1994). In the redwood region, 11% of the nest trees were hardwoods, primarily California bay laurel and tanoak (*Chow 2001*). In a study of the Klamath region and California Coast Range, Northern Spotted Owl nest trees included small numbers of tanoak, California live oak, California black oak, and golden chinkapin (LaHaye and Gutiérrez 1999). Effects on thermal cover would depend on the percentage of the stand overstory that was composed of susceptible hardwood species, as noted in the previous paragraph.

4.7.5 PROSPECTS AND UNCERTAINTIES SURROUNDING SOD

SOD is of such recent origin that it is difficult to predict the impacts that it will have on Northern Spotted Owls, even in the near future. Based on initial observations of vulnerable species it appears very likely that there will be a significant impact on Northern Spotted Owl habitat on sites occupied by stands with a significant component of tanoak, especially when associated with susceptible tree species that are major sources of inocula, such as California bay laurel. This will include negative impacts, at least initially, on prey species, thermal cover, and nest sites.

Stands with a major susceptible evergreen hardwood component are probably the most common type of Northern Spotted Owl habitat with the Klamath-Siskiyou region. Consequently, if other evergreen hardwood species, such as Pacific madrone, Canyon live oak, and golden chinkapin, ultimately suffer significant mortality from SOD, the potential impacts of SOD could be large in terms of the acreage of Northern Spotted Owl habitat affected.

In the (hopefully) unlikely event that major coniferous species, such as Douglas-fir and coast redwood, prove to be seriously affected by SOD, than impacts to Northern Spotted Owl habitat could be even more dramatic and potentially extend beyond the mixed-evergreen forests of southwestern Oregon and northwestern California.

Fuel loadings and architecture associated with high levels of mortality in the hardwood component of mixed-evergreen forest stands will also increase the risk of intense wildfire if SOD causes widespread mortality of trees and shrubs.

To conclude, there currently are many uncertainties regarding the eventual impact of SOD on Northern Spotted Owl habitat. It is very likely that, at least, SOD will have significant local impacts on Northern Spotted Owl habitat with a major component of tanoak, given this species' evident vulnerability. Possible, but less likely, would be impacts on all stands with major components of madrone, chinkapin, and Canyon live oak. The worst case will be if native conifers suffer significant growth reductions or mortality from SOD.

4.7.6 ASSESSMENT OF RISK FROM NATURAL DISTURBANCE

At the time of listing a significant risk to habitat was recognized from the vulnerability some habitat had to catastrophic wildfire (*USDI 1992*; 41 and Appendix F). Especially vulnerable are the provinces in eastern Oregon and eastern Washington and some areas of the Klamath province. Several elements of the Forest Plan were designed to provide adequate resiliency to prevent isolation due to catastrophic events. Action has not been taken to significantly reduce the uncharacteristic accumulations of fuels and thus the threat of catastrophic fire. The risk to habitat has continued to increase. Management requires the must balancing of the short-term impacts of risk reduction management on the Northern Spotted Owl versus long-term risks of catastrophic losses of habitat.

Judicious thinning and partial harvest is believed to reduce the risk of habitat loss for Spotted Owls from catastrophic wildfires *(Irwin 2003). Irwin and Thomas (2002)* explore the policy conflicts of managing for long-term habitat in fire-adapted forests. They emphasize that Federal land managers must be willing to tolerate important short-term risk in restoring landscapes with altered fire (and insect and pathogen) disturbance regimes. King et al. (1997) promote the use of a mixed landscape and site-based protections to high-quality fairly continuous dispersal habitat and well-distributed nesting, roosting, and foraging habitat on a fire prone east Cascade landscape.

4.8 HABITAT DEVELOPMENT

The development of suitable Northern Spotted Owl habitat is a vital part of the long term habitat management approach of the Forest Plan. Losses of habitat typically occur in a tangible time frame, such as with harvesting or catastrophic fire; rates of habitat development on the other hand, are influenced by many variables (such as site type and disturbance history) as to make the accuracy of predictions limited.

Habitat development is an important aspect of habitat change. Management activities designed to accelerate development of new habitat are becoming an important part of forest management. Carey (2003) and Franklin et al. (2002) provide background for management and the processes that can accelerate the development of habitat. It is assumed that retention of legacy components in current areas of timber harvest will shorten the time needed for them to achieve the habitat complexity to be suitable as Northern Spotted Owl habitat.

4.8.1 EXISTING ESTIMATES OF HABITAT DEVELOPMENT

In contrast to the habitat effects due to management and natural disturbances, available existing estimates of habitat development were calculated at the regional scale rather than at the project scale. Regional estimates of habitat development were derived as a modeled projection (*USDI 1993, 2004*). Habitat removal estimates are an aggregation of smaller scale estimates from local surveys and have not been validated with field information. The USFWS (*USDI 2004:13*) contends that "given the differences in the approach, describing a net rate of habitat change would be misleading when compared with project level habitat loss estimate." We do not concur. The intention of the analysis is to scale the effects to the province scale; habitat losses are already being portrayed at that scale. These are averages to be applied over vast acreages and are consistent with the goals of the assessment.

Ideally, field-measurement or inventories should be used to track changes in suitable habitat development. Unfortunately, this lack field work has resulted in the Federal agencies using modeled age-based projection approach based on general forest inventories. Projected forest development across the range of the Northern Spotted Owl (*USDA/ USDI 1993, 2004*) are used to help evaluate the consequences of different conservation or management alternatives.

4.8.2 PREVIOUS USE OF HABITAT DEVELOPMENT ESTIMATES TO ASSES IMPACTS

Net increases in late-successional forest of 600,000 acres per decade have been included in range-wide projections of Spotted Owl habitat development (*USDI 2004*) to evaluate management alternatives. This rate represents about an 8% decadal increase in forest over 80 years of age on federal lands relative to the Forest Plan baseline. Raphael et al. (1992) used a similar rate in 1992 to model the influence of habitat changes on possible survivorship.

Existing calculations are based on forward projection (*USDI 1993, 2004*) starting with data used in development of the Forest Plan in 1994 *(Martin Raphael and Chris Cadwell, pers. comm.).* As the Forest Plan baseline assumes that mature forest conditions have the function of suitable habitat, so do estimates of habitat development. In reality, projecting the transition of a forests age and size classes to different levels of habitat function requires extensive field verification. We recognize that the accuracy of both estimates is unknown without field validation.

Validation of potential habitat development is a difficult task. In part, validation of stand development will be part of the new suitable habitat baselines developed from the Interagency Vegetation Mapping Project. Remote sensing approaches have already demonstrated value in tracking both negative and positive changes in forest cover. For example, in an analysis of forest disturbance in the Klamath-Siskiyou ecoregion, Staus et al. (2001) found that forest disturbance was somewhat offset by approximately 220,096 ha (2%) of regrowth in areas that were non-forested in 1972 but forested in 1992.

We agree that the USFWS can appropriately utilize habitat development averages. Habitat development certainly is not a mechanistic process and there is considerable variability with predictions of habitat development. The habitat complexity that most definitions project as suitable habitat develops over multiple decades and is not a threshold that is achieved with an average size class. Stand age or size does not account for the history, growing conditions, species composition, and other factors that determine the rate of habitat development. There is considerable uncertainty in the transition between mid-seral stage stands and suitable habitat. These uncertainties still exist with remote sensing information or inventory methods that are not specifically designed to sample the key components of suitable habitat. Utilizing new remote sensing approaches that better portray the 3-dimensional structure of the stand, such as LIDAR, might allow quantification of Northern Spotted Owl habitat.

Estimates of habitat development were calculated by a modeled projection of stands at the regional scale. Stands that reach the age of 80 years are assumed to become habitat. Net increases in late-successional forest (80 years or greater) were estimated by decade. The lack of more detailed stand condition information precluded alternative methods of habitat development assessment. In reality, projecting the transition of a forests age and size classes to different levels of habitat function requires extensive field verification. We recognize that the accuracy of both estimates are approximations to be used on range-wide scales.

Given the uncertainty about the rate of complex forest structure development in the 80+ year-old stands, habitat development was likely overestimated. We cannot determine the extent of overestimation. However, since many of the stands that are projected to become habitat originated after natural disturbances, it is highly plausible that the majority of the projected new habitat would function as suitable habitat when predicted, and the remainder would follow within additional projection periods.

4.9 CHANGES ON NON-FEDERAL LANDS

There have been two major changes on non-Federal lands concerning suitable habitat protection since 1990: increased state regulation and the emergence of Habitat Conservation Plans (HCPs). The USFWS proposed a special rule under section 4(d) (*USDI 1995*) for non-Federal lands. It was never finalized, and the prohibition on take remains as it was when the species was listed.

State regulations have changed considerably since 1990. In 1993, the State Forest Practices Board in Washington adopted rules that would "contribute to conserving the Northern Spotted Owl and its habitat on non-Federal lands," (*WA Forest Practices Board 1996*) and recommended roles for those lands in owl conservation (*Hanson et al. 1993*, *Buchanan et al. 1994*). Seven HCPs with owl protection provisions covering 1,952,730 acres have been approved in Washington. These plans are designed to provide the demographic support and connectivity support that are recommended in draft recovery plan (*USDI 1992b*), and provide support to the Northwest Forest Plan. *Buchanan and Swedeen (2004)* examined the current known distribution of territorial Spotted Owl centers in relation to management designation. Of the approximately 1027 owl centers known in Washington, 86% were on primarily Federal lands, about half of the owl centers on non-Federal lands are on ownerships managed under an HCP.

In 2000, the Oregon Forest Practices Act provided for protection of 70-acre owl core areas around known nest sites on State and private lands, but did not provide for protection of owl habitat beyond these areas (*ODF 2000*). In general, there has been no large-scale Northern Spotted Owl habitat protection strategy or mechanism on non-Federal lands in Oregon. The four owl-related HCPs currently in effect included 303,541 acres of land and will provide some nesting habitat and connectivity over the next few decades.

Detrich et al. (1993) documented the evolution of management planning efforts in California. In 1990, the California State Forest Practice Rules were amended to require surveys for Northern Spotted Owls in suitable habitat and to provide protection around activity centers (O*DF 2001*). Under the these rules, no timber harvesting plan can be approved if it is likely to result in incidental take of Federally-listed species, unless authorized by a Federal HCP. The California Department of Fish and Game reviewed all timber harvest plans to ensure that take was not likely to occur, and the USFWS took over that review function in 2000. Several large industrial owners operate under Northern Spotted Owl Management Plans, with concurrence by the USFWS, in which they've specified the basic measures they will undertake for owl protection. Three HCPs authorizing take of Northern Spotted Owls in California have been approved on lands covering 594,580 acres.

Since 1990, 13 Habitat Conservation Plans have been issued that address the Northern Spotted Owl and provide habitat functions across the landscape. Since implementation of the Forest Plan in 1994, the USFWS's expectations for non-Federal lands are for contributions to demographic support or to provide connectivity with Forest Plan lands by providing dispersal habitat.

Poor documentation of initial baselines for most HCPs precludes estimates of habitat modification. In addition, the implementation schedule and rate of habitat removal and development would require frequent updates. As with Federal lands, there is a time scale difference between HCPs and actions consulted on for the Forest Plan and other agencies; the term of most large-scale HCPs covers periods of 20 to 100 years (and more), whereas the term of actions on Northwest Forest Plan lands is from one to five years. For this reason, comparisons are difficult.

4.10 NON-FEDERAL LANDS CHANGE EVALUATION

Significant changes in conservation have taken place on non-Federal lands since the listing of the owl. Federal conservation efforts recognized that contributions from non-Federal lands (State, Tribal, and private) were important to the goal of achieving the owl's conservation and recovery (Thomas et al. 1990 and 1993, *USDI 1992a* and *b*). The need for non-Federal contributions in areas of special concern was reiterated in the FEMAT Report (*USDA 1993*). The specific importance of the role of non-Federal lands will vary by individual physiographic province and conditions within each province. Holthausen et al. (1995), Raphael et al. (1995), *Michaels (1996)* and Hof and Raphael (1997) discuss possible contribution of non-Federal lands to Federal Northern Spotted Owl conservation efforts. They concluded that the retention of non-Federal habitat would make a biologically significant contribution to the maintenance of the Northern Spotted Owl population on the western Olympic Peninsula in Washington State.

State Forest Practice Rules offer some level of suitable habitat protection in each state. However, timber harvest on non-Federal lands still has the potential to displace owls and affect suitable habitat. Harvest of suitable habitat has been documented in Washington State *(Buchanan, pers. comm.),* and elsewhere in unknown amounts on non-Federal lands. In general, states do not require comprehensive monitoring of Northern Spotted Owl habitat loss. Efforts are currently ongoing to attempt to estimate habitat change on non-Federal lands in Washington State.

We remain poorly informed concerning habitat trends on non-Federal lands. A recent report (*American Resource Council, 2004*) illustrates the difficulty in obtaining data that could relate to habitat change on private lands. Each state has their own accounting systems and the data once obtained require considerable interpretation in terms of the impact of treatments and the time frame in which the treatments were conducted. The USFWS examined information submitted by private entities as well as information contained in Habitat Conservation Plans and associated reports to determine if the information was sufficient to calculate a rate of change on non-Federal lands. The USFWS determined there was insufficient documentation of the habitat baseline and lack of information about habitat change to allow the estimation of habitat trends on non-Federal lands. The panel recognizes that this information is usually maintained by private landowners and may be proprietary. Future habitat trends analysis of all forested lands within the range of Northern Spotted Owl using remote sensing could provide valuable insight to the continued role of non-Federal lands in supporting conservation of owl habitat.

Habitat Conservation plans will provide a more consistent role for owl conservation on non-Federal lands and should increase confidence that continued and often increasing habitat will be a management goal on some non-Federal lands. Implementation of these HCPs will provide for owl demographic and connectivity support to lands managed under the Forest Plan. Most physiographic provinces are influenced by one of the 13 HCPs for the Northern Spotted Owl that have been issued to date, covering periods from one to 100 years. Habitat conservation plans represent a significant positive development over State Forest Practices Rules alone in terms of reduced habitat risk. In concert with the Forest Plan, HCPs offer the opportunity to develop landscape scale approaches to habitat conservation and development, rather than focusing on individual owl sites. Increased assurances of habitat maintenance and development on non-Federal lands should promote the planning and analysis of management alternative for habitat on a landscape scale as illustrated by McComb et al. (2002). We believe that HCPs should be encouraged, and the continued cooperation between the USFWS and private land owners to seek creative ways to manage habitat in working forests is a positive development since listing.

5 ASSESSMENT OF RISK

5.1 FEDERAL LANDS

Our evaluation is that the reductions of Northern Spotted Owl habitat on Federal lands since 1994 are lower than those originally anticipated by the USFWS and the Forest Plan. The Northwest Forest Plan has maintained large blocks of suitable owl habitat on federal landscapes. While some of the suitable habitat is at risk of loss or degradation from pests and fire, these risks appear consistent with historical norms. Fire risk and the forest health situations on the east side of the Cascade Range and within Klamath provinces may be exceptions.

We have considerable uncertainty about how to estimate future habitat development, but development of mature forests will undoubtedly continue to add suitable Northern Spotted Owl habitat. Conclusions about the changes in the distribution of suitable habitat are restricted to the provincial level. However, given the low rate of suitable habitat change, these province-wide estimates are adequate to assess habitat risk range-wide.

It is clear that the threat from habitat loss on Federal Lands has been reduced from the time the owl was listed. Since the adoption of the Forest Plan, habitat loss has been lower than anticipated. Our best qualitative assessment is that losses (*USDI 2004*) have been overestimated. The current methods used to assess habitat trends on federal lands have significant sources of uncontrolled and difficult-to-document bias, such as what the baseline represents in terms of functional owl habitat and the imprecise approximations of trend assessments. However, the estimated rates of suitable habitat change on federal lands are small. A precise assessment of impact to owl habitat is not possible because of uncertainty in the baseline and the quality of data available; however, the risk of reaching the wrong conclusion in terms of the scale of habitat loss is low.

The annual estimated rate of habitat development is about 8% and is perhaps another overestimate because it is difficult to predict the establishment of the key components of habitat that are believed to render it functional. For the sake of argument, if half of the estimated long term habitat development was accepted, the net change in suitable habitat range-wide would probably balance approximated losses. Inclusion of estimates of habitat development would have helped the USFWS provide perspective on their estimated suitable habitat trends. However, current estimated rates of habitat development need to be considered cautiously because the growth models used to develop those estimates have not been adequately evaluated in the field.

Given the low estimates of suitable habitat loss, the consequences of error are low. We believe that it is an acceptable risk to wait for new monitoring approaches such as the Interagency Vegetation Mapping Project to be developed.

The trends discussed in the USFWS's habitat analysis are more important than precise acreage values. The trends are consistent with range-wide expectations about effects of Forest Plan implementation. The focus in habitat assessment should turn to other emerging threats to habitat utilization (e.g. Barred Owls) and managing threats to the current reserve system (e.g. fire). Because the habitat trends databases are not spatially specific, further interpretations of the implications of habitat trends are limited. A synthesis of habitat trends in relation to spotted owl population change is not possible with the information made available to us. We are unable to make any conclusions concerning the implications of the distribution of habitat loss. However, readers should be warned that habitat losses are not evenly distributed and that range-wide averages can be deceptive. For example, range-wide trends are low, but the majority of habitat losses has occurred in a portion of the range where Northern Spotted Owls are most densely populated in the Klamath region. The interpretation of the habitat loss is complex and beyond the scope of this review, but Bond et al. (2003) suggest that at least short-term fire effects are often overestimated. See the Demography section of this report for a discussion of the possible impacts of habitat loss.

5.2 NON FEDERAL LANDS

Data are insufficient to determine the rate of change on all non-Federal lands in the last 13 years. However, two conclusions are inescapable. First, the regulatory environment has significantly changed forest management on non-Federal lands. The management of significant acreages are now under Habitat Conservation Plans and State regulations that provide for significant contribution to Northern Spotted Owl habitat.

Second, the type of harvest on non-Federal lands has resulted in a different type of habitat configuration that is often highly fragmented and generally of younger age (Richards et al. 2002, Staus et al. 2002). The influence of this landscape for the long-term conservation of the Northern Spotted Owl will be highly variable by ownership.

Monitoring habitat changes on non-Federal land does not appear to be sufficient to determine trends. This may be particularly important in Oregon where state regulations provide minimal protection of suitable habitat. The impact of habitat change on non-Federal lands needs to be interpreted in terms of efforts on Federal lands to recovery of the Northern Spotted Owl.

5.3 INFORMATION NEEDED RELATIVE TO RISK ASSESSMENT

Our current understanding of Northern Spotted Owl habitat amount and distribution is limited by data quality that will remain as long as the assessments are done on a project by project basis. We encourage developing a coordinated effort to validate all aspects of habitat trends across the range of the Northern Spotted Owl, to help validate options to encourage the coexistence of forest management and Northern Spotted owl.

We believe the persistence of the NWFP reserve system will be critical to maintaining owls and other old forest associated species. We also believe that there needs to be a concerted effort to implement strategies to reduce risk of catastrophic habitat loss, particularly n the East Cascades Province and the Klamath Province. Moreover, there is a need to understand the relationship between these risk reduction endeavors and the persistence of owls and the viability of LSRs.

Creative solutions have been perused in the efforts to reduce the risk of catastrophic loss. Historical landscape patterns and disturbance regimes can be used as a guide for landscape management. Cissel et al (1999) illustrated the use of historical fire regimes in the landscape planning on the Blue River in Oregon. Their plan compared the future forest development on an extensive reserve system and standard matrix prescriptions in the Northwest Forest Plan. Their hypothesis was that the use of historical information to guide management recognizes the dynamic and variable character of the landscape and may offer an improved ability to meet ecosystem management objectives. We would promote adaptive management where forest management programs are designed to yield learning opportunities. The design of active adaptive management should include replication in space and time, implementation of different treatment alternatives and the maintenance of untreated controls. These are all part of operational activities that will help validate options to encourage the coexistence of forest management and Northern Spotted owl habitat.

The following points are expanded on in the information needs section:

A Range-wide, spatially explicit database would make it possible to effectively track changes in forest condition from individual management activities and natural disturbance.

More information is needed on changes on non-Federal land to provide a more complete picture of habitat change within the range of the Northern Spotted Owl.

An improved ability to differentiate different types of disturbance would be valuable. Assessments of fire and insect damage are particularly problematic in terms of defining the effect on owl habitat. There appear to be considerable inaccuracies in estimates of habitat impact by fire. Improved confidence in remote sensing methodologies to describe habitat condition would be very valuable, such as Light Detection and Ranging (LIDAR). Increased emphasis on non-clearcut harvest methods may limit traditional remote sensing disturbance detection.

An improved confidence in our ability to track and validate the suitability of newly developed habitat would be very valuable.

More information on the actual impacts of Sudden Oak Death on Northern Spotted Owl habitat would be valuable.

SCIENTIFIC EVALUATION OF THE STATUS OF THE NORTHERN SPOTTED OWL

CHAPTER SEVEN

Assessment of the Potential Threat of the Northern Barred Owl

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1 INTRODUCTION

The historic range of the Barred Owl (*Strix varia*), prior to the mid 1900's was confined to eastern North America, from southeastern Canada through the eastern United States, south through eastern Mexico, and then north into some mountain ranges of western Mexico (Rignall 1973, Mazur and James 2000). For at least the past 50 years the Barred Owl has been expanding its range into southwestern Canada, northern Rockies and Pacific states where it has invaded the range of the Northern Spotted Owl (*Strix occidentalis caurina*). We do not know if this range expansion was natural or facilitated by anthropogenic habitat change. Although it is assumed that the Northern Barred Owl (*Strix varia varia*) is the subspecies now found in the Pacific Northwest based on geographic proximity, there are no studies that confirm this systematic relationship. Therefore, throughout most of this document we reference the species in general, *Strix varia*, rather than to a particular subspecies.

The U.S. Fish and Wildlife Service (USFWS) identified the Barred Owl as a potential threat to the Northern Spotted Owl in the Final Rule listing the Northern Spotted Owl as a threatened species (Federal Register 50 CFR 17, June 26, 1990:26191):

> "The Barred Owl's adaptability and aggressive nature appear to allow it to take advantage of habitat perturbations, such as those that result from habitat fragmentation, and to expand its range where it may compete with the Spotted Owl for available resources. The long-term impact to the Spotted Owl is unknown, but of considerable concern. Continued examination is warranted of the role and impact of the Barred Owl as a congeneric intruder in historical Spotted Owl range and its relationship to habitat fragmentation. The potential for interbreeding of the two species also merits concern and monitoring."

The Northern Spotted Owl Final Draft Recovery Plan (*USDI 1992:21*) stated:

> "The recent invasion of the Barred Owl into the range of the Spotted Owl (Taylor and Forsman 1976) is an example of potential competition between closely related species. Barred Owls are larger and more aggressive than Spotted Owls in interspecific interactions. They also feed on a broader range of prey, occupy a wider range of habitats, and have smaller home ranges than Spotted Owls do *(Hamer 1988).* Further, they are known to have displaced Spotted Owls from their territories…. Thus, Barred Owls are a potential competitive threat to Spotted Owls."

2 APPROACH

The USFWS initiated a five-year status review of the listing classification of the Northern Spotted Owl in 2003. One component of this review is to evaluate whether Barred Owls pose a threat to the continued existence of Northern Spotted Owls and, if so, to evaluate the magnitude of that threat. This section provides that evaluation.

A literature review of Barred Owls was conducted by a Sustainable Ecosystems Institute, Inc. (SEI) panel of experts. More than 80 articles and/or journal papers were reviewed that specifically discussed Barred Owls in North America, and many of those relate to the Barred Owl in the Pacific Northwest. This report is intended to serve as a synthesis of the best available information, including a discussion of data limitations for many of the studies, summarized from these articles. This report also examines 1) the similarities and differences between Spotted Owls and Barred Owls in terms of their physical characteristics, systematics, habitat use, food habits, behavior, and population dynamics, as well as the probable impacts facilitated by or resulting from these similarities and differences; 2) the magnitude of these impacts on Spotted Owl numbers, distribution, and reproduction; and 3) whether the Barred Owl poses a significant threat to the continued existence of the Northern Spotted Owl.

Despite the unambiguous warnings and suggestions for evaluating the impact of Barred Owls on Spotted Owls noted above in the listing decision (Anderson et al. 1990) and the draft recovery plan (USDI 1992), there have been very few studies specifically designed to evaluate the interspecific interactions between these two species. Since *Hamer's (1988)* initial work, most published studies on Barred Owls in the Pacific Northwest have been ancillary to studies being conducted on Spotted Owls. That is, scientists studying Spotted Owls have attempted to report information on Barred Owls that was collected during the course of field studies on Spotted Owls. Another important caveat on Barred Owl data concerns accuracy of detections and population estimates. Because the information on detections of Barred Owls has been collected incidental to Northern Spotted Owl surveys, the data are neither consistently collected nor consistently reported, and are usually reported in the literature either as a ratio of Barred Owls to Northern Spotted Owls or as numbers of Barred Owls detected over time. Consequently, there is a great deal of uncertainty about the Barred Owl's pattern of range expansion, its interaction and the consequences of those interactions with Spotted Owls, and the contribution of Barred Owls to the decline of Spotted Owls both in terms of direct effects (competition, predation, social harassment, hybridization) or indirect contributing effects (e.g., additional pressure on Spotted Owls in combination with habitat loss and/or lag effects associated with previous habitat loss; weather; or other factors). Despite this scientific uncertainty, some biologists are passionate in their views that Barred Owls are the most serious threat to the Spotted Owl. Yet, because of this uncertainty, it is impossible to predict with a high level of accuracy or confidence the ultimate impact of the Barred Owl on the Spotted Owl in the Pacific Northwest. However, it is apparent that Barred Owls have greatly and rapidly expanded their distribution within the range of the Northern Spotted Owl and that they have demonstrated negative interspecific interactions with the Spotted Owl. Therefore, in our concluding remarks we discuss plausible alternative scenarios regarding these interactions. Moreover, we focus on the uncertainties throughout this chapter not because we think that the Barred Owl is not a threat, but that simply documenting or claiming the Barred Owl is a major threat to the Spotted Owl is not helpful to those whose concern is to manage or conserve the Spotted Owl and its habitat. That is, a solution to such a problem requires an understanding of the mechanism involved not just that it is occurring.

The varied opinions of biologists working with owls, the presentations about Barred Owls made at the initial Northern Spotted Owl forum, and the growing literature on possible negative effects of Barred Owls on Spotted Owls allowed us to develop a series of hypotheses about the direction and magnitude of the Barred Owl's effect on the Spotted Owl. The following hypotheses represent a range of possible outcomes with respect to the Barred Owl's effect on Spotted Owl. This is not an exhaustive list of potential outcomes. This list is primarily intended to illustrate a range of potential outcomes relative to interspecific interactions. These hypotheses are listed in order of their outcome from most serious to least serious effect. Some of these are nearly equivalent (e.g., 3 and 4; 5, 6, and 7; 8 and 9) only the mechanism by which the impact occurs is different.

Our alternative hypotheses about the consequences of the Barred Owl invading the range of the Northern Spotted Owl are:

1. Barred Owls will replace the northern spotted owl throughout its range (behavioral and competitive dominance hypothesis).

2. Barred Owls will replace the northern Spotted Owl in the northern, more mesic areas of its range (moisture-dependent hypothesis).

3. Barred Owls will replace northern Spotted Owls over much of its range, but the Spotted Owl could persist in some areas with management intervention (management hypothesis).

4. Barred Owls will replace northern Spotted Owls over much of its range, but the Spotted Owl will persist in refugia (refugia hypothesis).

5. Barred Owls will replace northern Spotted Owls in the northern part of its range but the Spotted Owl will maintain a competitive advantage in habitats where its prey is abundant and diverse (specialist vs. generalist hypothesis).

6. Barred will replace Spotted Owls only where weather and habitat change have placed Spotted Owls at a competitive disadvantage (synergistic effects hypothesis).

7. Barred Owls will replace northern Spotted Owls in some habitats but not in others (habitat hypothesis based on structural elements of forest, which confer a maneuverability advantage to the smaller Spotted Owl).

8. Barred Owls and Spotted Owls will compete, with the outcome being an equilibrium favoring Barred Owls over Spotted Owls in most but not all of the present NSO habitat range (interference competition hypothesis).

9. Barred Owls will increase to a peak number, then decline or stabilize at a lower density, which will permit the continuation of Spotted Owls (dynamics hypothesis).

In the remainder of this section we first provide a brief review of coexistence patterns and interspecific relationships in other owls, both congeneric and allogeneric, in order to provide a perspective on the observed interaction between Barred and Spotted Owls in the Pacific Northwest. We then discuss actual and potential interactions between these two species in detail. Using the information developed in this section we will revisit our hypotheses at the end of the section and provide a qualitative assessment of their likelihood.

3 SYMPATRY AND COEXISTENCE IN OWLS

3.1 SYSTEMATICS, DIVERSITY, DISTRIBUTION

Owl systematics have been relatively conservative over the history of their scientific classification, although the precise relationships between owls and their putative close relatives in nightjars (Caprimulgi), parrots (Psittaci) and cuckoos (Cucculi) remain obscure (Mayr and Amadon 1951, Wetmore 1960, Sibley and Ahlquist 1990). Using DNA-DNA hybridization methods, Sibley & Ahlquist (1990) placed owls in two families (Tytonidae and Strigidae) within order Strigiformes, the latter also including owlet-nightjars (Aegothelidiae), nightjars (Caprimulgidae), and their relatives the frogmouths (Podargidae), Batrachostomidae, oilbirds (Steatornithidae), potoos (Nytibiidae), and eared-nightjars (Eurostopodidae). Earlier work often classified barn owls and typical owls as subfamilies Tytoninae and Striginae within Strigidae (Stresemann 1934, Sibley and Ahlquist 1972, Amadon and Bull 1988), but the most recent treatments, including the molecular phylogeny of Wink & Heidrich (1999) based on the cytochrome b gene, have supported segregation at the family level.

Species delineation of owls has been refined using both ear morphology and molecular/genetic information. Cryptic species with weak morphological divergence have been recognized as distinct via their acoustic repertoires (mostly in *Glaucidium* and *Otus*; König 1991a, 1991b, 1994), and these distinctions have been upheld by, and correlate well with, divergence in the molecular phylogeny (Wink and Heidrich 1999). Thus Amadon and Bull (1988) recognized 162 species in Strigidae (plus Tytoninae), Sibley and Monroe (1990) recognized 17 species in Tytonidae and 159 in Strigidae for 176 total species, and König et al. (1999) recognized 18 species in Tytonidae (*Tyto* and *Pholidus*) and 184 species in Strigidae (24 genera), or 212 total species.

Species-level radiations among owls clearly have been promoted by the fact that most owls are non-migratory, and thus form genetic discontinuities when populations are isolated. Thus many species are members of sister species complexes, and are allopatric “ ” replacements, in different parts of the superspecies’ geographic range. Further, owls readily form vicariant populations, and persist well, on continental islands formed by rising sea levels (e.g., on Indonesian islands of the Sunda Shelf, SE Asia). In all, 10 *Tyto* species and nearly one-third of the Strigidae are island endemics, and many other species are local endemics in island-like situations, such as on isolated mainland mountain ranges (König et al. 1999).

3.2 BODY SIZE PATTERNS IN COEXISTING SPECIES

Given the uncertainty about the Barred Owls' ultimate impact on Spotted Owls, in this section we examine patterns of body size in coexisting species for the purpose of understanding the potential effect of invading Barred Owls on Spotted Owls in the Pacific Northwest. Although we cite numerous published studies, these studies vary in depth and quality. Thus, it is likely that some of these relationships or inferences could change with expanded data or more rigorous data acquisition.

We examine coexistence patterns in owls from local and regional to global perspectives, with a view toward the identification of characteristics of owl species that commonly co-occur within the same habitat (syntopically). The identification of these characteristics, and generalizations produced from them, may shed some light on the potential for coexistence of barred and Spotted Owls in their area of sympatry in northwestern North America. This is an area of sympatry generated by the recent range expansion of the Barred Owl (see below).

With exceptions detailed below, most congeneric owls are separated by geographic range (allopatry), and of those with some degree of sympatry in range, many segregate by their use of different habitat types, and therefore are not syntopic. For example, the Western Screech-Owl (*Otus kennicotti*) occupies more open habitats than the sympatric Whiskered Screech-Owl (*O. trichopsis*) (Arizona) and Eastern Screech-Owl (*O. asio*) (Texas), avoiding denser habitats occupied by the congenerics (Marshall 1957, Gehlbach 1995). The Western Screech-Owl is generally segregated from flammulated owl (*O. flammeolus*) by its use of lower elevation woodland (McCallum 1994). In most cases, owls that coexist within the same habitat belong to different genera, and coexistence is apparently promoted by interspecific differences in behavior, such as hunting modes, and diet (i.e., prey selection) (Mikkola 1983, Jaksic and Carothers 1985, Johnsgard 2002). Owls share with diurnal raptors conspicuous differences in body size among coexisting species, size differences that co-vary with prey choice and perhaps also with hunting mode. Size differences among species are further accentuated by gender-based size differences within species. Reverse sexual size dimorphism is typical of owls, as it is in diurnal raptors, with females larger than males in body size (Earhart and Johnson 1970). Dunning (1993) presents male and female body mass data for 40 owl species; these include species from various geographic regions, and also a few subspecies (for a total of 46 taxa). The data set is expanded to 53 taxa with body mass data from König et al. (1999), Earhart and Johnson (1970), and Gutiérrez et al. (1995) (see Table 7.1). Females (F) average 20% ($1.202 = 10^{0.080}$ [equation allows translation to a ratio of female to male mass]) larger than males (M) over a wide range of species' size ($\log F = 0.080 + 1.002 * \log M$; $R^2 = 0.987$, $p<0.001$). The degree of the dimorphism is not dependent on absolute size in this family-wide regression analysis (1.002 is not statistically different from 1.000; p=0.878). Sexual size dimorphism has been related to territorial defense, nest site defense, the size and defense of clutch and brood, and size-related access to prey of different sizes and densities (for examples see, Lundberg 1986, Mueller 1986, for owls in general, Hakkarainen and Korpimäki 1991, Korpimäki 1986 for Boreal Owls *Aegolius funereus*, and Sunde et al. (2003) for European Tawny Owls *Strix aluco*).

Size relationships among coexisting owl species are derived from a variety of sources, some of which document specific differences in prey utilization (e.g., Korschgen and Stuart 1972), others which come from site-specific surveys, and a few which are derived from regional ornithological treatments and field guides. Body mass data for the listed species are included in Table 7.1. We present 21 data sets in Table 7.2. For a few of these species, body mass was not available from standard sources, and we estimated mass from linear body size measurements. For instance, for *Strix albitarsus* (Site S, Pakistan) body mass was computed from the linear regression of body length (L) against mass (WT) using 12 *Strix* species (males plus females) for which both variables are known. From the relation WT = -380.6 + 20.51*L (R^2 = 0.96, p<0.001), *Strix albitarsus* mass is estimated at 286g. Because we estimated body mass data for some species, most notably *S. v. sartorii* (see below), we view the inferences about size relationships between the Barred Owl and Spotted Owl as preliminary. Most coexisting owl assemblages contain either three species (*n* = 9) or four species (*n* = 8). However, the five- and six-species assemblages found in African savannah and neotropical rainforest, respectively, indicate that owl species richness mirrors the general trends of avian species richness, conspicuously high in both neotropical forests and the African savannahs relative to temperate woodlands. Log (body mass) of coexisting owl species is represented in Figure 7.1, in which male and females body sizes are averaged. Conspicuous size segregation is seen at all sites except in the two Australian habitats (Q, R), which lack small owls and differ also in that the larger *Ninox* species do not show reversed sexual dimorphism. For these reasons the Australian sites are omitted from the following analysis.

Overall, size ratios (logA/logB, where A and B are body size masses of adjacent species in a size series) tend to become smaller in assemblages with larger numbers of coexisting species: 3-species: 0.485; 4-species: 0.398; 5-species: 0.332; 6-species: 0.240. However, size ratios are not significantly different between the smaller and larger adjacent species pairs in either 3-species or 4-species assemblages, and mean size ratios do not differ significantly between 3-species (0.485 ± 0.184SD; n = 18) and 4-species assemblages (0.398 ± 0.177SD; n = 24) by t-tests (df= 34, t = 1.446, 0.2>p>0.1). Thus, in general, adjacent species in a size series differ by a factor of 3.05 in body mass in 3-species assemblages of coexisting owls, and by a factor of 2.50 in 4-species assemblages.

Most of these sets of coexisting species consist of species in different genera (as well as different body sizes); this is the case with the six species at Cocha Cashu, Peru (Terborgh et al. 1990). Site M (Andean forest, 2000-m elevation; Graves 1985) and site Q (African savannah; Voous 1966) support two *Otus* species of different sizes, and the latter also supports two *Bubo* species of different size. Roberts (1991) reports that as many as three *Otus* species may be found together in the Murree Hills of Pakistan during the summer (*O. spilocephalus*, *O. bakkamoena*, *O. sunia*). Two species of *Strix* occur at sites G (humid pine-oak, Colima; Schaldach 1963), I (Chiapas rainforest; Howell 1999), J (Guatemala rainforest; Land 1963) and K (Costa Rica rainforest; Enriquez Rocha and Rangel-Salazar 2001). Indeed, *S.virgata* and *S. nigrilineata* coexist throughout a broad range of neotropical forest (e.g., SE Nicaragua [*Cody, unpublished*]). Thus, although most congeneric species are segregated by geographic range or by habitats, in some cases congenerics coexist at the same site and contribute to local -diversity. However, coexisting congeneric species display a comparable degree of size divergence to that which characterizes coexisting species in different genera.

4 SYMPATRY AND COEXISTENCE IN THE GENUS STRIX

König et al. (1999) list 21 species in the genus *Strix*, distributed throughout Eurasia, Africa, North and South America. Most are medium to large owls, but body size varies from 175 g (male *S. butleri*, Arabian Peninsula) to 1280g (female *S. bartelsi*; Sumatra); female *Strix* exceed male mass by a factor averaging 1.28, with a tendency for this factor to increase with absolute size. There are numerous examples within the genus of sympatric species, and some of these sympatries are examined here with respect to differences in habitat use and body size.

4.1 EUROPEAN SPECIES

Three *Strix* species occur in Europe and western Asia, broadly segregated by latitude of breeding range, with *S. nebulosa* in the north, *S. aluco* in the south, and *S. uralensis* in between. All three species are sympatric in central Sweden and southern Finland: there are overall habitat differences that correspond to differences in geographic ranges, with northern *S. nebulosa* in open conifer forests, *S. uralensis* in deciduous to mixed conifer forests, and *S. aluco* in deciduous woodlands to park- and farm-lands. All feed mainly on small mammals. Mean body sizes (average male and female) are ranked 390-785-1080g, *aluco-uralensis-nebulosa* (Sweden, Finland). Thus, body size ratios are 2.01 and 1.38, the larger pair considerably smaller than the norm for coexisting owl species in general (Mikkola 1983, Vrezec 2003).

The Tawny Owl (*Strix aluco*) has expanded its breeding range north in historical times, being absent from Finland and other Scandinavian parts of its present breeding range prior to 1875 (Mikkola 1983). In Finland, territory sizes of *S. aluco* are much smaller (ca. 50 to 100 ha) than those of *S. uralensis* (ca. 450 ha); where the two occur in similar habitat, nests are generally 2 to 4 km apart (Lammin-Soila and Uusivuori 1975, in Mikkola 1983). These two species are known to engage in strongly aggressive interactions, especially when in competition for nest sites, and some degree of spatial segregation may result from this (data summarized in Mikkola 1983). The Great Grey Owl (*S. nebulosa*) is more distinct in range and habitat than the former two *Strix*, is more nomadic in following microtine cycles, less sedentary in winter, takes smaller prey, hunts somewhat more diurnally, and occupies larger breeding territories (ca. 650 ha). Predation by *S. nebulosa* on *S. uralensis* and by *S. uralensis* on *S. aluco* is known, but is apparently infrequent (Mikkola 1983).

4.2 ASIAN SPECIES

Strix ocellata and *S. selaputo* are similar in size (M/F approximate weights 690/870g), and have abutting, allopatric ranges in India and Burma-Malaysia respectively. Their combined range is shared with the larger *S. leptogrammica* (M/F weight 845/1055g). Their size difference (a factor of 1.22) is much less than in most coexisting owls, but the species with overlapping geographic ranges are segregated largely by habitat, with the latter in dense tropical forest and the former two in more open, lightly-wooded country and plantations (König et al 1999).

4.3 NEOTROPICAL SPECIES

In southeast Brazil and northeast Argentina, three *Strix* species (*S. virgata, S. hylophila*, and *S. huhula*) occur sympatrically in lowland, humid forest, but their ecologies are not well known. *S. virgata* (M/F weights 222/278 g) is smaller, but the remaining two are quite similar in size (*S. hylophila* M/F weights 302/395g; *S. huhula,* 329/411g). In northwest South America and throughout Central America, *S. virgata* and *S. nigrolineata* commonly co-occur in lowland rainforests (see above). No interactions between them, nor differences in habitat use have been recorded, but the two species have distinct diets. *S. nigrolineata* is a bat-eating specialist, and *S. virgata* eats mostly small rodents (Ibañez 1992, Gerhardt et al. 1994). Their difference in weight (by a factor of 1.78) presumably relates to hunting and diet differences, and denotes a degree of ecological segregation sufficient for their coexistence. *S. virgata* extends north into Mexico, and from Nicaragua to Chiapas overlaps in range with *S. fulvescens*, which is very much larger (by a comfortable factor of 2.29; M/F weights 506/640 g). A third *Strix* species, the Barred Owl (*S. varia*) reaches the southern limit of its range in Oaxaca, and thus is allopatric from *S. fulvescens* (which occurs to the south across the Isthmus of Tehuantepec, and with which *S. varia* was previously considered conspecific).

4.4 NORTH AMERICAN SPECIES

Strix nebulosa is holarctic in distribution, and its North American range has partial overlap with more southerly and smaller species *S. varia* and *S. occidentalis* in a way similar to its overlap in northwestern Eurasia with the more southerly and smaller *S. uralensis* and *S. aluco.* Interestingly, the size differences between the three North American *Strix* species parallel those of the European species: mean masses, north to south in western North America, are *nebulosa-varia-occidentalis* (974-717-621g). Thus, the trio is closer interspecifically in mean mass than is the European trio (1080-785-475g), since *S. aluco* is much smaller (475g) than *S. occidentalis/caurina* (610g) and *S. nebulosa* is a little larger in Europe than North America. Unlike northwestern Europe, there was until recently (see below) relatively little sympatry in the North American *Strix*, with *S. nebulosa* occupying a geographic range north of and almost completely allopatric to *S. varia*, and only marginally sympatric with *S. occidentalis* in the Cascade Range and Sierra Nevada. Note that the size difference between *S. nebulosa* and *S. occidentalis* is considerable (factor of 1.6); but beyond this, *S. nebulosa* occupies the high-elevation, more open, subalpine woodland and meadow regions of the western mountains, whereas *S. occidentalis* occurs at lower elevations and in more contiguous and dense forest and woodland (*Winter 1986*, Johnsgard 2002). *S. nebulosa* is much closer in size to *S. varia* (a factor of 1.36), but because both *S. varia* and *S. occidentalis* are species of forest and woodland in lowlands and foothills, there appears to be little in the way of potential interaction between either of the two species and *S. nebulosa*.

S. varia helveola is a comparatively large Barred Owl subspecies that extends from the lowlands north of the Isthmus of Tehuantepec along the Caribbean coast to Texas. The range continues north with contiguous subspecies *S. v. georgica* and ultimately *S. v. varia*. The Barred Owl now occurs in all Canadian provinces bordering the lower 48 states, and all but six of the contiguous states in the United States (Mazur and James 2000). The primary concern addressed by the committee is the recent sympatry of *S. varia* with the northern subspecies of Spotted Owl (*S. occidentalis caurina*) in the Pacific Northwest and south to the central Coast Province of California (i.e., the range of the Northern Spotted Owl). However, the two species are sympatric in south Central Mexico, and have presumably been sympatric there for a long period of time. There are, apparently, differences besides the presumed temporal extent of sympatry between the species in this old (southern) area versus the new (northwestern) areas of sympatry. The fourth subspecies of Barred Owl (*S. v. sartorii*) occupies mountainous areas of west central Mexico in the Sierra Madre Occidental and the transverse Eje Volcanico from Durango south through Jalisco, Nayarit, and Colima to Michoacan and Guerrero. From Michoacan north, its range overlaps that of the Mexican Spotted Owl (*S. o. lucida*), which extends from the southern Rocky Mountains south to Michoacan, thence north in the Sierra Madre Oriental. Both species are reported to occupy similar conifer and mixed woodlands, humid to semi-arid pine-oak and pine-fir, at similar elevations (1,500 to 2,500 m), although Spotted Owls may range lower (to 1,200m) (Howell and Webb 1995), however, there appear to be no published ecological studies of the Barred Owl subspecies in Mexico.

S. o. lucida is the smallest of the three Spotted Owl (*S. occidentalis*) subspecies. (M/F weights for *S. o. lucida* are 509/569g for Arizona and New Mexico birds. Specimens from the Museum of Vertebrate Zoology (Berkeley) record the masses of five male *S. o. lucida* from Chihuahua as 483g ±31.0SD, and four females as 518g ±30.3SD. Thus the trend for decreasing mass among subspecies, north to south, appears to be continued within subspecies; birds at southern end of range of *S. o. lucida*, where it contacts *S. varia*, therefore may be even smaller. On the other hand, *S. v. sartorii* is the largest of the Barred Owl subspecies, with relatively larger bill and feet. No mass data on this subspecies have been published, but lineal measurements reported by Ridgway (1914) suggest that *S. v. sartorii* may be around 1.39 larger in mass than typical *S. v. varia* (Table 7.3). If this estimate proves correct, coexisting *S. v. varia* at (estimated) M/F weights of 878/1113g (these masses are based on estimates from regression analysis), and *S. o. lucida* at M/F weights of 509/569g, would differ in mass by a factor of almost two, possibly enough to ensure the coexistence of these two southern races. This contrasts with the much more similar masses of *S. v. varia* and *S. o. caurina* in the Pacific Northwest, where the Barred Owl (*S. v. varia*) is the smallest subspecies and the Spotted Owl race (*S. o. caurina*) is the largest of its species. The results of the regression estimate is opposite to predictions based on biogeographic rule (i.e., animals decrease in size from north to south), but they are the best we have at this time because there are very few museum specimens from Mexico. The main issue is that the mass is so different not that they are not structurally bigger in southern Mexico. In the Pacific Northwest, the two differ in mass by a factor of about 17.5%, which appears too slight to permit coexistence by dint of size and size-related ecology alone. In this area it might be might expected that range differentiation would result from the evolution of habitat use differences (i.e., forest type or elevation), as is the case in similarly-sized sympatric *Strix* elsewhere.

Enríquez-Rocha et al. (1993) provided a general distributional summary of Mexican owls based on museum and literature records. Their data show sympatry, at the (political) state level, in Barred and Spotted Owls in the southern Sierra Madre Occidental and the transverse Eje Volcánico, south from Durango, San Luis Potosí, Colima, Jalisco, to Michoacan and possibly to Puebla. Within this range, it is likely that the two species co-occur also in Aguascalientes and Zacatecas, and beyond this range the two may be sympatric further north (to Sinaloa) and further south (to Guerrero), but this is difficult to confirm from the literature, and the distributions of both species might well be discontinuous in the mountains of western Mexico. There are studies on Spotted Owl within the zone of sympatry (Aguascalientes) and north of it (Chihuahua); Young et al. (1997) described the diet of Spotted Owls in pine-oak, pure pine and mixed conifer habitats in these two states, where the species eats mainly woodrats (*Neotoma* spp.), mice (various genera and species) and cottontail rabbits (*Sylvilagus floridanus*). Other studies have described roost site characteristics, in Aguascalientes (Tarango et al. 2001) and in Chihuahua (Young et al. 1998), where they roost generally in dense vegetation on steep, well-shaded north-facing slopes. However, little is known of the ecology and behavior of Barred and Spotted Owls in these regions at sites where they are know to co-occur. There is some indication from Enríquez-Rocha et al. (1993) that Barred Owls are found higher (1500-3000m) than Spotted Owls (1200-2500m), but these are range (=country) -wide limits that might not accurately reflect the degree of syntopy where the two co-occur, other than to indicate a potential for broad overlap. Clearly, far more research on Barred and Spotted Owls in their Mexican areas of sympatry and syntopy is required.

5 RANGE EXPANSION OF THE BARRED OWL

The Barred Owl has rapidly expanded its range in North America over the past 50+ years, and may now be entirely sympatric with the Northern Spotted Owl. In the early 1900s, the Barred Owl began to expand its range westward, moving into Saskatchewan (Mazur et al. 1997, Mazur et al. 1998), Alberta (Preble 1941, Oeming and Jones 1955, Boxall and Stepney 1982), British Columbia (Rand 1944, Grant 1966, Campbell 1973, Dunbar et al. 1991), Montana (Shea 1974, *Wright 1976*, Holt et al. 2001), Idaho (Wright and Hayward 1998), Washington (Reichard 1974, Leder and Walters 1980, *Hamer 1988*, *Hamer et al. 1989*, Sharp 1989), Oregon (Taylor and Forsman 1976), Alaska (Gibson and Kessel 1992), and California (Dark et al. 1998). Barred Owls were first detected in Montana in 1922 (Weydemeyer 1927), Washington in 1965 (*Rogers 1966*), Oregon in 1974 (Taylor and Forsman 1976), and California in 1981 (Evens and LeValley 1982). In less than 10 years the Barred Owl expanded its range from western Washington to northern California (Taylor and Forsman 1976, Evens and LeValley 1982).

The exact mechanisms by which Barred Owls moved westward and the factors that permitted the range expansion are unknown. It is also not clear if the expansion is a natural occurrence or human influenced. Grant (1966:44) suggested that "some barrier to its westward spread – perhaps the Rockies, but more likely some ecological barrier further east" was bridged. Other hypotheses explaining the relatively recent arrival of the Barred Owl in western North America include: 1) an increased adaptation to coniferous forests (Boxall and Stepney 1982); 2) changing climate conditions (e.g., an increase in summer rainfall and/or mean temperature), in regions outside of the Barred Owl's historical range (Johnson 1994); 3) the creation of shelterbelts, urban parks and woodlands, and riparian woodlands in the Great Plains (Dobkin 1994, Dark et al. 1998); 4) environmental changes resulting from forest management practices, specifically clearcut logging (Root and Weckstein 1994, Dark et al. 1998, König et al. 1999); and 5) a conversion from more open habitats to larger areas of closed canopy forests, as a result of fire suppression activities (Wright and Hayward 1998). Relatively little is known of the dispersal ability of Barred Owls. Five juveniles banded in Nova Scotia moved between 0.8 and 64 km (Mazur and James 2000). A single juvenile banded in another study moved approximately 994 miles (1,600 km, Mazur and James 2000), which suggests that some birds have the potential to disperse long distances.

The Barred Owl now occupies a range roughly coincident with that of the Northern Spotted Owl. Within this range, Barred Owls continue to move into new areas (Dark et al 1998, *Gremel, pers.comm. 2003*). For instance, the species is beginning to use higher elevation forests on the Olympic peninsula, having earlier colonized lower forest (*Gremel, pers. comm. 2003.*). At the edges of their current distribution there is continued expansion. For instance Barred Owls have recently colonized Marin County, California and the central Sierra Nevada. The rate of spread appears to be unequal. Most notably, the species does not appear to be expanding rapidly into interior Douglas fir forests to the east of Redwood National Park in California (*Franklin and Gutiérrez, pers. comm.*). Numbers of Barred Owls in Redwood forests monitored incidental to Spotted Owls under The Simpson Timber Company's habitat conservation plan (now Green Diamond) have also remained low (*Diller, pers. comm. 2004*). Similarly the Timber Products Company (*Farber et al. 2003*) has detected only a single Barred Owl in its California Cascades timberlands, and none on its Klamath province lands, although 388 Spotted Owls have been detected in these surveys (*Farber et al. 2003*). Again, Sierra Pacific Industries (SPI) has surveyed for owls on its lands, which extend from coastal Redwoods to the Sierra Nevada and they have only detected five Barred Owls in all these surveys (*Murphy 2003*). This finding is especially interesting in that the disturbed landscapes of industrial forests might be presumed to offer enhanced opportunities for species using early successional forests (as has been postulated for Barred Owls). However, most of their land holdings are typically in more xeric areas than the forests on the Olympic Peninsula and Cascades of Washington. In the Sierra Nevada, Barred Owl numbers are currently low, but there has been little systematic effort to survey for the species. Barred Owls detections are made incidental to Spotted Owl surveys by SPI and the U.S. Forest Service. In addition, there are four large, long-term Spotted Owl demographic studies in the Sierra Nevada which devote much more effort to Spotted Owl surveys than does SPI, and they report very few Barred Owl detections (Franklin et al. 2004, *R. J. Gutiérrez, pers. comm. 2004*). Thus, although the current number and distributional limit of Barred Owls in the Sierra Nevada are unknown, the number of Barred Owls is low, but the range is expanding (*R. J. Gutiérrez, pers. comm.*).

6 BARRED OWL DETECTION AND BIASES IN BARRED OWL DATA

Numerous studies of Spotted Owls have occurred over the past three decades. In contrast, very few studies have been conducted on the Barred Owl in the Pacific Northwest where the initial study was designed specifically to answer questions about Barred Owls. Thus, most Barred Owl population data are largely incidental encounters made during Spotted Owl surveys. Because of these facts there is an unknown bias in Barred Owl estimates of density, population levels, and trends. Spotted Owl studies are often based on detection surveys that are based on eliciting a response from an owl by imitating the species' call. With the exception of *Hamer's (1988)* study, there are no designed detection surveys for Barred Owls. Although, it is known that Barred Owls respond to Spotted Owl calls (Dunbar et al. 1991), such responses may not always occur *(Hamer 1988). Hamer (1988)* presumed that Barred Owls would be behave aggressively toward Spotted Owls because they behaved more aggressively toward humans, which is supported by some anecdotal information of species interaction. These facts confound the efficacy of using Spotted Owl calls to elicit a vocal response from a Barred Owl. In fact, we cannot estimate trends or numbers of Barred Owls from existing information. We do know that Barred Owls have increased in number and distribution over the past 50 years, and in some areas there have been substantial increases (Anthony et al. 2004). However, individual counts of Barred Owl detections are sometimes reported as cumulative detections of owls and/or nighttime detections, which both would lead to over estimates of Barred Owl numbers (e.g., Pearson and Livezey 2003, Kelly et al. 2003). On the other hand, the fact that Barred Owls are usually only detected incidental to Spotted Owl surveys suggests that Barred Owls could easily be more abundant than recognized. The problem is that we simply do not have reliable estimates of Barred Owl numbers, density, or population trends. Gross evaluation of population trends is useful in that it alerts biologists and managers of a looming problem, and help them focus on more critical questions and experimental study designs. However, even gross evaluation is quite variable across space such that in at least one area (British Columbia) the Barred Owl population may have reached its peak, areas experiencing rapid growth, areas that are showing gradual increase, and still others that have maintained low population densities for some time. Therefore, critical estimation of Barred Owl population characteristics is important if we are to understand this issue over the range of the Spotted Owl.

Barred Owls respond to Spotted Owl calls in various ways, which may have different effects on their detection rates. For example, Barred Owls may not always respond to Spotted Owl calls. In this instance, Barred Owls would be underestimated. Alternatively, unpaired Barred Owls may move among territories of Spotted Owls if they are interspecifically agonistic toward Spotted Owls, which could result in overestimates of Barred Owls in local areas. That is, Barred Owls may move among several Spotted Owl territories within a drainage and, hence, be counted more than once during surveys.

The typical vocalization of the Spotted Owls is a four-note call, whereas the Barred Owl has an eight-note call and hybrids have a five- or six-note call (Mazur and James 2000, *Pearson and Livezey*, *Presentation at Panel Meeting 2003*). Vocalizations of hybrids are very different than vocalizations of either pure Spotted Owls or pure Barred Owls (Hamer et al. 1994). *Pearson and Livezey (Presentation at Panel Meeting 2003)* also observes that Barred Owls may emit short calls in 10-15 minute intervals or only one short call before going silent. In either instance, the call may be missed or not recognized. They have a wide variety of vocalizations in addition to the standard call. Therefore, as was the case with inexperienced Spotted Owl surveyors, less experienced surveyors may not recognize Barred Owl or hybrid owl vocalizations.

Areas outside the preferred or occupied habitat of the Spotted Owl have received little attention for owl surveys of any kind, thereby restricting the availability of data on Barred Owl habitat preference and occupancy in the Pacific Northwest. Some historical sites and areas with low Spotted Owl densities are no longer surveyed (e.g., Schmidt 2003). These include but are not limited to Washington DNR, tribal land, commercial forestland, and private lands surrounding Olympic National Park (*Gremel, Presentation at Panel Meeting 2003*) and some areas in California.

Olympic National Park surveys have followed individual Spotted Owls as they move to higher elevations. When Spotted Owls are known to move to higher elevations within the "same territory," the old site center is only visited once or twice during a given season (*Gremel, pers. comm. 2003*). This may be a bias that reduces counts and trends in Barred Owls in historically occupied but now unoccupied Spotted Owl habitat because the survey effort is reduced at old sites. Carrying capacity, reasons for increase, and demographic information on Barred Owls cannot be estimated in these areas without further study.

Survey effort per territory varies greatly by study area. Information has been collected from a variety of sources with limited consistency. The use of sporadic site surveys where sites are not visited annually (for example *Pearson and Livezey, Presentation at Panel Meeting 2003*) limit our ability to determine the exact time sequence when Spotted Owls move out of a site and Barred Owls move in, and, more important, whether the Barred Owls were the direct or indirect cause of the displacement or merely incidental to the displacement. Without this knowledge, direct displacement of Spotted Owls by Barred Owls can only be assumed.

Surveying directly for Barred Owls, using Barred Owl calls, is problematic in Spotted Owl habitat due to the potential negative impact Barred Owl calls may have on Spotted Owl behavior. That is, some Spotted Owl researchers are reluctant to survey for Barred Owls because of the perceived negative effect of Barred Owl hooting on Spotted Owls. If the presence of Barred

Owls affects the response rate of Spotted Owls or perhaps causes some other negative effect, designing a suitable Barred Owl survey with an emphasis on consistent effort in areas historically and currently occupied by Spotted Owls must recognize the possibility of attendant consequences for co-occupant Spotted Owls, and these difficulties must be addressed and resolved.

In summary, counts and trends in Barred Owl detections are probably underestimates of the species' true abundance. Barred Owls may not respond to all Spotted Owl calls imitated by biologists conducting surveys. If they do respond, they may do so silently, or with sporadic responses that an inexperienced observer will miss. Most importantly, many areas where Barred Owls are potentially present are not surveyed. This includes different habitats on the same landscape, or historically occupied Spotted Owl habitat that is no longer occupied and is also not being surveyed. All these potential biases would lead to an underestimate of Barred Owl numbers.

6.1 POPULATION INCREASE OF THE BARRED OWL

Populations of the Barred Owls have increased in most areas of the northern Spotted Owls range that it has invaded. Direct estimates of density or trends over time are unavailable, because most Barred Owl detections are incidental to Spotted Owl surveys, there has been little systematic effort to document Barred Owl numbers, and Barred Owl detections are often reported as cumulative detections rather than annual detections (e.g., Pearson and Livezey 2003, Kelly et al. 2003). Given these caveats, population data and inferences about trends should be treated with caution (see Table 7.4); true Barred Owl numbers and densities could be very different than those reported in the literature or perceived by biologists. For example, *Pearson and Livezey (Presentation at panel meeting 2003), Gremel (pers. comm. 2004)* believe, but no formal estimates are available for their study areas, that Spotted Owl surveys are detecting between half and two-thirds of Barred owls present.

Barred Owl populations appear to be continually increasing almost throughout the range of the Spotted Owl (Dark et al. 1998, Wiedemeier and Horton 2000, Kelly et al. 2003), and Barred Owls are thought to now outnumber Spotted Owls in some areas (*Hamer 1988, Kuntz and Christoperson 1996*). Based on the overall numbers and distribution, populations of Barred Owls in the Pacific Northwest appear to be self-sustaining (i.e., not dependent on immigration from populations outside the range of the Northern Spotted Owl [*Biota Pacifica 2003*]). Anderson et al. (1990) provide a table showing relative densities of Spotted and Barred Owls in surveys up to that time. They concluded that at that time "detection rates of Barred Owls do not approach those of Spotted Owls except in the northern Washington Cascades and British Columbia" (Anderson et al. 1990:42)

By the mid-1980s Barred Owls were more common than Spotted Owls in British Columbia (Dunbar et al. 1991). However, some Barred Owl populations may have reached local saturation. For example, *Blackburn and Harestad (2002)* reported that both Northern Spotted

Owl and Barred Owl numbers decreased over a 10-year period (1992-2001) on one study area in southern British Columbia. This has been the only study area to reliably report a recent decline in Barred Owl detections.

Spotted Owl demography studies in Washington and Oregon have documented a steady increase in Barred Owl detections in the Olympic Peninsula and Western Washington south through the Oregon Coast and Cascade ranges since the early 1990s (Kelly et al. 2003). Trends relative to Spotted Owl numbers are discussed in section 10 below. The overall pattern may be due to rapid growth of Barred Owl populations. On the Olympic Experimental State Forest, where Wiedemeier and Horton (2000) calculated detection rates as detections per visit, Barred Owl *detection rates increased rapidly* in the period 1991 to 1999. Similarly, at the Bureau of Land Management Salem District in Northwest Oregon surveyors first detected a Barred Owl in 1985; by 2002, the total was 59 sites (*S. Hopkins, pers. comm. 2003*). Again, in southwestern Oregon, the Bureau of Land Management Coos Bay District reported Barred Owl sites increased from one known site in 1990 to 40 sites in 2001, despite greatly reduced survey efforts between 1995 and 2001; by 2002 Barred Owls were approximately one-third as common as Northern Spotted Owls (*J. Guetterman, pers. comm.*). On the southern Cascades study area of *Anthony et al. (2002)* the first Barred Owl was seen in 1981. At this study this area detections of Barred Owls in historic Spotted Owl sites increased five fold in the five years 1997 to 2002. The invasion can sometimes be quite abrupt: Zabel et al. (1996) record that the numbers of sites with Barred Owls in consecutive years at Coos Bay were 1 (1990), 0 (1991), 12 (1992) and 11 (1993). However not all sites have shown a continual increase: on the Yakama Reservation in Washington, Barred Owl numbers appeared to increase rapidly from 1991 to 1998, but thereafter appeared to have stabilized or fallen (King 2003). In another case, Barred Owls have been present for decades yet have not increased rapidly (*Franklin, pers. comm. 2004*). These observations (perhaps when fully documented) suggest that their may be several patterns of colonization by Barred Owls. If this is true (i.e., if we assume that situations where Barred Owls are present, but not expanding is not a temporary phase in the process), then the ultimate outcome of some these colonizations is not clear. Yet, the fact that there are several examples of Barred Owls increasing and Spotted Owls decreasing warrants concern about their impact on Spotted Owls.

Barred Owls were first detected in California in 1981 (Dark et al. 1998), and were seen in Redwood National and State Parks beginning in 1983 (*Schmidt, pers. comm. 2003*). By 2003, there were 32 known Barred Owl sites (Schmidt 2003), and there were 36 known Spotted Owl sites by 1995 (*Tanner 1999*, Schmidt 2003). Schmidt (2003) reported that Spotted Owl site occupancy was the lowest since *Tanner's (1999)* original surveys. Schmidt could not determine whether the low occupancy was the result of downward trend of the owl population or that surveys were inadequate to detect the birds. However, Schmidt (2003) suggested that the territories probably had been abandoned by Spotted Owls based on survey results, and in some cases probably "displaced" by Barred Owls. Of particular interest was Schmidt's (2003) Appendix B, which provided a matrix of survey results (i.e., whether or not surveys were conducted or not conducted), Spotted Owl detections, Barred Owl detections, and occupancy status of the site. We use the data in Schmidt's Appendix B to illustrate alternative ways of examining Barred Owl effects on Spotted Owls (see Appendices). These examples cannot be used to make inferences about Barred Owl effects on Spotted Owls, rather they can be used to show that the use of cumulative vs. annual number of Barred Owls, and the choice of covariates are important issues to consider when assessing similar data.

Given the inherent inaccuracies in counts of Barred Owl numbers, it is probably appropriate to treat estimates of population growth rates with caution. Nevertheless, a useful approximation for the overall population growth rate is the total number of territories identified in Oregon in combination with the spatial distribution of those territories (Kelly et al. 2003). Kelly et al. (2003) estimated there were 706 Barred Owl territories in Oregon based on 2468 detections of Barred Owls. More importantly, these territories were spread over most of western Oregon and the forested regions of northeastern Oregon. Another useful approximation of gross increase is the annual proportion of Northern Spotted Owl territories with Barred Owl detections from 1985-2003 (see Appendix D in Anthony et al. 2004). Among the 14 demographic studies, the four Washington and six Oregon study areas showed general increasing trends in the proportion of Spotted Owl territories with Barred Owl detections, while the four California study areas showed relatively low proportions, which did not appear to be increasing rapidly over time. These proportion varied in 2003 from approximately .02 (Marin study area) – 0.45 (Southern Cascades study area), and there was substantial variation in the pattern of this metric over time on these 14 study areas (Anthony et al. 2004). Consistent with these patterns for California has been the apparent lack of Barred Owl detections on industrial forest lands in California (*Murphy 2003, Diller, pers. comm. 2004*).

7 BREEDING BIOLOGY

Barred Owls have a larger range of clutch sizes than Northern Spotted Owls (1-5 vs. 1-3; Gutiérrez et al. 1995, Mazur and James 2000). However, it is not clear that they produce more young on average than Spotted Owls (i.e., are more productive than Spotted Owls in the Pacific Northwest). For example, in a study with a limited sample size in Washington, productivity ranged from 1.85 (n = 6) to 2.29 (n = 7)*(Hamer 1988).* Several pairs in *Hamer's (1988)* 3-year study produced young every year while others did not produce any young. However, these birds did produce more young than the sympatric study group of Spotted Owls. Estimates of Barred Owl *productivity* (number of young per successful nest) taken from the literature ranged from 1 to 2.4 young *per successful nest* (Mazur and James 2000) whereas estimates of *reproductive output* (number of young fledged per pair) for adult female Northern Spotted Owls averaged 0.744 (range = 0.432 -1.148; n = 9,828 broods observed on 14 study areas) young *per female in the population over all years of study regardless of breeding status* (Anthony et al. 2004). Thus, given that the recent Northern Spotted Owl meta-analysis estimate considered all adult females regardless of the year (i.e., both good and bad years included) and breeding condition of the individual, the difference in reproductive output between the two species may not be different. Like Spotted Owls, Barred Owl reproductive activity appears to be quite variable from year to year (Mazur and James 2000).

8 HOME RANGE AND HABITAT USE OF THE BARRED OWL

Barred Owls have smaller home ranges than Spotted Owls in Washington (321 - 644 ha for breeding and annual ranges, *Hamer 1988*). In the Washington Cascades, Spotted Owl home ranges east of Mt. Baker were 3.5 to 7.4 times larger than Barred Owl home ranges *(Hamer et al. 1989).* Spotted Owls in Washington also have the largest home ranges among those estimated for the various provinces inhabited by Northern Spotted Owls (range = 2060 – 4020 ha, n=23 pairs and 11 individuals; Gutiérrez et al. 1995). There are no estimates of Barred Owl home range size in Oregon where Spotted Owl home ranges vary from 520 – 2590 ha (n = 42 pairs and 19 individuals) and California where Spotted Owl home ranges vary from 370 – 1030 ha (n = 2 pairs and 48 individuals). Northern Spotted Owl home range size is significantly smaller in Oregon and California than their home ranges in Washington (Gutiérrez et al. 1995).

Barred Owls use the same habitats as Spotted Owls in addition to habitats not used by Spotted Owls *(Hamer 1988).* In several cases Barred Owls nested in the specific nest hole formerly used by Spotted Owls *(Buchanan et al. In Review).* In general, both species nested in broken-topped snags, cavities in large trees, abandoned platform nests, and on clumps of mistletoe (*Arceuthobium tsugense*) (Forsman et al. 1984, *Hamer 1988,* Devereux and Mosher 1984, Postupalsky et al. 1997).

8.1 DOUGLAS-FIR FOREST TYPE

Barred Owls occur in old deciduous forest and old mixed-wood forest in Saskatchewan (Mazur et al. 1997, Mazur et al. 1998); mixed-wood boreal forest, conifer forests, and montane forests in Alberta (Boxall and Stepney 1982); mixed stands of hardwoods and conifers in riparian areas as well as old-growth and mature conifer forest separated from riparian areas in British Columbia (Dunbar et al. 1991); low elevation mixed deciduous-coniferous forests and old-growth forests in Oregon and Washington (*Hamer 1988,* Pearson and Livezey 2003).

In British Columbia, *Blackburn and Harestad (2002:27)* found that "most Barred Owls detected during Spotted Owl surveys tend to occur along the valley bottom near riparian habitats; Spotted Owls tend to occur at the mid to upper elevation where the majority of old forest exists." In the northern Washington Cascades, *Kuntz and Christopherson (1996)* similarly found many low elevation, riparian areas were occupied by Barred Owls. However Barred Owl activity sites were also found in upland areas, and there was a complete overlap in elevation of Spotted Owl and Barred Owl sites. Similar results were shown by *Iverson (1993)* where Spotted Owl sites with Barred Owls were no different in elevation than sites without Barred Owls. In the central Washington Cascades, Barred Owl sites generally were located in moister forest, such as those along rivers, streams, and lakes, or at higher elevations with more annual rainfall than Spotted Owl sites (Herter and Hicks 2000). At Mount Rainier National Park, the elevational range of both species completely overlapped (*George and Lechleitner 1999*). Sites in the Gifford Pinchot National Forest occupied by Barred Owls averaged significantly lower in elevation and in areas with less steep slopes than Spotted Owl sites (Pearson and Livezey 2003). Similarly the spread of Barred Owls in the Olympic peninsula was initially into lower elevation, moister habitats (*Gremel, pers. comm. 2000*, *Presentation at panel meeting 2003*), but have subsequently entered higher elevation sites.

In addition to their ability to use slightly different habitats when sympatric with Spotted Owls, Barred Owls also use many areas that Spotted Owls do not use. Barred Owls throughout eastern and northwestern United States and southern Canada use a wide variety of habitats. The distribution of Barred Owls in Washington and Oregon is far broader than that of Spotted Owls, for it includes much of the forested areas of both States (*Smith et al. 1997*, Kelly et al. 2003). *Blackburn (1992)* noted that Spotted Owls were rare in British Columbia, and found only in old forest stands. By contrast, Barred Owls were common in all forest types, including both fragmented and second growth forests.

Hamer et al. (1989) found that in western Washington, on average, Barred Owl home ranges had approximately seven percent more pole stage forest (dominated by trees of 8 to 14 inches [in] dbh [20-36 centimeters (cm)], usually with one closed canopy layer and an understory with few shrubs) than did Spotted Owl home ranges; while Spotted Owl home ranges had approximately six percent more old-growth forest than Barred Owl home ranges. Even though there was little difference in the proportions of forest cover types within the home ranges of the Barred Owl and the Spotted Owl, the two species spend differing amounts of time in the various forest types. Barred Owls used old-growth and large saw timber (dominated by trees of 20 to 32 in dbh [50-80 cm], often having three canopy layers, and less down woody material than old-growth) approximately 17 percent and 13 percent of the time, respectively *(Hamer et al. 1989).* In contrast, Spotted Owls spent twice as much time in old-growth and large saw timber (44% and 20% respectively). Barred Owls were relocated a little over half of the time (53%) in pole and small saw timber (dominant trees 14-20 in [36-50 cm], having one but sometimes two canopy layers, and little or no dead woody debris). Barred Owls also were relocated in sapling and deciduous forest types three times more frequently than were Spotted Owls *(Hamer et al. 1989).* In the radio-telemetry study by *Hamer et al. (1989)*, 38% of the area within Spotted Owl home ranges (n = 10) was comprised of older stands while those of Barred Owls (n = 17) averaged 31% older stands; however, Spotted Owls spent only 31% of their time in younger stands, while Barred Owls spent 68% of their time in younger stands. *Iverson (1993)* also argued that Barred Owls were more strongly associated with second growth than with old-growth.

In the Gifford Pinchot National Forest, Spotted Owl (n = 145) and Barred Owl sites (n = 98) did not differ relative to the amount of different forest-age classes within core-circles having a radius of 0.8-kilometer (km) (0.5 miles [mi]) (Pearson and Livezey 2003). On average, core-circles of both species contained more forest at least 180 years old and less forest 50 to 79 years old than random circles (Pearson and Livezey 2003). In an area with extensive old-growth (Mt. Rainier National Park), a majority of Spotted Owl nests were in stands classified as more than 700 years old, and 70% of Spotted Owl activity centers were found in such ancient stands, with only one site in forest aged 100 to 200 years. In contrast, Barred Owls were more common (42% of activity sites) in stands less than 200 years old. Nevertheless, some Barred Owls were found in stands over 700 years in age. *George and Lechleitner* (1999) speculated that the Barred Owl would eventually invade the oldest forest stands, leading to an increase in competition. In central Idaho, nine of 10 sites occupied by Barred Owls in wilderness areas – areas without any timber harvest – were located in "upland, mature to old growth, mixed-conifer forests" (Wright and Hayward 1998:79).

Currently there are no studies specifically describing Barred Owl habitat in Oregon or California. In general, Barred Owls in Oregon are found in habitats similar to those in other states: conifer and mixed conifer forests. In California, Barred Owls are found in redwood forest and mixed conifer forest (Dark et al. 1998, *A. Franklin, R. Gutiérrez, pers. comm.*).

Several studies have suggested that Barred Owls initially colonize moister forest types, with the species spreading along river valleys and riparian areas in particular (*Pearson and Livezey, Presentation at panel meeting 2003*, *Gremel, Presentation at panel meeting 2003*). However, it is apparent that Barred Owls will also colonize drier areas (*Gaines, pers. comm.*), or higher elevation sites (Pearson and Livezey 2003, *Gremel, Presentation at panel meeting 2003*) later in the invasion sequence. It is unclear if the drier interior Douglas-fir forests of the Klamath Province will allow species coexistence: we note that dry sites on the Olympic Peninsula and Washington Cascades are considerably more mesic than are Klamath Province forests.

8.2 MIXED FOREST TYPES

In the central Cascades of Washington, Herter and Hicks (2000) found that Barred Owl sites in the far west (west of the Cascade Crest) and the far east (east of the 150-cm isopleth) contained more young forest habitat within 0.8 kilometers (km) (0.5 miles [mi]) than did Spotted Owl sites. Spotted Owl sites also contained significantly more old forest closer to the site center across the study area than did Barred Owl sites (Herter and Hicks 2000). Sympatric Barred Owls in some areas used significantly younger forest than Spotted Owls, and they nested both lower and higher in elevation than at any known Spotted Owl sites (Herter and Hicks 2000).

On both slopes of the Cascades, Barred Owl sites were located in deciduous and mixed forest stands within large river valleys, in areas not considered suitable for Spotted Owls (Herter and Hicks 2000). However, west of the 150-cm isopleth and outside of the river bottoms, Barred Owl sites were similar to Spotted Owl sites. In the drier zone of the study area (east of the 150-cm isopleth), eight of 12 Barred Owl sites were located in moister locations where the true amount of precipitation may have exceeded 150-cm isopleth, such as along river drainages, near lakes, or at higher elevations.

Buchanan et al. (In review) examined habitat characteristics around 10 Barred Owl nest sites located on the eastern slope of the Cascades in Washington from 1988 to 1994. They found that Barred Owl nest sites were "embedded within the range of the Spotted Owl, and occurred within the elevation range and forest associations used by the Spotted Owl." In general, Barred Owl nestsites were situated on flatter bottomlands, closer to water, and with a more diverse tree community (greater hardwood component) than Spotted Owls. They also found no difference in total height of canopy of dominant or intermediate trees, in the basal area of living trees, but did find significantly lower snag basal area at sites occupied by Barred Owls (mean = 6.35m^2/ha [27.6ft^2/ac]) vs. 14.6m^2/ha (63.6ft^2/ac) than those used by Spotted Owls. However, *Buchanan et al. (In review)* note that the Barred Owl population has expanded since their study, and that Barred Owls are now found in areas previously used only by Spotted Owls. Hence, it is not known if the differences seen in their study have been maintained as the Barred Owl population has grown. As with other habitat types (see above) the initial colonization of Barred Owls along water courses may lead to only a temporary segregation in habitat use between the species.

8.3 REDWOOD FORESTS

Barred Owls have been documented in the coastal redwood (*Sequoia sempervirens*) forests, Douglas-fir forests, and mixed conifer forests in California (Dark et al. 1998). In Redwood National and State Parks, the majority of the 36 Barred Owl sites documented by 2002 were in "large, unfragmented stands of old growth" (Schmidt 2003:15). Similarly, *Chinnici* (*pers. comm. 2003*) noted that the only observations of Barred Owl breeding on Pacific Lumber lands were in old-growth redwood reserves.

Schmidt (2003: 15) reported that Barred Owls used "large, unfragmented" old growth forest, but were largely absent from structurally complex older second growth (including residual stands). In contrast, *Tanner (1999)* reported that Spotted Owls used these structurally complex residual stands in Redwood National and State Parks. However, they appeared not to use second growth stands as they did on adjacent private timber lands *(Tanner 1999).*

All 12 Barred Owl nests initially described in western Washington were cavity nests (*Hamer 1988*; Leder and Walters 1980). The first nest was located in a big-leaf maple (Leder and Walters 1980) and all of the other nests located in western redcedar *(Hamer et al. 1989). Buchanan et al. (In review)* found 10 nests on the eastern slope of the Cascades in Washington in the following tree species: 3 black cottonwood, 3 Douglas-fir, 2 grand fir, 1 western hemlock and 1 western larch. Eight nests were cavities or chimney platforms, one was on dwarf mistletoe, and one was a goshawk platform. This contrasted with Spotted Owls in the same area, which predominantly used mistletoe or goshawk nests.

Given the lack of information regarding nest tree use vs. availability in the West, it cannot be determined if Barred Owls are selecting nest sites in larger trees than in other parts of their range, or if trees with suitable nest structures are larger in the West. The general pattern seems to be one of opportunistic use of nest structures (*Buchanan et al. In review*). In their eastern slope study area, *Buchanan et al*. did find that Barred Owls nested in bigger trees than did Spotted Owls in nearby areas. They attributed this to three possible causes: 1) Barred Owls were nesting in cottonwoods which are generally larger; 2) trees are generally larger in bottomlands where Barred Owls occur, and 3) cavities are more common in larger trees. Barred Owls in this area did not use trees of different age than those used by Spotted Owls.

8.4 SUMMARY OF HABITAT DIFFERENCES

Initial reports suggested that Barred Owls were more strongly associated with younger forest types than were Spotted Owls (e.g., *Hamer 1988, Iverson 1993*). However, it was reported to us that Barred Owls are often found in mature or old-growth forests (*Gremel, Presentation at panel meeting 2003, Pearson and Livezey, Presentation at panel meeting 2003,* Schmidt 2003; see also Pearson and Livezey 2003).

There are also indications that in some areas, Barred Owls initially colonize watercourses and riparian areas (i.e., moister habitats). However, it is not clear that this apparent habitat preference will be maintained in later stages of an invasion sequence. That is, once Barred Owls arrive and use moister habitats they may then spread to upland (drier) sites. On the other hand, "drier" sites on the Olympic Peninsula and Washington Cascades where this expansion of habitat use has been reported are more mesic than drier habitats that are occupied by Spotted Owls in other areas (e.g., Klamath Province). Indeed, the expansion of Spotted Owls into inland areas of the Klamath Province either may have been slowed by the unsuitably dry conditions of the interior forests and woodlands or it is still in the very early phases of colonization and may yet be followed by a rapid population increase and expanded habitat use.

Since Barred Owls are known to use a range of habitats typical of Spotted Owls, coexistence by habitat segregation will be possible primarily where Northern Spotted Owls occupy habitat outside of the preferred habitat of Barred Owls. However, two aspects of this situation remain unclear: 1) the degree to which Northern Spotted Owls will have a refuge in drier inland habitats such as the Klamath Province if they prove to be uninhabitable by Barred Owl, and 2) the degree to which both species might in fact co-occupy drier habitats, should Barred Owl invade them.

9 FOOD USE

Spotted Owls prey almost exclusively on small mammals, particularly northern flying squirrels (*Glaucomys sabrinus*), dusky-footed woodrats (*Neotoma fuscipes*), and bushy-tailed woodrats (*N. cinerea*). The dominance of these two species can vary by area, and the diet may include a larger component of other small mammals in some regions (*Forsman 2004 presentation to panel*). Nevertheless, northern Spotted Owls can be considered specialists on these medium-sized small mammals. They also occasionally prey on songbirds, small owls, and, rarely, on amphibians and insects (*Solis 1983*, Forsman et al. 1984, Carey et al. 1992, Forsman et al. 2001, Hamer et al. 2001).

On the other hand, Barred Owls have a more diverse distribution of prey taxa than do Spotted Owls. In the eastern United States, Barred Owls eat birds as large as Screech Owls (*Otus asio*), Bobwhite (*Colinus virginianus*), and Ruffed Grouse (*Bonasa umbellus*); mammals as large as opossums (*Didelphis marsupialis*) and mink (*Mustela vison*); and they also eat fish, skinks, frogs, snails, crabs, and slugs (Smith et al. 1983, Devereux and Mosher 1984, Cook 1992, Dodd and Griffey 1997). In one study in Missouri, as much as 31% of the Barred Owl's diet was crayfish (Korschgen and Stuart 1972). The winter diet of Barred Owls in Montana contained the remains of Sharp-Shinned Hawk (*Accipiter striatus*), Grey Partridge (*Perdix perdix*) and Ring-Necked Pheasant (*Phasianus colchicus*) (Marks et al. 1984), but *Microtus* made up the largest percentage of their diet (96.4% of individuals identified).

Where Spotted Owls and Barred Owls are sympatric, there is diet overlap. Hamer et al. (2001) estimated Pianka's index of dietary overlap was 76% in an area of sympathy in northern Washington. Barred Owl diets were more diverse and prey species more evenly distributed than Spotted Owl diets. Small mammals comprised 96.2% and 76.1% of the diets of Spotted Owls and Barred Owls, respectively (Hamer et al. 2001). Snowshoe hares comprised 35% of the biomass of Barred Owl diets, while flying squirrels comprised 57% of the biomass of Spotted Owl diets. Barred Owls ate many species associated with riparian and other moist habitats such as fish and frogs. They reported observations of Barred Owls perched at the edge of such habitats (Hamer et al. 2001: 225). Barred Owls also tended to take more mammals with diurnal habitats than Spotted Owls. In contrast, Spotted Owls took more prey that were arboreal and semiarboreal in habits (Hamer et al. 2001). Despite these observations, Hamer et al. (2001) concluded that the two species were food competitors based on the degree of diet overlap.

Barred Owl diets in northern Washington included significantly more diurnal prey than Spotted Owl diets (Hamer et al. 2001), suggesting that Barred owl foraging activity is distributed across an extended time period including daylight or at least crepuscular hours rather than being limited to strictly night-time hours (but see Laymon 1991, Sovern et al. 1994 for diurnal foraging in California and Northern Spotted Owls, respectively). Studies of food habits are one of the historical staples of ornithological and wildlife research. There is a plethora of spotted owl diet studies, so it is noteworthy that so few studies have been conducted on diet overlap of Barred and Spotted owls. Such investigations seem crucial to understanding the potential for competition and coexistence between these two species.

10 COMPETITION WITH AND PRESUMED DISPLACEMENT OF SPOTTED OWLS

10.1 MECHANISMS

10.1.1 INTERFERENCE AND AGGRESSION

Some surveyors have witnessed a Barred Owl physically attacking a Spotted Owl (e.g., *T. Fleming, E. Forsman, J. Mowdy, G. Stagner, and T. Snetsinger, pers. comms.*). In one instance, circumstantial evidence suggested that a Barred Owl killed a Spotted Owl (Leskiw and Gutiérrez 1998). Similarly, *Johnston (2002)* provides circumstantial evidence of predation on a juvenile Spotted Owl. Surveyors imitating Spotted Owl calls have been attacked by Barred Owls (*A. Ellingson, R. Pearson, J. St. Hilaire, pers. comm.*), which could indicate the potential for aggressive interactions between these species or the propensity for Barred Owls to defend its territory against other owls in general.

In contrast, there are few observations of a Spotted Owl aggressively chasing or physically attacking a Barred Owl, despite numerous instances of Spotted Owls attacking field biologists. However, the data on heterospecific responses, particularly Spotted Owls responding to Barred Owls may not have been detected because there are relatively few surveys conducted for Barred Owls relative to Spotted Owl surveys. In addition, there are reports of a nesting Spotted Owl pair aggressively confronting Barred Owls (*A. Ellingson, pers. comm.*), of a male Spotted Owl in a family group pursuing a Barred Owl out of an area (*George and Lechleitner 1999*), and of a Spotted Owl pair responding in an agitated manner to a Barred Owl (*P. Loschl, pers. comm.*). Although aggression from Northern Spotted Owls directed toward Barred Owls seems to be more the exception than the reverse, an experiment approach is needed to determine the direction, degree of intensity, and consequences of these interspecific interactions.

If individual Spotted Owls respond to the presence of Barred Owls by avoidance, it is possible that nest sites and habitat areas could be preempted by Barred Owls. Under these circumstances, the extent of the interaction between the species will depend on the extent of habitat overlap. Since Barred Owls occupy a wider diversity of habitat types (including nest sites) than do Spotted Owls (section 9 above) there may be some degree of separation between the two species. Similarly the relatively slow invasion of Barred Owls into second growth redwood forests and other (more xeric) habitats in northern California, suggests an alternative hypothesis that Spotted Owls are either superior competitors in some habitat types or the diversity and abundance of prey is sufficient to allow some degree of coexistence between the species (i.e., Spotted Owls may be more fit as a specialist while the Barred Owl may be more fit as a generalist). Under these scenarios, reproductive success of Spotted Owls in preferred habitats may be sufficiently high that the species could coexist in some areas.

Conversely a wider use of younger forest habitat by Barred Owls may allow this species to maintain overall high rates of population growth, even when Spotted Owls are competitively superior in certain habitat types (e.g., interior forest). Under these circumstances, the high overall productivity of Barred Owls may swamp the Spotted Owl population, even in the latter's preferred habitat types. The sequential displacement of Spotted Owls by Barred Owls on the Olympic peninsula is consistent with such a hypothetical scenario: Barred Owls initially colonized low elevation forests before moving into higher forests (displacing Spotted Owls in one area after another). It is also consistent with other alternative hypotheses (see below).

A potential additional form of interference competition between the species is the effect of interference by Barred Owls on Spotted Owl social behavior. Numerous biologists have noted anecdotally or surmised that Spotted Owls are often silent after Barred Owls have entered an area (e.g., *Hamer 1988*, Kelly et al. 2003). This could potentially limit the ability of Spotted Owls to both locate mates and defend a territory against conspecific intruders. However, this has not been tested experimentally, and it appears inconsistent with recapture rates presented in the recent meta-analysis (Anthony et al. 2004). That is, recapture rates have remained relatively constant, and, for the most part, high on all the study areas. Even on the Wenatchee and Olympic Study Areas, where there appears to be a Barred Owl effect, there does not appear to be declining recapture rates, which would be expected if Barred Owls were increasing and simultaneously interfering with or suppressing Spotted Owl response rates (see Appendix G in Anthony et al. 2004).

10.1.2 COMPETITION FOR FOOD

An alternative scenario for competition between the two species supposes that prey populations are depressed by owl presence. Barred Owls have a wider diet than Spotted Owls (Section 10) and in some areas have a smaller home range. It is possible that within this area, Barred Owls may sufficiently reduce the density of Spotted Owl prey (small mammals) that the smaller owl cannot find sufficient food for maintenance and reproduction. This scenario is plausible, given that Spotted Owl presence is thought to depress flying squirrel abundance (Carey et al. 1992) and Spotted Owl reproduction is influenced by prey abundance (Rosenberg et al. 2003). Hence, indirect competition through resource depletion of shared prey may be a factor in determining whether the two owl species can coexist. Yet, another alternative hypothesis (see list of alternative hypotheses below) could place the Spotted Owl at a competitive advantage when foraging in some forest conditions if it selects food resources in a different state (e.g., flying squirrels available for capture on the ground is the same resource but in a different state than flying squirrels available for capture in trees). That is, Spotted Owls will take prey from the canopy (arboreal hunting). While it is not known if Barred Owls and Spotted Owls have different hunting strategies in the Pacific Northwest, one study (Hamer et al. 2001) reports that Spotted Owls have a higher proportion of arboreal mammals in their diet than do sympatric Barred Owls. That is, some arboreal mammals like flying squirrels descend to feed on the ground at certain times, and may be available for capture there by either species. Thus, it is not known if the diet differences reflect differences in foraging tactics or prey selection, but this would be a useful area of scientific investigation. If the smaller size and high wing loading of the Spotted Owl confers an advantage because of greater maneuverability in dense forest, it may allow some degree of coexistence as long as complex forest structure is maintained through management. However, *Hamer (1988)* showed that wing loading is similar between the larger Barred Owl and the smaller Spotted Owl.

10.2 PRESUMED DISPLACEMENT

Northern Spotted Owls have been declining in several areas of their range over the past two decades (Anthony et al. 2004). In some areas such as the Olympic Peninsula, this decline has been dramatic. Concomitant with the decline of Spotted Owls has been a general increase in Barred Owls, again particularly in the northern part of the owl's range. These changes are correlative and do not prove causality; however, a logical and reasonable interpretation, given the potential and known extent to which the two species share habitat and food resources, and interact behaviorally, is that one change is probably causing (or at least interacting among causes) the other change. Thus, many biologists are concerned that the invasion of the barred owl is having a direct effect on the viability of the spotted owl.

At the northern edge of the range of the Northern Spotted Owl, there were four times more Barred Owl sites than Northern Spotted Owl sites in British Columbia during the late 1980s (Dunbar et al. 1991). *Blackburn and Harestad (2002)* surveyed 40 Spotted Owl sites in British Columbia that represented the presumed majority of the Canadian Spotted Owl population. Spotted Owl occupancy on these sites declined 49% from 1992 to 2001. This decline was 4.8 times the rate of decline predicted by their simulation model, based on the amount of suitable habitat, and it took place in spite of assumed adequate protection of suitable habitat within 39 of 40 sites. They concluded that unless additional management actions are implemented, the Spotted Owl "will likely be extirpated soon in Canada" (*Blackburn and Harestad 2002:19*). They estimated that, as of 2001, there were less than 50 breeding pairs of Spotted Owls in British Columbia. Interestingly, Barred Owl occupancy in the same 40 Spotted Owl sites also declined, but less than the decline in Spotted Owl occupancy *(Blackburn and Harestad 2002).* This conclusion assumes that surveys were adequate to detect the true trends or that some factor other than (or in addition to) interspecific interaction may be affecting owl trends. Furthermore, the high rate of timber harvest in British Columbia over most of the historic range of the Spotted Owl is a confounding factor in these declines because extensive habitat loss has occurred simultaneously with Barred Owl invasion.

High numbers of Barred Owl sites relative to Northern Spotted Owl sites have also been reported in the North Cascades National Park, Washington, between 1993 and 1996 (*Kuntz and Christopherson 1996*), and other Washington areas where Spotted Owl numbers have declined rapidly. Barred Owls were twice as abundant as Northern Spotted Owls in the northern Cascade Mountains east of Mt. Baker in the late 1980s *(Hamer et al. 1989),* and almost as numerous as Spotted Owls in the mid 1990s just north of Mt. Rainier (Herter and Hicks 2000). Herter and

Hicks (2000) monitored 62 Spotted Owl sites from 1991 to 1998. During that period, five sites had Barred Owls at or near site centers that were once occupied by Spotted Owls. In most of these areas, Barred Owls had been present before the Spotted Owls disappeared. By 2001, Barred Owl territories exceeded Spotted Owl territories by a ratio of 38 to 27, with 49 vacant territories (of an original 107 original Spotted Owl sites from 1995). This large number of vacant territories suggests that the rate of territory occupancy may be influenced by other factors in addition to Barred Owls. These trends continued through 2003 (*Hicks, pers. comm.*). In addition, surveyors reported apparent displacement of Spotted Owls by Barred Owls in the Naches Ranger District of the Okanogan/Wenatchee National Forest (n = 18) (*J. St. Hilaire, pers. comm.*), the Lake Wenatchee and Leavenworth Ranger Districts of the Okanogan/Wenatchee National Forest (n = 7) (*G. Roberts, pers. comm.*). These reports are consistent in their depiction of changes in owl numbers. However, it is often unclear in some unpublished reports and published papers if the numbers of Barred Owls are cumulative (i.e., annual numbers are better indicators than cumulative numbers) number of detections over time rather than identified sites or known individual Barred Owls, whether Spotted Owls are declining independently of Barred Owls, or whether nocturnal detections of Barred Owls are the same birds or different birds attracted from adjacent areas. Thus, there is uncertainty over the nature of Barred Owl population trends, and whether the changes in numbers of Barred Owls and Spotted Owls are causally related.

In the Gifford Pinchot National Forest, the percentage of Barred Owl detections (n = 403) relative to all *Strix* detections (n = 2431) increased significantly each year from 1982 to 2000 (Pearson and Livezey 2003). Pearson and Livezey (2003) studied Spotted Owls and Barred Owls in the 217,812-ha (841-square mile [mi^2]) Cowlitz Valley Ranger District from July 1978 to November 2001. Of the 129 Spotted Owl sites with at least 10 surveys during the last five years of the study, 25 (19.4%) apparently were unoccupied by Spotted Owls by 2001. There were significantly more Barred Owl sites within circles with radii of 0.8-km, 1.6-km, and 2.9-km (0.5-mi, 1.0-mi, and 1.8-mi), centered on Spotted Owl site-centers in unoccupied Spotted Owl sites, than in occupied Spotted Owl sites. Barred Owl sites were situated in areas of flatter slope and lower elevation than Spotted Owl sites, whereas occupied Spotted Owl sites were on significantly steeper slopes and were significantly higher in elevation than Barred Owl sites, and unoccupied Spotted Owl sites were not significantly different than Barred Owl sites in slope or elevation. Both species appeared to preferentially occupy older forest habitats.

On the Olympic peninsula, Wiedemeier and Horton (2000) were able to calculate per visit detection rates for both Barred and Spotted Owls at the Olympic Experimental State Forest. There was a large increase (approximately 5-fold) in Barred Owl detection rate over the period 1991 to 1999, despite inherent biases in their methods against detecting Barred Owls. At the same time, there was a decline in Spotted Owl detections, although this was not linear. By 1999, only four (12.1% occupancy) of an original 33 Spotted Owl sites were still occupied, while six (18.1% occupancy) sites were known to be occupied by Barred Owls; 23 (69.7%) sites were ‘vacant’ (i.e., had no owl detections). However, it is not entirely clear from their paper if these 23 “vacant” sites were adequately surveyed. These findings suggest, like the Redwood Park situation, that there probably are other factors influencing Spotted Owl occupancy rates in this area.

Gremel (pers.comm. 2000, 2003), working at Olympic National Park established a sequential correlation of local Barred Owl invasion and Spotted Owl decline. This is interesting because it has occurred in an area that has never been subjected to timber harvest, which suggests that either Barred Owls or some other unidentified factor (e.g., weather; see Franklin et al. 2000) may have had a role in the Spotted Owl's decline. The first record of Barred Owls in this area was in 1985, when birds (including reproductive pairs) were seen in several locations in the Park (suggesting invasion prior to 1985) (Sharp 1989). By 2003, 69% (based on cumulative numbers) of Spotted Owl sites were documented as having had Barred Owls nearby, and 20% of Spotted Owl sites had been unoccupied for five years or more (all but one of these sites had previous barred owl detections) (*Gremel, pers. comm. 2003*). These effects show no sign of attenuation – the numbers of Barred Owls detected in 2003 were 55% higher than the previous maximum count (based on annual counts). However, Gremel (2000) reported that two Spotted Owl territories that were occupied by Barred Owls (i.e., presumed displacement) were reoccupied by Spotted Owls, and in one case the original occupants of a territory were detected in an adjacent territory. These observations suggest that either displacement did not occur or that Spotted Owls will reoccupy sites if Barred Owls leave. Like most of observations of Barred Owl-Spotted Owl interaction, we are uncertain of the actual events that led to occupancy or loss of a site.

Gremel (Presentation at panel meeting 2003) examined the details of the interaction in different parts of the Olympic peninsula. He showed that Spotted Owl pair occupancy was lower when Barred Owls were present, and after Barred Owls arrived in an area. He also showed a significant movement displacement of Spotted Owls following Barred Owl detections, coupled with elevational changes on the east side of the Park. In Oregon the correlation between Spotted Owl decline and Barred Owl invasion is less clear. Spotted Owls in the Tyee (Roseburg) Study Area have been "relatively stable in 1985-2002" and "there is little evidence that the increasing presence of Barred Owls on the study area is causing the Spotted Owl population to decline" (Forsman et al. 2002:6). The 2002 annual report for the Southern Oregon Cascades (*Anthony et al. 2002*) noted that the percentage of historic Spotted Owl territories having both Spotted Owls and Barred Owls or having Barred Owls only has increased from 3.0 to 17.3%, and that additional work is needed to evaluate the effects of Barred Owls on Spotted Owls for that area. However at Crater Lake National Park, *Johnston (2002)* reported a rapid rise in Barred Owl detections following the first record in 1993, so that by 2001 Barred Owls were almost as common as Spotted Owls, which had disappeared from several eastside locations during this time period.

In Redwood National and State Parks 37 occupied Spotted Owl sites had been documented by 1995 (*Tanner 1999*, Schmidt 2003). In 2002, only 36% of the Spotted Owl sites were occupied by at least one Spotted Owl, and only 17% of the sites were occupied by a pair of Spotted Owls. Although Schmidt (2003) thought that displacement of Spotted Owls by Barred Owls was occurring, reanalysis of the data (Appendices) suggests that Spotted Owls could also have been declining independent of Barred Owl colonization. In addition, survey effort was inconsistent subsequent to *Tanner's (1999)* study (Schmidt 2003). Given the nature of the terrain, vegetation, and climate of this area surveys to protocol may not be adequate to determine occupancy of historic territories because more surveys may be needed than outlined in the protocol (*Gutiérrez, pers. comm.*).

By contrast, in areas of California, where Barred Owls have not invaded in large numbers, populations of Spotted Owls have had a mixed performance. The population inhabiting Simpson Timber land is declining, but the other three study areas have not shown a decline. Of particular interest is that the Spotted Owl populations on both Simpson Timber land and Redwood National Park have apparently declined, but one presumably has more Barred Owls than the other. This suggests that something other than Barred Owls is negatively affecting these adjacent Spotted Owl populations. *Chinnici (pers. comm. 2003)* noted that on Pacific Lumber lands occasional sightings of Barred Owls in areas has not precluded successful nesting by Spotted Owls. On Sierra Pacific lands, occupied in different areas by Northern and California Spotted Owls there have been few documented Barred Owl detections during the period 1991-2003. No Barred Owl activity centers have been documented within this region, and the few (n = 5) observations of Barred Owl responses (all in areas of Northern Spotted Owls) did not produce additional responses during follow-up surveys (*Murphy 2003*).

Kelly et al. (2003) examined the interaction and presumed displacement of Spotted Owls by Barred Owls in a series of detailed analyses. They examined the effect of Barred Owls on territory occupancy by Spotted Owls at demography study areas in Washington and Oregon (Olympic Peninsula, Cle Elum [WA Cascades] Oregon Coast Range, H. J. Andrews, and Roseburg). Barred Owl occupancy increased significantly at all five study areas, increasing linearly with time (though Kelly et al. (2003) argue that their 'data undoubtedly underestimate the total Barred Owl population in Oregon'). When Barred Owls were detected within 0.8 km (0.5 mi) of Spotted Owl territory centers, Spotted Owl occupancy was significantly less than in Spotted Owl territories where no Barred Owls were detected. However, there was no significant difference in Spotted Owl territory occupancy after Barred Owls were detected between 0.8 and 2.4 km (0.5 to 1.5 mi) – and absent within 0.8 km (0.5 mi) – of the center of the territory compared to occupancy of Spotted Owl sites where Barred Owl were not detected. Kelly et al. (2003:51) found that occupancy of Spotted Owl sites declined ($P < 0.001$) when Barred Owls were detected within 0.8 km, but that occupancy was "only marginally lower" ($P = 0.06$) if Barred Owls were located more than 0.8 km from Spotted Owl territory centers.

In the Roseburg study area *(Kelly 2001)*, 46% of Spotted Owls moved more than 0.8 km, and 39% of Spotted Owls were not relocated again in at least two years after Barred Owls were detected within 0.8 km of the territory center ($n = 28$ of 251 total Spotted Owl territories monitored). In comparison, only 21% of Spotted Owls moved more than 0.8 km and just 11% were never found again at matching territories without Barred Owl detections during the same time period. The majority of Spotted Owl territories (88%) were surveyed at least three consecutive years after the year Barred Owls were first detected. When Barred Owls were detected between 0.8 and 2.4 km (0.5 to 1.5 mi) from Spotted Owl territory centers, there was no difference in rates of Spotted Owl movements between territories with Barred Owl detections (19%) versus those without detections (16%, $n = 28$). There was also no difference in the rate of disappearance of Spotted Owls at territories with Barred Owl detections (38%) and those without detections (47%). The majority of Spotted Owl territories (79%) were surveyed at least three consecutive years after the year Barred Owls were first detected.

There are only a limited number of cases where historic Spotted Owl sites that had been occupied by Barred Owls have been subsequently reoccupied by Spotted Owls (Gremel 2000, *Hane, pers. comm., 23 July 2003*, *Gremel, pers. comm. 2003*). But such documentation is limited because once Barred Owls occupy a Spotted Owl site, that site is not always monitored by biologists (e.g., Schmidt 2003)

One important caveat must be noted. Although there is a strong overall correlation between Barred Owl increases and Spotted Owl declines, many historical Spotted Owl sites are not currently known to be occupied by either species. As noted above Wiedemeier and Horton (2000) at the Olympic Experimental State Forest noted that of 33 occupied sites, four were now occupied by Spotted Owls, six sites by Barred Owls, and 23 were "vacant." Similarly, Herter and Hicks (2000) noted that of 107 original Spotted Owl sites in the Washington Cascades, 39 were occupied by Barred Owls, but 49 were vacant. Large numbers of truly vacant sites are not to be expected if the main cause of Spotted Owl decline is Barred Owl invasion and pre-emption of suitable sites. Vacant territories might indicate that something else is causing Spotted Owl decline. Habitat loss to timber harvest is often postulated to be a major factor in Spotted Owl decline, but habitat is still present in the study areas (indeed some areas where Spotted Owls are in the worst decline, such as Olympic National Park, have never been harvested). Yet, despite the presence of habitat, neither the quality of such habitat nor the influence of potential lag effects of past habitat loss are known. Further, these results are not inconsistent with other factors that are known to negatively affect Spotted Owls. For example, Franklin et al. (2000) predicted, based on past weather data that there could be long periods of decline in a Spotted Owl population due solely to weather effects. However, there is reason to believe that Barred Owls are under-detected based on our experience with Spotted Owls prior to the employment of specific Spotted Owl survey protocols.

On balance, the data of *Kelly (2001)*, Kelly et al. (2003) and *Gremel* (2000, *Presentation at panel meeting 2003*) suggest a direct response of Spotted Owls to Barred Owl presence, but the data are not inconsistent with alternative hypotheses. Taken with the widespread negative correlation between the numbers of the two owl species, the panel feels that displacement of Spotted Owls by Barred Owls is likely occurring, but the rate and extent of this are unknown, and, further, whether this effect is exacerbated by other confounding issues is also uncertain.

10.2.1 OTHER COMPETITIVE INTERACTIONS

Most discussion of Barred Owl/ Spotted Owl interactions has focused on competition in breeding areas. However, an important component of long-term Spotted Owl conservation plans has been the provision of dispersal habitat in the matrix of forest between reserve (breeding) areas. If Barred Owls now occupy this matrix habitat, such areas may be less suitable for dispersal of young Spotted Owls, due to both direct antagonism (and possibly predation) and indirect inhibition. It is possible that Barred Owl presence may decrease the effectiveness of matrix areas as suitable dispersal corridors (see Pearson and Livezey 2003). An alternative view, and tenable under the current understanding of dispersal dynamics of Northern Spotted Owls (Turchin 1998, Forsman et al. 2002), is that Barred Owl presence in matrix habitat will promote a faster progression of dispersing Northern Spotted Owl juveniles through lower quality habitat into that of higher quality with fewer Barred Owls. Spotted Owls disperse randomly and settle in temporary home ranges while searching adjacent habitat (Turchin 1998). If Barred Owls exclude Spotted Owls, then Spotted Owls will likely spend less time in matrix habitat occupied by Barred Owls. If this were accomplished without reduced survivorship, there might be few or no negative consequences to Barred Owls occupying matrix habitat.

Another area of uncertainty is the timing of possible impacts to Spotted Owls by Barred Owls. Studies of winter ecology of Barred Owls may prove useful in terms of understanding whether Barred Owls affect winter survival of Spotted Owls. At this time there is no information on winter ecology of Barred Owls relative to Spotted Owls in the Pacific Northwest.

11 HYBRIDIZATION

Hybridization between Spotted Owls and Barred Owls has been known for many years, but has been low (Hamer et al. 1994, Dark et al. 1998). Nevertheless, there was concern among some parties at the time of listing that hybridization of Barred and Spotted Owls would eventually lead to the loss of the Spotted Owl as a distinct species in this portion of its range.

More than 50 cases of interspecific hybridization between Spotted and Barred Owls have now been documented from 1974-1999 although the extent of hybridization is not known (Hamer et al. 1994, Gutiérrez et al. 1995, Dark et al. 1998, *Kelly 2001*, Haig et al., in press b). Some occurrences of hybridization have been documented by direct observation, while others have been inferred from morphological and genetic data (Haig et al. in press b). Backcrosses have also been found to occur (Hamer et al. 1994, Gutiérrez et al. 1995, *Kelly and Forsman in press*, Haig et al., in press b) and are extremely difficult to identify by any means (except perhaps by genetic AFLP [Amplified Fragment Length Polymorphism] markers, see below). Thus, the extent of introgression is likely to be higher than the level indicated by the >50 documented cases, unless later generation backcrosses are less viable.

Even though Barred Owls and Spotted Owls are congeneric, they show significant genetic divergence based on mitochondrial Control Region sequences (> 11% sequence divergence based on the data in Barrowclough et al. 1999, 13.9% from Haig et al., in press b) and AFLP markers (Haig et al., in press b). The two species are also differentiated morphologically, both in plumage characteristics and in body size, and, to some extent, are behaviorally and ecologically distinct (Gutiérrez et al. 1995, Mazur and James 2000). Thus far, there appear to be few strong isolating mechanisms. Some directionality of hybridization by sex has been documented *(Kelly and Forsman in press).* For example, six of seven genetically confirmed cases of hybridization involved parents that were female Barred Owls and male Northern Spotted Owls (based on mtDNA haplotype of the hybrid offspring, Haig et al., in press b), and all direct observations made by Kelly et al. (2003) and *Kelly and Forsman (in press)* were male Spotted Owls mating with female Barred Owls or female hybrids. This is consistent with the pattern of reversed sexual dimorphism exhibited by these owls. Apparently the large size of male Barred Owls (about the same size as female Spotted Owls) reduces the likelihood of hybridization. In addition, while the data are limited, there appear to be no barriers to backcrossing of hybrid individuals into the parental species (Gutiérrez et al. 1995, *Kelly 2001*, Haig et al., in press b). No cases of mating between hybrid individuals are known at present.

Two field studies that have documented Barred Owl and Spotted Owl hybridization have been based on direct observation, vocalizations or morphology (Hamer et al. 1994, Kelly et al. 2003). Kelly et al. (2003) summarize the number of hybrids that have been detected during field studies or spotted owl surveys. They queried all biologists in Oregon and Washington who either worked on Spotted Owls or conducted surveys of this species. They reported 47 hybrids had been observed up to 1999. This is a relatively small number of observations considering that over 9,000 Spotted Owl banding records were examined by *Kelly and Forsman (in press)*. They also queried wildlife biologists who have made thousands of observations of Spotted Owl and their broods during routine surveys over the past 30 years *(Kelly and Forsman in press).* Thirty-one of these hybrids were F1 generation and 16 were F2 suggesting that there is some potential for viability in hybrids. Many combinations of pairings were involved that produced these hybrids, but there was never a male Barred Owl and a female Spotted Owl (Kelly et al. 2003, *Kelly and Forsman in press*). These authors also suggest that hybridization may occur primarily in areas where Barred Owls are relatively uncommon (i.e., do not have access to mates of their own species).

Because of the work by Barrowclough et al. (1999) and Haig et al. (in press b), hybrids can be detected at any generation of backcrossing. Mitochondrial DNA is useful for some diagnoses, but not all. Hence, Haig et al. (in press b) developed a suite of diagnostic AFLP markers. Using this approach they found 14 fixed or nearly fixed alternative character states between 28 putatively pure Barred and 37 putatively pure Spotted Owls sampled from throughout their respective ranges. This approach (Haig et al. in press b) has the potential to monitor the extent of hybridization and introgression between Barred and Spotted Owls, and also among Spotted Owl subspecies.

Hybridization is often more prevalent when one species is rare or limiting (Randler 2002) or when one species is a recent invader of new habitat (Randler 2002, Riley 2003). Thus, as Spotted Owls become rarer, they are probably more likely to mate with Barred Owls, especially if Barred Owls are becoming more common or established. This may already be an important growing threat in areas such as southern British Columbia where Spotted Owls are already rare and Barred Owls are well established. Some other studies suggest that in some hybrid zones (such as where California and Gambel's Quail hybridize) the two species mix randomly (Gee 2003). In such cases again, when Spotted Owls become rare, we can expect that a greater percentage of Spotted Owl individuals would mate with Barred Owls. Thus hybridization with Barred Owls, although it may not be common now, is expected to be an increasing threat for Spotted Owls as the latter become more rare. However, the rate of hybridization may be partially related to the sex ratio of owls in a population because of apparent female choice relative to reversed sexual dimorphism.

12 MANAGEMENT IMPACTS

Because Barred Owls are known to use a wide variety of forest types, including early successional habitats, some authors have suggested that timber harvest activities may favor the species. For instance, fragmentation of forest habitat may have created favorable conditions for survival and reproduction. By contrast, Spotted Owls appear to be more generally associated with old growth forest or forests that are structurally complex over a greater part of the species' range. Under such conditions, timber harvest may have increased interpolation and contact of the two species' preferred and potential habitats, leading to increased competition between the species.

An alternative hypothesis is that Barred Owls have wider breadth in habitat use in the northern part of the Northern Spotted Owl's range, and the Spotted Owl has a narrower one. But in the southern part of the Northern Spotted Owl's range, the Spotted Owl has a wider habitat breadth than does the Barred Owl. We have only anecdotal information on habitat use by Barred Owl in the southern part of its range. Under such a scenario, timber harvest may have the effect of reducing Spotted Owl habitat in some areas, leading to a competitive advantage for Barred Owls, but perhaps not in others. This scenario envisages the Spotted Owl niche as closely overlapping that of the Barred Owl, but with some notable disjunct habitat use. *Hicks et al. (2001)* have attempted to examine this hypothesis in the northern part of the range by determining the amounts of different habitat types surrounding Spotted Owl territories that either have or have not been invaded by Barred Owls. They detected no effect of surrounding habitat on the probability of replacement. Also, under the Plum Creek HCP, harvest was deferred for areas of nesting, roosting and foraging habitat around 30 productive Spotted Owl sites. After six years, only 10 sites had any Spotted Owl presence – this rate of decline is very similar to that seen at other areas where timber harvest occurred. These results suggest something other than timber harvest is influencing occupancy in this location.

However, it is unclear if forest management affects the outcome of the interaction between the two species. Alternative hypotheses are plausible, and are consistent with known facts of the species' (owl) biology. The apparent slow rate of Barred Owl invasion in some redwood areas (including industrial forests with ongoing harvest activities) may be explicable in terms of the wider use of denser, second-growth habitat by Spotted Owl or a lack of preference for such areas by Barred Owls.

It is also clear that, in some portions of the Northern Spotted Owl's range, Barred Owls are increasing and Spotted Owls are declining to some degree independently of forest management history in the area. For example, the population of Spotted Owls has decreased on both the Plum Creek Cascades HCP area (with extensive harvest) and nearby reserve areas without harvest. Similarly, Barred Owls are increasing while Spotted Owls are declining throughout the Olympic peninsula in both industrial and national forest land, but also in the National Park (in areas never harvested) (see Anthony et al. 2004 for trend information). On the Gifford Pinchot National Forest (Washington), the density and impact of Barred Owls appears higher in areas without timber harvest (Pearson and Livezey 2003).

13 UNCERTAINTIES

The greatest uncertainties associated with the actual and potential effects of the Barred Owl on the Northern Spotted Owl is that we lack accurate information on Barred Owl density, numbers, and population trends, and that we are unable to resolve with certainty whether the observed changes of Barred Owls and Spotted Owls are causal or merely correlated in opposite ways with some other, unknown, factor(s). Most Barred Owls are detected incidentally using Spotted Owl calls. There is almost no effort to systematically survey for Barred Owls. In areas where Barred Owl home ranges are much smaller than Spotted Owls (e.g., Cascades of Washington), estimates of Barred Owl abundance are probably lower than the true numbers. On the other hand, where studies have used cumulative detections of Barred Owls over time and/or night time detections, the number of Barred Owls may be overestimated.

Given such uncertainty about Barred Owl presence, numbers, and effects on Northern Spotted Owls it is difficult at this time to evaluate the exact role of Barred Owls in Spotted Owl decline. For instance, Herter and Hicks (2000) report that many historical Spotted Owl locations in the Washington Cascades are now occupied by Barred Owls, but that many other sites have no owls of either species (see also Wiedemeier and Horton 2000). Therefore, it is impossible to infer whether Barred Owls are the preeminent cause of Spotted Owl decline (if for instance, most original Spotted Owl territories are now occupied by Barred Owls), or whether some other factors are also contributing (if for instance, Barred Owls are merely utilizing sites vacated by Spotted Owls for other reasons). A complicating factor is that there may be an interaction of habitat change and Barred Owl presence which leads to loss of Spotted Owls in many areas. No studies have attempted to assess such potential interactions.

A further complication is that some biologists studying Spotted Owls believe that Spotted Owls are silent in the presence of Barred Owls. Hence, an area may be recorded as vacated by Spotted Owls, when in fact the birds are merely unresponsive to surveyors' calls. Schmidt (2003), for instance, has noted that at Redwood National Park, Spotted Owls are "increasingly difficult to locate, unresponsive or absent" but it is unclear in this case if the survey effort was sufficient to detect the birds in this heavily forested area. Evidence contradictory to this hypothesis comes from the meta-analysis, where, if this scenario were true, we would expect to observe a decline in recapture rates for banded Spotted Owls in areas where Barred Owls are increasing, but this does not seem to be the case for any study area (see Appendix G in Anthony et al. 2004).

Given the difficulties in assessing the population ecology of Barred Owls and the interaction between the two species, it is difficult to provide a definitive and accurate assessment of the role of competition. More systematic surveys for both species are sorely needed, as well as experiments on the direct and indirect interactions between the species.

14 POPULATION TRENDS OF THE SPOTTED OWL IN RELATION TO THE BARRED OWL

Throughout the range of the Northern Spotted Owl, Barred Owls now occupy many territories once occupied by Spotted Owls. Early studies indicated that although some Spotted Owls were displaced by Barred Owls, it was not regarded as a common event *(Hamer et al. 1989). Iverson (1993)* similarly indicated that the status of Spotted Owl activity centers is independent of Barred Owl presence. Anderson et al. (1990:42) felt that “throughout most of the range of the Northern Spotted Owl, the Barred Owl seems to exist as scattered pairs or individuals.” However, recent evidence suggests that these assessments no longer hold true (section 10 above), especially in terms of the extent and numbers of Barred Owls.

Plausible explanations for the Spotted Owl decline in conjunction with the Barred Owl invasion is that the Barred Owls exclude Spotted Owls, either directly through aggression by Barred Owls and avoidance by Spotted Owls, or indirectly through depletion of local prey populations. There is little evidence that hybridization has had anything other than a minor impact on Spotted Owl populations. However, there are other plausible explanations or the decline of Spotted Owls (see also threats section below).

Demographic studies of Spotted Owls have recently incorporated presence of Barred Owls as a possible factor in population trends. Anthony et al. (2004) explicitly considered the annual proportion of Spotted Owl territories with Barred Owl detections as an exploratory covariate in the analysis of Spotted Owl population trends to assess whether Barred Owl were detectable with this coarse-scale covariate. In this analysis there was little effect of Barred Owls on fecundity of Spotted Owls, although they noted that there might be some effect at the Wenatchee and Olympic demographic study areas (Anthony et al. 2004). As was discussed by the meta-analysis participants, a territory-specific Barred Owl covariate would have been a more appropriate covariate than the study area-specific covariate used, but the study area- specific Barred Owl covariate was the only one that was available at the meta-analysis workshop (Anthony et al. 2004). Iverson (2004) also reported little effect of Barred Owl presence on Spotted Owl reproduction although his results could have been influenced by small sample size, unlike the very large sample sizes of Anthony et al. (2004). They did find a negative effect of Barred Owls on survival on the Wenatchee and Olympic study areas and possibly an effect at the Cle Elum study area in both the meta-analysis of the 14 study areas and the analysis of the individual study areas (Anthony et al. 2004). *Olson et al. (in press)* found a significant (but weak) negative effect of Barred Owl presence on Spotted Owl reproductive output but not on survival at Roseburg. Their top ranked model was complex and included age effects, temporal effects, interactions between age and even-odd year (temporal) effects, precipitation effects, and the presence of Barred Owls.

Given the observed inverse correlations of some Barred Owl and Spotted Owl population trends, it is important to evaluate the relative effects of such potential interspecific competition as a cause of Spotted Owl decline, as compared to other factors such as habitat loss, as well as their interactions. Historically, much of the observed loss of old-growth habitat occurred well before Barred Owls arrived in the region. Hence there must have been substantial effects of habitat loss on Spotted Owl populations prior to the period 1965 to 1980 (when the Barred Owl arrived in western states). Evaluations of habitat loss on Spotted Owls by USFWS (e.g. listing document; 1990 status review) are probably accurate in assessing such effects as a major cause of population decline from historical levels. However, the arrival of the Barred Owl has introduced a new factor. Previous estimates of Spotted Owl demographic parameters in 1994 (Burnham et al. 1996) and 1998 (Franklin et al. 1999) have produced substantial evidence that some populations at least are in decline. Of particular concern was the 1994 meta-analysis result that there was an accelerating rate of adult female mortality over the period study for the various demographic study areas. This trend was not apparent in the 1998 meta-analysis although some populations apparently were declining. Although habitat loss is one plausible explanation for such population trends, an alternative explanation is that Barred Owl invasion has been depressing Spotted Owl survival and reproduction. Recent studies have shown strong effects (Franklin et al. 2000) and relatively weak effects (Olsen et al. in press) of some habitat conditions on Spotted Owl survival and reproduction. In demographic study areas where Barred Owls have been present the longest, and have been increasing through time, Anthony et al. (2004, see above) noted strong evidence for negative effect of Barred Owl on survival on the Olympic and Wentachee, weak evidence for a Barred Owl effect on survival on the Cle Elum, but no effect of Barred Owls on fecundity on any demographic study population. Even a low level of competition may contribute to depressed demographic parameters. Since the covariate in these analyses was a study area-wide covariate it is likely that a territory-specific Barred Owl covariate(s) could strengthen these results. Therefore, it is conceivable that Barred Owl numbers have been underestimated over the last 25 years such that the true extent of the impact of competition was also underestimated.

The general timing of the Barred Owl invasion is known, but the subsequent decline of Spotted Owls will not be easy to establish. The first detection of Barred Owls in Washington was in 1965, and they arrived on the Olympic Peninsula in 1985 *(Gremel, pers. comm. 2004).* Barred Owl responses exceeded Spotted Owl responses in the northern and central Cascades by the mid 1980's (*Bjorklund and Drummond 1987, Hamer 1988*), but Spotted Owls were still responsible for the majority of responses at this time on the Olympic Peninsula (Anthony and Cummins 1989), in SW Washington *(Irwin et al 1989)* and in Oregon *(Johnson and Meslow 1989).* Anderson et al. (1990:42) felt that at the time of listing, "detection rates of Barred Owls do not approach those of Spotted Owls except in the northern Washington Cascades and in British Columbia." In retrospect it is possible that Barred Owls were having an impact on Spotted Owl populations as early as the late 1970s (British Columbia), early 1980s (northern and central Washington Cascades) and early 1990s (southern Washington, Olympic Peninsula, Oregon).

The true impact of Barred Owls in the past will probably never be decipherable from the limited data that are available. Nevertheless, it appears that Barred Owls have probably been having a negative impact on Spotted Owls in some areas for some time. Yet, it is unclear how such competition is interacting with past habitat deterioration (including lag effects) and other factors that can affect Spotted Owl fecundity and survival (e.g., weather, see Franklin et al. 2004, Seamans et al. 2002, LaHaye et al. in press).

15 FUTURE POPULATION TRENDS AND IMPACTS

It is important to assess the likely future development of the Barred Owl invasion of western North America. This will include evaluating both the likely change in Barred Owl numbers in areas where the species is already present, and also the potential for invasion of new areas and habitats.

At almost all survey sites and most demographic study areas in Washington, the increase of Barred Owls remains strong (Anthony et al. 2004, Kelly et al. 2003). Only in British Columbia surveys have the numbers of Barred Owls shown any sign of stabilizing or even decreasing *(Blackburn and Harestad 2002).* By contrast in the Washington Cascades, on the Olympic peninsula, and in some areas of Oregon, the numbers of Barred Owls continues to increase rapidly. Associated with such population increases are movements of Barred Owls into some habitats, such as high elevation sites, that were considered potential refugia for Spotted Owls. Hence we believe that the Barred Owl invasion has probably not reached its peak over most of the Northern Spotted Owl's range, and that there are no grounds for optimistic views suggesting that Barred Owl impacts on Northern Spotted Owl have been already fully realized.

In a few areas, most notably some redwood forests, the Klamath province and the California Cascades and Sierra Nevada in northern California, Barred Owls have not yet invaded in large numbers. Barred Owls are present in these areas at low numbers; hence there is nothing to suggest that the habitat is unsuitable or that the species has not reached the locations. It is possible that Spotted Owls will be able to maintain their viability in spite of the Barred Owl invasion in such habitats (see section above); alternatively the current low densities of Barred Owls may be nothing more than a historical accident or temporal lag, soon to be swamped by rapid population growth, higher density, wider habitat use. The history of the Barred Owl invasion elsewhere is consistent with the latter hypothesis: Barred Owls were initially thought to exist "throughout the range of the Northern Spotted Owl…. as scattered pairs or individuals" (Anderson et al. 1990:42), but have increased rapidly in the last decade. We have no means of distinguishing between alternate scenarios, which carry different risks for Spotted Owl conservation.

Peterson and Robins (2003) recently developed a predictive model on the geographic spread of Barred Owls, based on general habitat variables from throughout the species' United States range. The prediction of these models, based purely on habitat characteristics and without consideration of other potential factors (such as prey, predators, competitors, etc.), is that Barred Owls will continue to spread and will essentially extend throughout the original range of the Northern Spotted Owl (which had already occurred well before model construction). However, the model predicted that Barred Owls will not continue to spread very far south into the range of the California Spotted Owl.

Current conservation plans for the Northern Spotted Owl include substantial forest reserves, separated by matrix habitat (suitable for dispersal and some breeding) and non-federal lands (which also have some roles as breeding and dispersal habitats). Invasion of protected reserves (such as the Olympic National Park area) by Barred Owls may lead to the loss of some conservation function of the reserve network. Schmidt (2003) reported a decline of Spotted Owls in one such reserve, leading her to question the effectiveness of the reserve in contributing to recovery (but see comments in several places above). Similarly, *George and Lechleitner* (1999) consider that the Barred Owl invasion of Spotted Owl habitat at Mount Rainier National Park reduces the likelihood that these lands will serve as a source of Spotted Owl recruits for the surrounding National Forest LSR (Late Successional Reserve). Pearson and Livezey (2003) establish that in at least one important Spotted Owl conservation area (Gifford Pinchot National Forest), the density of Barred Owls was highest in LSRs and other reserve areas and lower in areas subject to harvest. If late successional reserves fail to protect breeding populations of Spotted Owls, then the overall conservation strategy for the species is based on an untenable premise and may similarly fail (unless the LSRs are not optimal habitat for Spotted Owls; see Franklin et al. 2000). We note here that the National Parks within the range of the Spotted Owl were not established to conserve Spotted Owls, but rather were delineated as reserves that represented a variety of unique plant and animal communities and geologic features. Similarly, the function of LSRs under the Northwest Forest Plan was much broader than Spotted Owl conservation.

16 ASSESSMENT OF THREAT

The USFWS, when listing the Northern Spotted Owl as threatened, recognized the Barred Owl as a potential threat to the viability of the Spotted Owl. Similarly, the 1990 status review and subsequent conservation plans also have acknowledged that Barred Owls could have an increasing negative impact on Spotted Owl populations. This prediction appears to have been borne out in some areas. While the evidence for a negative effect of Barred Owls is clearly correlational, we believe the Barred Owl is having a substantial effect on the Spotted Owl in some areas because of the preponderance of circumstantial and anecdotal information.

In our evaluation, the Barred Owl currently constitutes a significantly greater threat to the Northern Spotted Owl than originally envisaged at the time of listing. While there are some areas and habitats that are not yet occupied by Barred Owls, this may not continue to be the case. Nevertheless, there is substantial uncertainty associated with the effect of Barred Owls on Spotted Owls. Because of this uncertainty, we briefly summarize our current understanding and assess the uncertainties discussed in this section.

Barred Owls have colonized essentially the entire range of the Northern Spotted Owl and they have done so rapidly. The Barred Owl is larger and apparently more aggressive in heterospecific interactions than the spotted owl, which has led many biologists to believe that Barred Owls may be able to displace Spotted Owls. It also uses more habitats and has a more broad prey selection than Spotted Owls. Further, the difference in mass between the two *Strix* species may not be sufficient to preclude competition between them, which could possibly lead to competitive exclusion. On the other hand, we do not know in detail, or with any degree of precision, the rate of Barred Owl range expansion, the magnitude of the increase of population density, or of the rate of colonization of different forest types. The widespread presumption that the Barred Owl is replacing the Spotted Owl on a large scale is confounded by potential effects of habitat change (such as cumulative or lag effects associated with historic changes or reduction in habitat quality) and by year-to-year weather effects on Spotted Owl population trends via reduced reproduction, and adult or juvenile survival. Evidence suggests that the Barred Owl is having a negative effect on Northern Spotted Owl in some areas, but in other areas the Barred Owl has not had an effect because either the conditions are not entirely suitable for its occupation or it has yet to increase to sufficient density to have an impact on the Spotted Owl. It will be critical to monitor areas where Barred Owls are currently low in numbers because if they increase in these areas, and Spotted Owls subsequently decline, it will provide additional evidence supporting an effect. Therefore, we cannot be certain of the ultimate outcome of the interspecific interactions between of the two species. Here we return to the alternative hypotheses presented in the introduction of this chapter concerning the potential outcome of Barred Owl-Spotted Owl interactions. Although all of these are more or less feasible with our current state of knowledge and understanding, we reorganize them under three categories of likelihood given the information presented in this chapter. These three categories are: 1) *clearly plausible* given the increase in number and distribution of Barred Owls and their interactions with Spotted Owl; 2) *plausible* given the ambiguous nature of the spread of Barred Owls and their interaction with Spotted Owls; and 3) *not plausible or not clear* given the patterns of Barred Owl expansion and general ecology. We chose not to rank these hypotheses numerically in terms of their plausibility for two reasons: 1) the data are unclear in some critical areas, and 2) there was disagreement among the panel members about which of these was more likely (see Chapter 10 for questionnaire of panel members). These hypotheses are:

16.1 CLEARLY PLAUSIBLE

Alternative Hypothesis 1: Barred Owls will replace the Northern Spotted Owl throughout its range (behavioral and competitive dominance hypothesis). A failure to reject this hypothesis clearly confers the most serious risk to the Northern Spotted Owl. The panel was in disagreement about the likelihood of this outcome. The evidence in favor of this hypothesis was both theoretical and observational (empirical). A position favoring this outcome is based on the theoretical prediction that the similarity in morphology, diet, and feeding habits of these two species will lead to strong competition if not competitive exclusion. In addition, there is no indication at this time, based on field observations from the northern part of the range, that Barred Owls are limited to specific habitats; 1) that they appear to be increasing across most of the range, 2) that they occasionally hybridize with Spotted Owls, and 3) that there are anecdotal observations that Barred Owls are behaviorally dominant to Spotted Owls. A position not favoring this outcome is based on the lack of information about the process of (or lack thereof) presumed displacement of Spotted Owls by Barred Owls, a lack of knowledge about the synergistic effects of weather, past habitat loss, and Barred Owls on loss of Spotted Owls, the lack of increase in Barred Owls in the southern part of the range, and the anecdotal data that Barred Owls might be stabilizing in number in some northern areas of the range. In addition, there are no explicitly designed studies of interspecific interactions, displacement probabilities, trends and abundance estimates of Barred Owls, diet similarity in all areas of sympatry, physiological tolerances of Barred Owls, and detailed mode of foraging of either species (such information could be key to predicting the strength of the Barred Owl threat). Moreover, much of the data we have concerning Barred Owls effects on Spotted Owls are confounded statistically. All of the former favoring categories bode poorly for Spotted Owls, while all of the latter suggest that Spotted Owls might be capable of neutralizing the competition in certain habitats or parts of its range.

Alternative Hypothesis 2: Barred Owls will replace the Northern Spotted Owl in the northern, more mesic areas of its range (moisture-dependent hypothesis). This alternative has support from the panel because the pattern of Spotted Owl decline is strongest in the northern part of the range and less in the south. However, the panel recognized that this difference could simply be due to the phase of colonization in more southern areas.

Alternative Hypothesis 3: Barred Owls and Northern Spotted Owls will compete, with the outcome being an equilibrium favoring Barred Owls over Spotted Owls in most but not all of the present NSO habitat range (quasi-balanced competition hypothesis). This alternative has support from the panel as a viable hypothesis because such situations have occurred in other species.

16.2 PLAUSIBLE

Alternative Hypothesis 5: The Barred Owl will replace the Northern Spotted Owl over much of its range, but the Spotted Owl will persist in some areas with management intervention (management hypothesis).

If Alternative Hypothesis 1 appears to be a reality, Northern Spotted Owls could very likely be maintained in limited areas by control of Barred Owls. This would be particularly true in areas that are isolated or otherwise “defensible” (e.g., National and State Parks in Marin County, California).

Alternative Hypothesis 6: Barred Owls will replace the Northern Spotted Owls in the northern part of its range but the Spotted Owl will maintain a competitive advantage in habitats where its prey is abundant and diverse (specialist vs. generalist hypothesis). This alternative could be explored by defined studies investigating key areas of uncertainty, but is not implausible given the specialist nature of the Spotted Owl, and its rather limited prey base in the northern part of its range. Limited evidence on food habits suggests that there may be some food partitioning occurring, at least in the northern part of its range where Spotted Owls take more arboreal mammals than do sympatric Barred Owls.

16.3 NOT PLAUSIBLE OR NOT CLEAR

Alternative Hypothesis 4: Barred Owls will replace the Northern Spotted Owl over much of its range, but the Spotted Owl will persist in refugia (refugia hypothesis). This alternative is unlikely because should Barred Owls effectively colonize all the range of the Spotted Owl, no refugia are conceived that could allow persistence of Spotted Owls without some Barred Owl presence or interference.

Alternative Hypothesis 7: Barred Owls will replace the Northern Spotted Owl in some habitats but not in others (habitat hypothesis based on structural elements of forest, which confer a maneuverability advantage to the smaller Spotted Owl). Although this alternative is not entirely implausible given the ability of Spotted Owls to inhabit some very dense habitats (e.g., second-growth redwood forests, complex structured mixed conifer forests of the Klamath Mountains), the similarity in wing loading between the two species suggests that Spotted Owls may not have greater maneuverability that Barred Owls.

Alternative Hypothesis 8: Barred Owls will increase to a peak number, then decline or stabilize at a lower density, which will permit the continuation of Spotted Owls (dynamics hypothesis). This alternative is not clear given the anecdotal evidence that this may be occurring in at least one area (but the data are not extensive), and this pattern has been seen in other invasive species.

Alternative Hypothesis 9: Barred Owls will replace the Northern Spotted Owl only where weather and habitat perturbations have placed Spotted Owls at a competitive disadvantage (synergistic effects hypothesis). This alternative is not inconsistent with the current state of Barred Owl expansion and Spotted Owl ecology (they are known to be negatively affected by weather and habitat loss), where northern areas that have had significant past habitat loss and poor weather show the primary Barred Owl effects.

As noted above, most studies of Barred Owls in the Pacific Northwest have been ancillary to studies of Spotted Owls. While conducting such studies in addition to their required research and other duties is a credit to the biologists involved, there are many gaps in our understanding both of Barred Owl biology and the nature of interspecific interactions between Barred and Spotted Owls. However, unlike many facets of Spotted Owl research, some of the questions expressed as hypotheses above are amenable to experimental evaluation. Thus, while we are convinced that Barred Owls are having a negative impact on Spotted Owls at least in some areas, the extent of this impact and its ultimate outcome is uncertain.

17 TABLES

TABLE 7.1

Table 7.1. Body mass (in grams and rounded to the nearest gram) data for owl species. Most data are taken from Dunning (1993), which citation is used rather than the original source of the data. Other sources listed are Earhart & Johnson (1970), Konig et al (1999), and Gutiérrez et al. (1995). Some data are approximate (e.g., due to small sample sizes--see numbers in parentheses), others are extrapolated from linear measurements of near relatives. See text for additional explanation.

Species	Male (n)	Female (n)	M-F mean, or unsexed	Region	Source
Tyto alba pratincola	495 (33)	568 (41)	531	Utah	Dunning
Tyto novaehollandiae	545	673	609	Australia	Dunning
Tyto soumagnei	323?	435	379*	Madagascar	K,W&B
Tyto tenebricosa	600	875	737	Australia	Dunning
Aegolius acadicus acadicus	75 (27)	91 (18)	83	N, W N America	Dunning
Aegolius funereus funereus	101 (74)	167 (96)	134	Germany	Dunning
Aegolius funereus richardsoni	101 (5)	139 (4)	120	N America	E&J
Asio clamator	341 (2)	459 (3)	400	Surinam	Dunning
Asio flammeus flammeus	315 (20)	378 (27)	346	N America	Dunning
Asio madagascariensis	estimated from *Asio* spp:		700*	Madagascar	K,W&B
Asio otus wilsonianus	245 (38)	279 (28)	262	N America	Dunning
Asio stygius			675*	C, S America	K,W&B
Athene cunicularia	151 (15)	159 (31)	155	SW USA	Dunning
Bubo africanus	585	685	635	Africa	Dunning
Bubo bubo	2380 (14)	2992 (12)	2686	Norway	Dunning
Bubo capensis	929 (4)	1347 (3)	1138	S Africa	Dunning
Bubo lacteus	1704 (4)	2625 (6)	2165	Africa	Dunning
Bubo leucostictus	511 (2)	555 (3)	533	Africa	Dunning
Bubo poensis	575 (1)	746 (4)	661	Africa	Dunning
Bubo virginianus pacificus	992 (26)	1312 (23)	1152	California	E&J
Bubo virginianus virginianus	1318 (22)	1769 (29)	1549	Midwest	Dunning
Bubo virginianus pallescens	914 (18)	1142 (12)	1028	SW N America	Dunning
Glaucidium brodiei	52 (2)	63 (1)	58	India	Dunning
Glaucidium (gnoma) californicum	61 (42)	73 (10)	67	California	Dunning
Glaucidium cuculoides	164 (2)		150-176	India	Dunning,K,W&B
Glaucidium gnoma			55-64	NW Mexico	K,W&B
Glaucidium griseiceps	49-51		56*	S Mexico	K,W&B
Glaucidium jardinii			60 (4)	Peru	Dunning
Glaucidium (minutissimum) hardyi	59 (2)		62*	Peru	K,W&B
Glaucidium nanum	61 (8)	80 (8)	70	S America	Dunning
Glaucidium perlatum	69 (12)	91 (13)	80	Africa	Dunning
Glaucidium (brasilianum) ridgwayi	61 (29)	75 (16)	68	SW USA, W Mexico	Dunning
Glaucidium siju siju	55 (3)	70 (2)	62	Cuba	Dunning
Glaucidium siju vittatum	66 (2)	87 (6)	76	Isle of Pines	Dunning
Glaucidium tephronotum			87 (10)	Africa	Dunning
Gymnoglaux lawrencei	from *Otus* relatives:		124*	Cuba	K,W&B
Micrathene whitneyi			41 (20)	Arizona	Dunning
Ninox connivens			462	Australia	Dunning
Ninox rufa	1150-1300	700-1020	1043	Australia	Dunning
Ninox strenua	1130-1700	1050-1600	1370	SE Australia	Dunning
Lophostrix cristatus	468 (2)	620 (1)	544	Mex., Peru	Dunning
Otus albogularis			185*	Peru	K,W&B

Otus asio naevius	167 (31)	194 (66)	180	Ohio, USA	Dunning
Otus atricapillus	170 (7)	190 (8)	180	Brasil	Dunning
Otus bakkamoena everetti	125 (4)	152 (3)	138	India	Dunning
Otus bakkamoena lettia	108 (3)	142 (4)	125	India	Dunning
Otus clarki	135 (3)	186 (1)	160	C America	Dunning
Otus flammeolus	53 ((56)	57 (9)	55	N America	Dunning
Otus guatemalae			107 (9)	C. America	Dunning
Otus ingens	151 (3)	196 (2)	173	Peru	Dunning
Otus kennicotti (cineraceus) aikeni	111 (35)	123 (18)	117	SW USA	Dunning
Otus kennicotti kennicotti	153 (14)	187 (11)	170	NW N America	Dunning
Otus kennicotti (quercinus) bendirei	134 (26)	152 (10)	143	California	Dunning
Otus (Ptilopsis) leucotis			204 (16)	Africa	Dunning
Otus marshalli			115*	Peru	K,W&B
Otus roboratus roboratus	144 (7)	162 (3)	153	Peru	Dunning
Otus rutilus	87-107	112-116	102	Madagascar	K,W&B
Otus scops scops			92 (169)	France	Dunning
Otus senegalensis			46-62	Africa	K,W&B
Otus spilocephalus			67 (16)	Malaysia	Dunning
Otus trichopsis trichopsis	84 (23)	92 (8)	88	C Mexico	Dunning
Otus watsoni	117 (4)	134 (2)	125	Brasil	Dunning
Pulsatrix perspicillata			873 (13)	C, S America	Dunning
Scotopelia ussheri	743 (1)	834	789	Africa	Dunning
Strix albitarsus	From *Strix* relatives:		286*	S America	
Strix aluco	426 (11)	524 (7)	475	Italy	Dunning
Strix aluco			390	Norway	RJGutiérrez
Strix aluco			261	Asia, Spain	RJGutiérrez
Strix huhula			370	Peru	Dunning
Strix hylophila	302 (2)	395 (1)	349	Brasil	Dunning
Strix nebulosa	789 (17)	1159 (21)	974	W Europe	Dunning
Strix nigrolineata			446 (5)	C America	Dunning
Strix occidendalis caurina	579 (68)	663 (65)	621	NW USA	G,F&L
Strix occidendalis occidentalis	556 (218)	646 (195)	601	California	G,F&L
Strix occidendalis lucida	509 (68)	569 (68)	538	S USA, Mexico	G,F&L
Strix uralensis macroura	706 (40)	863 (57)	785	Romania	Dunning
Strix varia varia	632 (20)	801 (24)	716	N, E USA	E&J
Strix varia sartori					
Strix virgata			250 (8)	C, S America	Dunning
Strix woodfordi			257 (2)	Africa	Dunning
Surnia ulula	299 (16)	345 (14)	322	N America	Dunning
Xenoglaux loweryi			48 (3)	Peru	Dunning

TABLE 7.2

Table 7.2. Examples of coexisting owl species, over a range of habitats and geographical regions. Codes A-U are used in Figure 7.1.

Code	Region	Habitat	Species	Reference
A	Missouri	Hardwood forest	*Bubo virginianus virginianus* *Otus asio* *Strix varia varia*	Korschgen LJ & Stuart HB. 1972.
B	California	Oak woodland	*Tyto alba* *Bubo virginianus pacificus* *Glaucidium californicum* *Otus kennicotti*	Root 1969
C	California LA Co.	Oak woodland	*Tyto alba* *Bubo virginianus pacificus* *Otus kennicotti*	*Cody (Pers. Obs.;* *28y monitoring study, Topanga, CA)*
D	California Amador Co.	Foothill oak-pine	*Bubo virginianus pacificus* *Otus kennicotti* *Strix occidentalis occidentalis*	*Cody (Pers. Obs.)*
E	Wyoming Grand Teton Nat. park	Lodgepole pine Forest	*Aegolius acadicus* *Asio otus* *Strix nebulosa*	*Cody (Pers. Obs.;* *monitoring of breeding birds, GTNP;* *e.g.* Cody 1997*)*
F	Arizona, Mexico	Sonoran Desert	*Asia otus* *Bubo virginianus pallescens* *Micrathene whitneyi* *Otus kennicotti aikeni*	Cody & Velarde 2002
G	Colima, Mexico	Montane pine- Oak woodland	*Asio stygius* *Glaucidium gnoma* *Otus trichopsis* *Strix occidentalis lucida* *Strix virgata*	Schaldach 1963
H	Veracruz, Mexico	Montane mixed oak woodland	*Glaucidium brasilianum* *Pulsatrix perspicillata* *Strix virgata*	Howell 1999
I	Chiapas, Mexico CR	Lowland Rainforest	*Glaucidium griseiceps* *Otus guatemalae* *Strix nigrolineata* *Strix virgata*	Howell 1999
J	Guatemala	Lowland Rainforest	*Glaucidium brasilianum* *Otus guatemalae* *Strix nigrolineata* *Strix virgata*	Land 1963
K	Costa Rica	Lowland rainforest	*Glaucidium griseiceps* *Lophostrix cristatus* *Otus vermiculatus* *Pulsatrix perspicillata* *Strix nigrolineata* *Strix virgata*	Enriquez Rocha & Rangel-Salazar 2001
L	Andes, Peru	Montane woodland 2500m elev.	*Glaucidium jardinii* *Otus albogularis* *Strix albitarsus*	Graves 1985
M	Andes, Peru	Premontane	*Otus ingens*	Graves 1985

		woodland, 2000m	*Otus marshalli*	
			Strix albitarsus	
			Xenoglaux loweryi	
N	Peru	Lowland rainforest	*Glaucidium hardyi*	Terborgh et al. 1990
			Lophostrix cristatus	Lloyd 2003
			Otus watsoni	
			Pulsatrix perspicillata	
			Strix huhula	
			Strix virgata	
O	Cuba	Forest	*Asio stygius*	Garrido & Kirkconnell 2000
			Glaucidium siju	
			Gymnoglaux lawrencei	
P	SE Europe	Oak woodland	*Asio otus*	
			Bubo bubo	*Cody, Pers. Obs.*
			Otus scops	
			Strix aluco	
Q	Africa	Dry woodland	*Bubo africanus*	Voous 1966
			Bubo lacteus	
			Glaucidium perlatum	
			Otus leucotis	
			Otus senegalensis	
R	W Africa Cameroon	Rainforest	*Tyto alba*	Anon 2002
			Glaucidium tephronotum	
			Otus senegalensis	
			Strix woodfordi	
S	W Madagascar	Forest	*Tyto soumagnei*	Langrand 1990
			Asio madagascariensis	
			Otus rutilus	
T	Pakistan	Indus forest	*Bubo bubo*	Roberts 1991
			Glaucidium cuculoides	
			Otus spilocephalus	
			Strix aluco	
U	SE Australia	Forest	*Tyto novaehollandiae*	Loyn et al. 2001
			Tyto tenebricosa	
			Ninox connivens	
			Ninox strenua	

TABLE 7.3

Table 7.3. Size ratios for Barred and Spotted owls from the Pacific Northwest of the United States and from Mexico

			Mexico		
	Pacific Northwest		Actual	Extrapolated	
Species	Male	Female	Male	Male	Female
Barred Owl	632[1]	801[1]	709[3]	878[5]	1113[5]
Spotted Owl	579[2]	646[2]	484[4]	509[6]	569[6]
Size Ratio (M/F)	1.09	1.24	1.47	1.72	1.96

[1]Mass for *Strix varia varia* from Table 7.1
[2]Mass for *Strix occidentalis caurina* from Table 7.1
[3]Single mass for *Strix varia sartorii* specimen in Museum of Vertebrate Zoology, Berkeley
[4]Mean of mass from five *Strix occidentalis lucida* specimens in Museum of Vertebrate Zoology, Berkeley
[5]Mass extrapolated from linear measurements in Ridgeway (1914).
[6]Mass on *Strix occidentalis lucida* from Table 7.1

TABLE 7.4

Table 7.4. Potential biases associated with determining the number of Barred Owls (BO) and their impact on Northern Spotted Owls (NSO) in the Pacific Northwest. The potential effect on estimating numbers of both Barred Owls and Northern Spotted Owls are indicated. The direction of the bias is denoted by + (would result in an overestimate) or – (would result in an underestimate). The category of "knowledge" is used here to denote that there is either knowledge that the bias exists or that the potential bias has occurred but its effect has not been ascertained. A 1 or 0 indicates whether we have scientific knowledge of this bias (i.e., do we have information that supports the basis for estimating bias), and a 1/0 indicates that there is anecdotal or correlative information or support for the presence of the bias (but the scale is unknown). The letter "N" denotes that the bias or effect is neutral or is not an issue for the species. A superscript asterisk indicates that the extant data indicate a response has been measured that is opposite to the predication.

Bias	Direction		Knowledge	
	BO	NSO	BO	NSO
Behavioral Influence:				
BO do not respond to NSO calls	-	N	0	N
BO investigate NSO hoots by arriving silently	-	N	1/0	N
BO affect the response rate of NSO	N	-	1/0	1*
BO have the ability to disperse long distances	+	N	1	N
BO move among NSO territories	+	N	1/0	N
Variation in BO vocalizations results in missed or unrecognized detections	-	N	1/0	N
Ecological Influence:				
Small BO home range size lowers detection probability due to NSO survey point distribution across study areas	-	N	0	N
Survey Extent:				
BO are not surveyed in most areas	-	N	1	N
BO Survey locations restricted to NSO habitat	-	N	1	N
BO are detected incidentally during NSO surveys	-	N	1	N
Biologists are reluctant to survey for BO	-	N?	1/0	N
Procedural Inconsistency:				
Few studies are designed specific to BO	-	N	1	N
Inconsistent BO survey effort	-	N?	1/0	N
BO detections are reported as cumulative detections	+	-	1	1
Nighttime responses are reported as BO detections	+	N	1	0
Data on BO detections not consistently reported	-	N	1	N

18 FIGURES

FIGURE 7.1

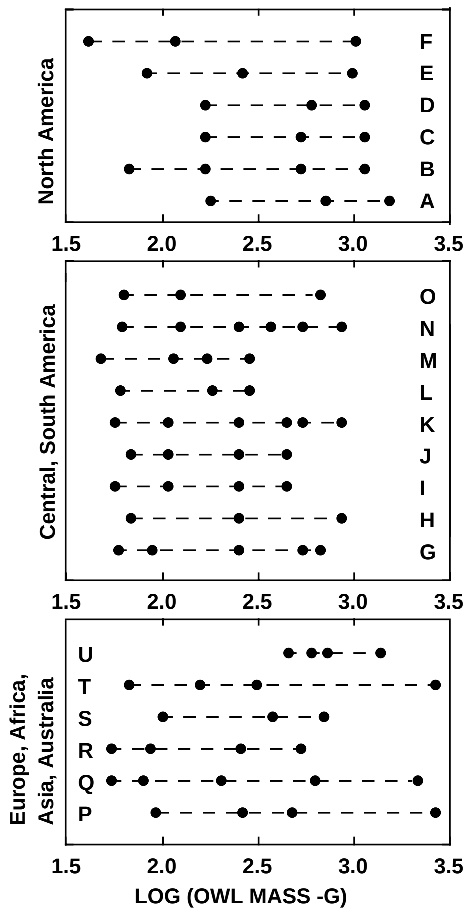

Figure 7.1. Sets of coexisting owl species on six continents, showing conspicuous size segregation of coexisting species (except site U). Sites A – U as listed in Table 7.2. See text for discussion.

FIGURE 7.2

Figure 7.2: Barred Owl Range Map

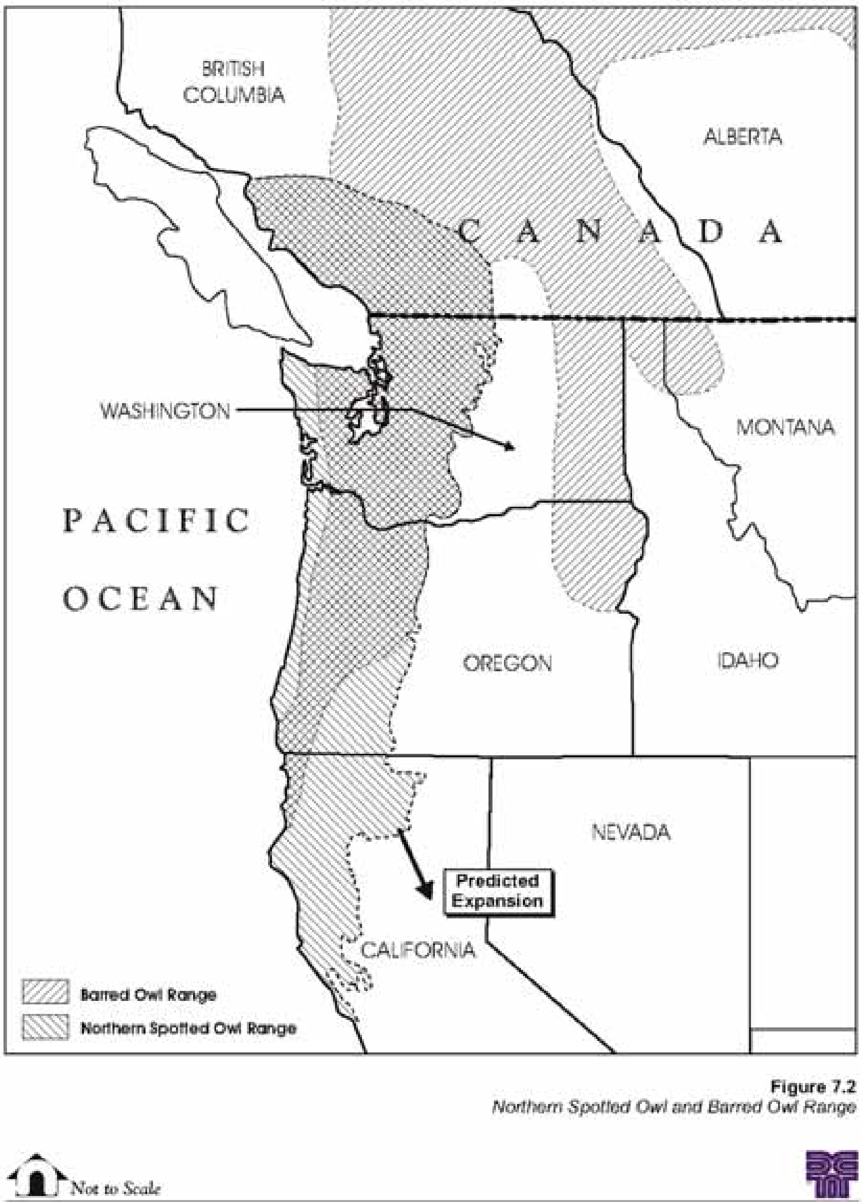

Figure 7.2
Northern Spotted Owl and Barred Owl Range

SCIENTIFIC EVALUATION OF THE STATUS OF THE NORTHERN SPOTTED OWL

CHAPTER EIGHT

Demography

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1 INTRODUCTION

This chapter discusses demographic performance in Northern Spotted Owls. After summaries of information on vital rates, we discuss population trends, regionally and nationally (with particular reference to the demographic meta-analysis of Anthony et al. 2004). We then discuss factors affecting demographic performance that may explain observed trends (such as competition, weather, etc.). In section 6 we draw together such information to consider the evidence for observed population trends.

In the remaining sections of the chapter, we focus on areas of particular importance or interest: small population size, extinction risks, predation (particularly with reference to fragmentation), and the emerging effects of West Nile Virus. This information is then summarized.

Throughout this chapter, our goal is to provide a comparison on information available now, as compared to that available either at the time of listing (1990) or at previous syntheses (mete-analyses reports).

Spotted Owls exhibit high adult survival, low and sporadic reproduction, and low recruitment rates. They have been characterized as having a bet-hedging life history strategy where they will forego reproduction in order to prolong survival (Franklin et al. 2000). The demographic parameters for Northern Spotted Owl are generally comparable to those seen in other subspecies of Spotted Owl (Seamans et al. 1999, Franklin et al. 2004) and for other owl species feeding on non-cyclic prey.

Spotted Owl population sizes may be limited by territorial behavior, with non-territorial floaters filling vacancies following mortality of territorial individuals (Franklin 1992). On a 292 km^2 study area in the Klamath Province, California, Franklin (1992) observed that the number of territorial male owls within the study area was maintained primarily by owls produced on the study area (recruitment) whereas the number of female owls was maintained primarily by immigration from outside the study area. These observations were consistent with longer natal dispersal distances of female owls compared to male owls (Forsman et al. 2002; see Section 3).

Little is known about mechanisms other than territoriality that may limit or regulate Spotted Owl populations (Gutiérrez et al. 1995). Owl demographic rates (reproduction, survival and population trend; Section 4) have been related to habitat, weather, competitors (Barred Owls), and/or the size of prey consumed (Section 5). Great Horned Owls and Northern Goshawks (and possibly Barred Owls) are predators of young and dispersing Northern Spotted Owls, and to a lesser extent, may prey upon territorial Spotted Owls (Gutiérrez et al. 1995; Section 7). Diseases, including West Nile Virus,(Section 10) have not yet had significant impacts on Spotted Owl populations; however WNV is a significant future threat that may affect owls in the near-term future.

2 DENSITY

Density of Northern Spotted Owls has been reported as both crude density (number of owls per area surveyed) and ecological density (number of owls per area of suitable habitat surveyed).

However, because suitable habitat was defined differently among studies, ecological density estimates from different study areas may not be directly comparable. Furthermore, density was most commonly reported as empirical numbers of owls encountered during surveys (*Woodbridge and Cheyne 1995*, *Chow 2001*; Table 8.1) and was only occasionally calculated using mark-recapture estimates (Diller and Thome 1999; Table 8.1). Crude densities of Northern Spotted Owls were previously reported as 0.063 to 0.274 owls/ km^2 (Thomas et al. 1993). At the time the Northern Spotted Owl was listed as Threatened, it was believed densities were low at the southern end of the range (USDI 1990). However, crude densities of Northern Spotted Owls in Marin County were recently estimated to be 0.376 owls/ km^2 (*Chow 2001*; Table 8.1). Crude density of Northern Spotted Owls in two areas of commercial timberland in Coastal California (0.313 and 0.351 owls/ km^2; Diller and Thome 1999; Table 8.1) was also higher than reported by Thomas et al. (1993).

3 POPULATION STRUCTURE AND DISPERSAL

Northern Spotted Owls may be regarded as comprised of a series of metapopulations, that is 'subdivided populations, with demographically significant exchange between them' (Gutiérrez and Harrison 1996). In some Spotted Owl subspecies and populations (primarily the California and Mexican subspecies), natural habitat distribution is such that different patches of habitat harbor quasi-independent populations of owls (e.g. La Haye et al. 1994). In some other areas of the California Spotted Owl range, and in most areas of the Northern Spotted Owl range, the species was probably originally distributed continually, but is now functionally a metapopulation as a consequence of habitat loss.

The metapopulation concept is a fundamental theory in conservation biology, recognizing that there is an interplay between factors affecting global trends, those affecting local dynamics, and also the factors which promote or discourage linkage between populations between dispersal. Gutiérrez and Harrison (1996) provide a lucid description of the concept and its application to the three Spotted Owl subspecies. The metapopulation concept underlies our current understanding of the distribution and demographic performance of Northern Spotted Owl populations, and is also a key concept behind the NWFP and other conservation plans. Models of Northern Spotted Owl populations, including those of Lande (1987), Doak (1989), Raphael et al. (1994), McElvey and Noon (1996) and others all rely on the basic insight that understanding Spotted Owl population dynamics involves understanding processes affecting not only reproduction and survival in populations, but also owl movement patterns between populations. See Section 8 of this chapter, and Appendix for a fuller discussion of the role of such models in understanding Northern Spotted Owl population extinction risks.

3.1 DISPERSAL

The following information was available at the time of listing:

> "Mortality rates of juveniles are significantly higher than adult rates (Forsman *et al.* 1984, Gutiérrez *et al.* 1985 a and b, Miller 1989). Recent studies of juvenile dispersal in Oregon and California indicate that few of the juvenile spotted owls survived to reproduce (Miller 1989, Gutiérrez *et al.* 1985 a and b). These research studies all report

very high mortality during pre-dispersal and the first months of dispersal. Using these data, Marcot and Holthausen (1987) estimated that about 60 percent of juveniles live until they disperse from their nesting areas, but only about 18 percent of those fledged survive for 1 year. In one study, only 7 out of 48 juveniles radio-tracked during a 3-year study (1982—1985), were known to be alive after 1 year (the fate of 4 was unknown because transmitter signals were lost) (Miller 1989). Survival of first year birds was estimated at 19 percent; predation by great horned owls and starvation were the two main causes of mortality (Miller 1989). Twelve of 23 juveniles in a 2-year study in California died during the dispersal period; the fate of the other 11 was unknown (Gutiérrez *et al.* 1985b). It is not known whether the use of radio transmitters attached to juveniles for tracking purposes contribute to juvenile mortality (Irwin 1987; Dawson *et al.* 1986); researchers using this technique believe it should not measurably influence juvenile survival if done properly (Foster *et al.*, unpub.ms.)."

Federal Register 26115

Forsman et al. (2002) studied natal and breeding dispersal in 1475 Northern Spotted Owls from 12 study areas in Oregon and Washington. Natal dispersal is the movement of an owl from its territory of birth to a new territory where it may potentially breed. Breeding dispersal is the movement of a territorial, non-juvenile owl between territories where it may potentially breed. Natal dispersal was studied by following 324 radio-marked owls for 1-2 years and by reobserving an additional 711 owls first banded as juveniles on demography study areas. Breeding dispersal was observed with colorbanded owls (4917 records of 440 non-juvenile individuals) that stayed on the same territory or moved to a new territory in subsequent years (Forsman et al. 2002).

Mean dates that juvenile Spotted Owls began dispersal were 19 September in Oregon (95% CI = 17-21 September) and 30 September in Washington (95% CI = 25 September – 4 October). Natal dispersal distance was skewed towards shorter distances with median dispersal distance of females (24.5 km for banded and 22.9 km for radio-marked owls) greater than that of males (14.6 km for banded and 13.5 km for radio-marked owls). Greater natal dispersal distances of females than males is typical among avian species (Greenwood and Harvey 1982, Greenwood 1983). Only 8.9% of juveniles dispersed > 50 km (maximum 111.2 km (Forsman et al. 2002).

Of radio-marked owls that were alive, 44% of females and 22% of males were paired at one year of age, and 77% of females and 68% of males were paired at two years of age. Among owls banded as juveniles, 9% were first reobserved as territorial individuals at ≥ five years of age (Forsman et al. 2002). Owls did not disperse across the Willamette, Umpqua nor Rogue Valleys of Oregon, but did disperse between the Coast Range and Cascade Mountains through forested foothills between the non-forested valleys (Forsman et al. 2002). An average of 6% of banded, non-juvenile owls exhibited breeding dispersal annually. Breeding dispersal distances were much shorter than those for natal dispersal. Probability of breeding dispersal was greater for females, younger owls, owls without mates in the previous year and owls that lost their mates from the previous year through death or divorce. Breeding dispersal distance was greater for 1- and 2-year-old than ≥ 3 year old owls but did not differ by sex (median = 3.5 km; Forsman et al. 2002).

Diller and Hibbard (*1996*) reported recaptures of 82 Northern Spotted Owls banded as juveniles on the Simpson study area, California Coastal province (see below) and 21 owls recaptured on the Simpson study area that were initially banded on other study areas from in 1990-1995. Straight-line dispersal distances of 51 males ranged from 1 to 58 km (mean = 12 km) and distances of 51 females ranged from 1 to 82 km (mean = 18 km). Of ten owls banded as juveniles in 1990 and recaptured in 1992-1995, five were first captured at 1- yr- old, one at 2-yrs-old, three at 3-yrs-old, one at 4-yrs-old, and none at 5-yrs old (*Diller and Hibbard 1996*).

4 DEMOGRAPHIC RATES

At the time of listing, it was recognized that:

> "The analysis used state-of-the-art methods both to estimate the demographic parameters and to estimate whether populations in the Willow Creek Study area of California, and in the Roseburg Study Area in Oregon, are reproducing at replacement rates. The conclusion was that resident birds in both populations are not reproducing at self-sustaining rates. The reproductive rate was 0.38 and 0.32 fledglings/adult female in the Willow Creek and Roseburg StudyAreas, respectively. These values are less than those cited by the commenter and in the Service's analysis were found to be insufficient to maintain a stable population size. Data are insufficient from other sites to make such an assessment."
>
> Federal Register 26173
>
> "In summary, the best and most current estimates of the finite rate of annual population change are those given above (e.g., 0.95 for northwest California and 0.86 for the Roseburg area in southwest Oregon). These results indicate a sharply declining population of resident, territorial owls due to habitat loss. The populations are above carrying capacity and are being temporarily maintained by immigration.
> It is unknown whether the amount and distribution of spotted owl habitat remaining at the end of commercial harvest of old-growth forests on public lands (USDI 1989) will be adequate to support a viable population of the northern spotted owl."
>
> Federal Register 26186

Survival and reproductive output of Northern Spotted Owls have been used to estimate the finite rate of population change (λ). Survival and reproductive output have been estimated using mark-recapture and mixed-model ANOVA analytical methods, respectively (Franklin et al. 1996, Anthony et al. 2004). Reproductive output was defined as the annual number of young fledging (leaving the nest) per territorial female and was determined by feeding live mice to owls and observing the owls' behavior (Forsman 1983, Franklin et al. 1996). Fecundity was defined as the number of *female* young fledged per territorial female because projection matrix methods used to model population trend (see below) used only the female portion of the population (Franklin et al. 1996). Because the sex of juveniles was not determined in many cases, a 1:1 sex ratio of juvenile owls was assumed; annual per-territory fecundity was therefore one-half of annual per-territory reproductive output. On some study areas, the assumption of a 1:1 sex ratio of juveniles has been met using genetic techniques to sex fledged young (*Franklin et al. 2004*)

Estimation of survival using mark-recapture methods was accomplished by capturing and banding Spotted Owls with uniquely-identifiable colored leg bands. Observation of unique bands was analytically equivalent to "recapture" of individuals (Franklin et al 1996). Over time, each banded owl in a study accumulated a capture history indicating whether the owl was observed or not each year. Statistical analysis of these capture histories originated in theory developed by Cormack (1964), *Jolly (1965)* and Seber (1996) and is reviewed in general by Lebreton et al. (1992) and explained specifically for Spotted Owl studies in Franklin et al. (1996). Briefly, analytical methods allow for simultaneous maximum-likelihood estimation of recapture and survival probabilities.

Because the Spotted Owl populations studied were not geographically closed to emigration or immigration, "open population" Cormack-Jolly-Seber (CJS) models were used in analyses. Open-population CJS models estimate apparent survival probability rather than true survival probability, although general discussion often refers simply to "survival rates" for Spotted Owls. Apparent survival is equivalent to 1- (mortality rate + emigration rate) whereas true survival is equivalent to 1-mortality rate (Franklin et al. 1996). Because juvenile owls are known to emigrate from study areas (see Dispersal section, above), estimation of juvenile survival probability has been problematic (see Raphael et al. 1996). However, emigration of territorial owls exhibiting breeding dispersal from study areas was thought to be infrequent (Raphael et al. 1996). For example, in one study area only 3.7% of recaptures of non-juvenile owls was outside of the study area boundaries over a 9-year period (Franklin et al. 1996b). This translated into a crude emigration rate for non-juvenile owls of 0.4%/year.

Van Deusen et al. (1998) modeled apparent survival of Spotted Owls on the Wenatchee study area (see below) by conditioning capture probability of female owls on capture probability of the male owls at the corresponding sites. Based on AIC model selection, models that included the conditional capture term were preferred over models without the conditional capture term (Van Deusen et al. 1998). The method of Van Deusen et al. (1998) has not been reported for any other study areas and was not used in Northern Spotted Owl meta-analyses. However, estimation of apparent survival probability in the meta-analyses used an empirical estimate of overdispersion for each data set, which measures lack of independence in the data and adjusts AIC values and estimates of standard errors accordingly. See Manly et al. (1999) for further details on this topic.

The finite rate of population change (λ), referred to here as "population trend", has been estimated for Northern Spotted Owls by two different methods, discussed in Section 4.3.1 (below). By either method, a stable population is indicated by $\lambda = 1$, a declining population by $\lambda < 1$, and an increasing population by $\lambda > 1$. If, for example, $\lambda = 0.970$, the population in question would have declined by three percent annually over the period for which λ was estimated. A population declining by three percent annually (with no variation) would experience a 24% total decline at the end of ten years $(1-(0.970)^9)$.

Interpretation of estimated λ has often been based on determining whether the 95% confidence interval around λ overlaps 1.000 and/or estimating the value of a t- or Z-statistic comparing estimated λ to 1.000 (e.g., USDI 1990, Anderson and Burnham 1992, Burnham et al. 1996, Franklin et al. 1999). However, the selection of 95% confidence intervals and/or a decision cut point for P-values of t- or Z-statistics is arbitrary (Taylor and Gerrodette 1993). Taylor and Gerrodette (1993) argued that estimation of power to detect population decline should be emphasized in studies of Northern Spotted Owls and other species of conservation concern, rather than focusing on the generally accepted level ($\alpha \leq 0.05$) of a Type 1 error (in this case, failing to detect a difference between estimated λ and 1.000).

At the time the Northern Spotted Owl was listed as threatened, demographic parameters had been estimated from two study areas, one primarily on National Forest land in the Klamath Province of northwestern California and the other primarily on BLM and Forest Service land in the Oregon Coast Range (USDI 1990). Two years later, demographic data were available from three additional study areas: the H. J. Andrews Experimental Forest and vicinity in the western Cascades of Oregon (HJA, 1987-1991), the Medford BLM Resource Area in the Cascades and Siskiyou Mountains of Oregon (MED, 1985-1991), and Olympic Peninsula of Washington (OLY, 1985-1991; Anderson and Burnham 1992). The five studies in the 1991 analysis were all extant in 2004.

In December 1993, December 1998, and January 2004, three Spotted Owl demographic meta-analysis workshops were conducted, with additional studies participating on each occasion and a few studies ending between workshops (n = 12 studies in 1993 [Forsman et al. 1996], n = 15 studies in 1998 [*Franklin et al. 1999*], n = 14 studies in 2004, Table 8.2 [Anthony et al. 2004]). Each analysis included data beginning from the initiation of individual studies, such that later analyses included all of the data from earlier analyses for a given study area. Because analyses were cumulative, later analyses superceded earlier analyses. In all meta-analysis workshops, data were analyzed separately for individual study areas, as well as simultaneously across study areas (true meta-analysis).

The Ecological Society of America (ESA) recently requested and received peer reviews of the latest meta-analysis report (Anthony et al. 2004) from four external scientists (ESA 2004). The reviewers were instructed to comment on the report's scientific credibility including representation of the data, objectiveness of analyses, presentation of all available data, information gaps and inadequacies. The reviews were favorable with respect to analytical and statistical methods used and the temporal and spatial scale of the meta-analysis. Two of the reviewers were particularly critical that the analysis did not include more exploration of possible mechanisms causing the observed trends in demographic rates (ESA 2004). This paralleled similar comments by the authors of a similar meta-analysis for the California Spotted Owl (Franklin et al 2004), who argued for work that would:

> "Analyze…data with covariates – such as climate, rates of timber harvest, presence of sequoia groves, and territory specific habitat configurations- combined with appropriate biologically based hypotheses that include both positive and negative influences of the covariates. In that manner, some of the processes influencing the initial patterns observed during this meta-analysis can be better understood"

Although the meta-analyses did not incorporate weather, habitat, or prey covariates, several individual studies examined the influence of weather, habitat, barred owls, and/or prey on one or more demographic rates of Northern Spotted Owls (Section 5).

4.1 REPRODUCTION

4.1.1 HISTORIC ESTIMATES

In all meta-analyses, fecundity (females offspring produced per territorial female) was lowest for one-year-old females (first year subadults), intermediate for two-year-old females (second year subadults), and highest for females ≥ 3 years old (adults). Despite initial concern, in 1993 and 1998 fecundity was observed to vary by year but did not appear to be decreasing over time (Burnham et al. 1996, *Franklin et al. 1999*).

The 1998 meta-analysis revealed an "even-odd year" trend in Spotted Owl reproduction, wherein reproductive output was generally greater in even-numbered years and lower in odd-numbered years (*Franklin et al. 1999*). Several hypotheses have been suggested for this pattern (see Franklin et al. 1999). Clearly range-wide synchrony suggests an effect or interaction involving climate, either directly or indirectly (such as through prey). Cody (*pers.comm. 2004*) has suggested that, if female owls do not generally breed successfully every year, then a climate/prey 'pulse' may synchronize breeding. Such synchrony would then persist, but would decay as non-breeding females enter the population (until another 'pulse' synchronizes the population again). The beginning of the odd-even year pattern in a strong El Nino year is consistent with such an hypothesis. Alternatively (or in addition) some conifers appear to seed on an alternate year cycle; this may trigger irruptions in populations of seed-eating prey (e.g. *Peromyscus*) with cascading effects on prey communities in subsequent years (see Chapter 4). This hypothesis would explain alternate-year cycles, but not their break-down in recent years.

4.1.2 CURRENT ESTIMATES

Recent estimates of reproductive rates for Northern Spotted Owls indicated that fecundity rates varied among 14 study areas, with the highest adult female fecundity rates in two studies in the eastern Cascades of Washington and in Marin County in the California Coast Range (Anthony et al. 2004; Table 8.3). The "even-odd" year effect was observed on most study areas, although it was less pronounced than was observed in the 1998 meta-analysis. Individual studies showed various weak time trends in fecundity (both positive and negative; Anthony et al. 2004; Table 8.3).

Anthony et al. (2004) modeled the effects of Barred Owls on Spotted Owl reproduction, using the number of Spotted Owl territories in which Barred Owls were observed each year as a covariate. Results did not indicate negative effects of Barred Owls on Spotted Owl reproduction. Anthony et al. (2004) recommended that future analyses use territory-specific Barred Owl covariates.

Meta-analysis confirmed regional differences in fecundity, with the highest rates in the mixed-conifer region (eastern Cascades) of Washington and the lowest rates in the Douglas fir regions of Washington and Coastal Oregon. Fecundity rates for all studies combined did not show time trends and averaged 0.074 for one-year-old females (SE = 0.029), 0.208 for two-year-old females (SE = 0.032), and 0.372 for adult females (SE = 0.029).

4.2 SURVIVAL

4.2.1 HISTORIC ESTIMATES

In the first meta-analysis of five study areas, adult survival had declined from 1985-1991 (Anderson and Burnham 1992). In 1993, the meta-analysis from 11 study areas confirmed a negative trend in female owl survival in both the long-term and shorter-term studies (Burnham et al. 1996). In 1998, estimates of female owl survival rate across study areas varied annually but did not show a decreasing trend over time (*Franklin et al. 1999*) and appeared to have increased since the previous (1993) meta-analysis.

4.2.2 CURRENT ESTIMATES

Survival rates varied by study area and were lowest on the Wenatchee study area (eastern Cascades, Washington), followed by Warm Springs (eastern Cascades, Oregon), Marin (coastal California, females only), and Rainier (western Cascades, Washington; *Anthony et al. 2004*; Table 4). Survival declined over time on five of the 14 study areas: the four study areas in Washington and the northwest California study area in the Klamath province (*Anthony et al. 2004*; Table 4). The Barred Owl covariate (see section 2.2) was negatively related to survival for two study areas, on the Olympic Peninsula ($\hat{\beta}$ = -4.24, 95% CI = -7.83, -0.65) and Wenatchee ($\hat{\beta}$ = -4.69, 95% CI = -7.32, -2.07) study area in the eastern Cascades, Washington (*Anthony et al. 2004*). However, the negative correlation of Barred Owls with survival on these two study areas does not differentiated between the hypothesis that Barred Owls are decreasing Spotted Owl survival and the hypothesis that some other factor is causing Spotted Owl survival to decline and that Barred Owls are filling the vacancies left by Spotted Owls (see Barred Owl chapter).

Meta-analysis revealed regional differences in Spotted Owl apparent survival rates (Anthony et al. 2004), with highest rates in Oregon Douglas fir regions and lowest rates in the Washington mixed conifer region. Annual survival was negatively associated with reproduction at the beginning of the annual survival interval for the Washington Douglas fir and Oregon Cascades regions.

4.3 POPULATION TRENDS

4.3.1 METHODS

Through 1993, the annual rate of population change (λ) was estimated using modified Leslie Projection Matrix methods (hereafter, PM and λ_{PM}). Projection matrix methods are based on age- or stage-specific estimates of fecundity and survival (Franklin et al. 1996). Projection matrix methods are predicated on assumptions which were not met with the Spotted Owl data, most notably that the population is geographically closed. Estimates of λ_{PM} were known to be biased low due to juvenile owl emigration from study areas which resulted in underestimation of juvenile survival rates. Efforts were made to correct juvenile survival rates for emigration using data from other sources (e.g., juvenile dispersal data). However, even after correcting estimates of juvenile survival, in the projection matrix, the survival and reproductive rates of a study are inappropriately assigned to juveniles that have left the study area (Franklin et al. 2004: Appendix 3). Furthermore, λ_{PM} represents the asymptotic rate of population change that would occur if the estimated average fecundity and survival rates occurred every year (it assumes a stationary population); evidence suggests that they do not (see below). It must be noted that the projection matrix method was the best available method for estimating λ at the time it was used.

In 1996, Pradel (1996) published a new analytical method for estimating λ, referred to as reparamaterized Jolly-Seber (hereafter, RJS and λ_{RJS}). λ_{RJS} is estimated directly from mark-recapture data and does not require the assumption of a stationary population. λ_{RJS} incorporates reproduction, survival, and recruitment, and allows for time-specific estimation of λ. The two estimates of population trend (λ) also differ in their interpretation: λ_{PM} reflects whether the population of territorial female owls within a study area were *replacing themselves if the system was geographically closed*, whereas λ_{RJS} reflects whether the population of territorial female owls *had been replaced* (*Franklin et al. 1999, Franklin et al 2004*). In both cases, $\lambda = 1$ indicates a stationary population, $\lambda < 1$ indicates a declining population, and $\lambda > 1$ indicates an increasing population.

In the 1998 meta-analysis, population trend was estimated by both the PM and RJS methods; the RJS analysis was considered to be exploratory. In 2004, the RJS method was recognized to be superior to the PM method for Spotted Owl mark-recapture data and was used exclusively at the meta-analysis workshop for estimating λ. The RJS method was also the single method used to estimate λ for the only meta-analysis of the California Spotted Owl (Franklin et al. 2004).

Inferences about the strength of evidence for $\lambda < 1$ were evaluated with a 1-sided t-test through 1993 (USDI 1990, Anderson and Burnham 1992, Burnham et al. 1996). In 1998 and 2004, 95% confidence intervals (CI) around λ were presented (Franklin et al. 1999, Anthony et al. 2004).

Note that Van Deusen et al. (1998) and Manley (2002) have discussed the effects of conditional effects on recapture probability (where female recapture probability is affected by the technique of finding them through breeding males). While this departure from strict assumptions of recapture models could potentially have affected estimates of λ and model selection, such effects are probably small. Nevertheless this may be an issue that could repay further exploration (for instance, by simulation).

4.3.2 HISTORIC TRENDS

In 1990, estimates of λ indicated that two populations of owls declined over the study periods ($\lambda_{PM} = 0.9524$, SE = 0.0284, $P < 0.05$ for northwestern California, 1984-1989, and $\lambda_{PM} = 0.8588$, SE = 0.0286, $P < 0.05$ for the Oregon Coast Range, 1985-1989; USDI 1990).

In 1992, estimates of λ from all five study areas indicated that owl populations had declined (all $\lambda_{PM} < 1.0$ and all five $P < 0.05$). Mean λ_{PM} across study areas was 0.902, indicating an average 9% annual population decline (SE = 0.017, $P < 0.05$). Because adult survival declined across study areas from 1985-1991, and because λ for Spotted Owls is strongly influenced by adult female survival, researchers inferred that rate of population decline accelerated during 1985-1991 (Anderson and Burnham 1992).

In 1993, estimated λ for 10 of 11 studies indicated that Spotted Owl populations had declined (10 study areas $\lambda_{PM} < 1.0$ and all 10 $P < 0.05$; Burnham et al. 1996). Mean λ_{PM} across study areas was 0.925, indicating an average 7.5% annual decline in Spotted Owl populations (SE = 0.015, $P < 0.05$) during the study period.

In 1998, 95% confidence intervals for estimates of λ_{PM} were < 1.0 for 11 of 15 individual study areas (Franklin et al. 1999). Mean λ_{PM} across study areas was 0.917, indicating an average 8.3% annual population decline (SE = 0.014, 95%CI = 0.889 - 0.945). The estimate of λ_{PM} from combined data was 0.961 (95% CI = 0.925 - 0.997). Estimated average λ_{RJS} for 12 individual study areas ranged from 0.969 to 1.027. Mean λ_{RJS} across study areas was 0.997, indicating essentially stationary Spotted Owl populations (SE = 0.003, 95% CI = 0.991 – 1.004). Differences between estimates of λ_{PM} and λ_{RJS} were attributed to different interpretations of the two metrics (see 4.1, above), the fact that data used for estimating λ_{RJS} was a subset of the data used to estimate λ_{PM}, and possibly modeling constraints that did not include temporally varying recapture rates (Franklin et al. 1999).

4.3.3 CURRENT TRENDS

Estimated λ_{RJS} from the most recent meta-analysis ranged from 0.896 to 1.005 and was < 1.0 on 12 of 13 study areas (Table 8.5, Anthony et al. 2004). However, in only four of these 12 were 95% confidence intervals for $\lambda < 1.0$: for the two study areas in the eastern Cascades, Washington, Warm Springs (eastern Cascades, Oregon), and Simpson (Coastal California). Evidence for decline was moderate (i.e. point estimate of $\lambda <1$) for Rainier and Olympic Peninsula, Washington, and the Oregon Coast Range and H. J. Andrews study areas. The Marin data set was insufficient to complete an analysis of population trend.

Two meta-analyses of λ_{RJS} were completed, one for all 13 study areas combined and one for eight study areas that were part of the Effectiveness Monitoring Program of the Northwest Forest Plan (Lint et al. 1999). The mean λ_{RJS} for all study areas was 0.959 (SE = 0.024, 95% CI = 0.908, 1.004), and for the eight monitoring study areas was 0.975 (SE = 0.023; 95% CI = 0.929, 1.021), indicating average annual population declines of 4.1% for all study areas and 2.5% for the monitoring study areas, neither of which were different from a stationary population based on the 95% confidence intervals. However, these averages across all study areas should be viewed cautiously because they ignore regional variation; the key point is that declines in Northern Spotted Owl populations may be occurring in some areas and not in others.

Therefore in general, calculated rates of decline for the 2004 study were lower than those observed in 1998, when (as noted) the data suggested a stable population. These results, which indicate lower demographic performance, may indicate a worsening of performance from 1998 to 2003, simple statistical variation, or both. Further analysis of time trends in λ_{RJS} over different periods would be valuable. It is difficult, on the information available, to be sure whether or not current conditions are worse now than they were five years ago.

The cause(s) of Northern Spotted Owl population declines from 1990-2003 are poorly understood. Hypothesized reasons for decline include displacement of Spotted Owls by Barred Owls, loss of habitat to wildfire, loss of habitat to logging on state, private and tribal lands, forest defoliation due to insects, and advancing forest succession toward climax fir communities in the absence of fire (*Anthony et al. 2004, L. Irwin, pers. comm*). Weather extremes may also be a factor in some populations. Franklin et al. (2000) predicted that Northern Spotted Owl populations may experience periods of decline, especially if habitat quality had been degraded from past land management practices.

Although the Barred Owl covariate used in the 2004 meta-analysis showed few meaningful relationships to fecundity and survival of Spotted Owls, many of the field researchers participating in the meta-analysis believed that Barred Owls had a greater effect on Spotted Owl site occupancy (Anthony et al. 2004; see also Barred Owl chapter of this report, and Kelly et al. 2003).

Loss of habitat to timber harvest was known to occur during the demographic studies on the Cle Elum, Warm Springs, and Simpson study areas (Anthony et al. 2004*, L. Diller pers. comm.*) In contrast, timber harvest was negligible on the Olympic study area (Anthony et al. 2004, *American Forest Resource Council 2004*). The USFWS estimated a loss of 2.11% of Northern Spotted Owl habitat range-wide on Federal lands due to management activities from 1994-2003 (mean = 0.23% loss annually; *USDI 2004,* see Habitat Trends chapter of this report). Unfortunately, these data are not spatially explicit; therefore, it is not possible to estimate the number of Northern Spotted Owl territories affected by timber harvest. USFWS also estimated an 8% increase in Northern Spotted Owl habitat from 1994-2003 (mean = 0.9% gain annually) resulting from development of younger forest (*USDI 2004*, see Habitat Trends chapter of this report).

AFRC (2004) provided the panel with an analysis of timber harvest on different demographic study areas. This commendable effort (carried out between meetings of the panel) showed that data are available that could usefully address the question of whether current timber harvest is an adequate explanation of differences in demographic performance among different study areas. There are significant inaccuracies in the data put forward, as recognized by AFRC; the data and their quality are insufficient at this time to determine unequivocally whether there is or is not any effect of current timber harvest. This initial study does suggest that there is no simple, strong and pervasive effect of current timber harvest that is immediately apparent: the location with highest demographic performance (Tyee) also had high harvest rates. Conversely, the study areas with lowest harvest rates (e.g. Olympic) had poor demographic performance. These results are discussed again below (section 4).

A significant problem with any correlation of demographic performance with habitat changes is that effects on survival and reproduction are likely to persist long after habitat change itself has ceased. For instance, although there is little current habitat loss on the Olympic peninsula, a pattern that has been in place since adoption of the NWFP in 1994, prior to that, there was extensive harvest on Forest Service and other lands (but not on National Park lands).

Loss of habitat to wildfire, forest defoliation due to insects, and forest successional changes were believed to be most relevant to decline in the Spotted Owl populations in the eastern Cascades of Washington (Anthony et al. 2004, *Irwin et al. in press*, see also Habitat Associations chapter of this report). On the Wenatchee study area, 20,024 acres of suitable Spotted Owl habitat were burned in 1994 within 3.36 km of 20 owl sites under study (*L. Irwin, pers. comm.*). The USFWS estimated a loss of 3.03% of Northern Spotted Owl habitat range-wide on Federal lands due to natural disturbances from 1994-2003 (mean = 0.34% loss annually; *USDI 2004*, see Habitat Trends chapter of this report). However, anecdotal evidence suggests that wildfires do not always have a negative effect on Spotted Owl survival, reproductive output and site fidelity (Bond et al. 2002).

In general, the panel believes that the most appropriate summary of demographic trends is that provided by the recent meta-analysis (Anthony et al, 2004). Detailed explanations are provided in that report, and we find no reasons to challenge any of the findings made there. Our comments here may be of value for context, and for exploration of potential causative agents. However, the meta-analysis report itself should serve as the appropriate source for information on trends and analyses.

4.4 REGIONAL TRENDS

4.4.1 BRITISH COLUMBIA

Dunbar et al. (1991) surveyed portions of the range of the Northern Spotted Owl in British Columbia, Canada in 1985-1988. Based on response rates of surveyed areas and the proportion of the range surveyed, Dunbar et al. (1991) guessed that there were fewer than 100 pairs of Spotted Owls in British Columbia. Subsequently, extensive surveys of Spotted Owls were conducted in British Columbia in 1992-2001 (*Blackburn and Harestad 2002*). Owls were not color-banded and areas were not surveyed consistently. However, post-hoc methods were used to estimate population trend based on survey results from 40 areas occupied by Spotted Owls in at least one year during the study period. Results indicated that Spotted Owls declined by approximately 7.2% annually, resulting in a 49% population decline between 1992 and 2001 (*Blackburn and Harestad 2002*).

4.4.2 REGIONAL SUMMARIES OF DEMOGRAPHIC RATES

<u>Olympic Peninsula</u> (Olympic study area) – Adult fecundity was stable but lower than the range-wide mean. Adult survival declined over time, was negatively associated with the number of barred owls detected on the study area annually and negatively associated with reproduction at the beginning of the annual survival interval. Evidence for population decline was moderate.

<u>Western Cascades, Washington</u> (Rainier study area) – Adult fecundity was stable but lower than the range-wide mean. Adult survival declined over time and was negatively associated with reproduction at the beginning of the annual survival interval. Evidence for population decline was moderate.

<u>Eastern Cascades, Washington</u> (Cle Elum and Wenatchee study areas) – Adult fecundity was highest among all regions, was stable on the Wenatchee study area, and showed some evidence of a decrease over time on the Cle Elum study area. Adult survival declined over time on both study areas and was lower on the Wenatchee than any other study area. Adult survival was negatively associated with the number of barred owls detected on the Wenatchee study area. Evidence for population decline was strong.

<u>Coast Range, Oregon</u> (Coast Ranges and Tyee study areas) – Adult fecundity was lowest among all regions, increased over time on the Tyee study area and showed some evidence of a decrease over time on the Coast Range study area. Adult survival was stable. Evidence for population decline was moderate on the Coast Range study area; however, the owl population appeared to be stable on the Tyee study area.

<u>Cascades, Oregon</u> (H. J. Andrews, Warm Springs and South Cascades study areas) – Adult fecundity similar to the range-wide mean and was stable or declined over time on the individual study areas. Annual survival was stable and was negatively associated with reproduction at the beginning of the annual survival interval. The Warm Springs study area, on the east slope of the Cascades, Oregon, was grouped with the two study areas on the west slope of the Cascades, Oregon, in the 2004 meta-analysis because of similar vegetation types (predominantly Douglas fir; Anthony et al. 2004). However, adult fecundity was fourth-highest and survival was second-lowest among all studies on the Warm Springs study area, which also showed strong evidence for population decline. Evidence for population decline was moderate on the H. J. Andrews study area and weak on the South Cascades study area.

<u>Klamath Province, Oregon and California</u> (Klamath, NW California and Hoopa study areas) – Mean adult fecundity in this province was similar to the range-wide mean. Fecundity was stable on one study area and declined over time on two study areas. Adult survival declined over time on the Northwest California study areas but was stable on the Klamath and Hoopa study areas. Evidence for population decline was weak.

<u>Coast Range, California</u> (Simpson and Marin study areas) – Adult fecundity was higher than the range-wide mean, was stable on the Marin study area, and showed some evidence for a decline over time on the Simpson study area. Adult survival was stable over time. Evidence for population decline on the Simpson study area was moderate.

Hicks et al. (2003) found clinal variation in productivity, subadult recruitment and adult turnover rates at 100 Spotted Owl sites in five vegetation zones spanning the Washington Cascade Range over a 10 yr period. (See Habitat Associations chapter for details). The number of young fledged per territory differed by vegetation zone, decreasing from east to west. Owls in the three westernmost zones had lower adult turnover rates and lower subadult recruitment rates than owls in the two easternmost zones. These trends were corroborated to some extent in that the demographic study area west of the Cascade crest had lower fecundity than the two study areas in the eastern Cascades, and one of the study areas in the eastern Cascades (Wenatchee) had the lowest survival rate among all studies. Fecundity and survival were not estimated by vegetation zone within study areas in meta-analyses.

5 FACTORS AFFECTING DEMOGRAPHIC RATES

5.1 HABITAT

The Federal Register recoginized that:

> "Current counts of owls may be misleading (optimistic) because the population was above the carrying capacity due to habitat loss. Thus, even if the loss of habitat were halted, these data suggest that the population would continue to decrease substantially for, at least, several generations (also see Thomas *et al.* 1990). At some future time, the population would come into a new equilibrium with the habitat and become somewhat stationary."
>
> Federal Register 26185

Franklin et al. (2000) analyzed data from a marked population of Spotted Owls for the first 10 years of study in the Klamath Province, California and evaluated the effects of weather variables and landscape characteristics on temporal and spatial variation of survival and reproductive rates. From the best models of these relationships, they estimated habitat fitness potential (λ_H) of individual owl sites (n = 95) using modified Leslie projection matrix methods, which did not include juvenile survivsl. Franklin et al. (2000) mapped vegetation within 158 ha around each owl site center, defining two habitat categories: suitable owl habitat or older forest (mature and old-growth conifer ≥ 53 cm dbh, percent of conifers ≥ 40%, overstory canopy cover ≥ 70%) and all other habitat. Survival was positively and non-linearly associated with the amount of interior older forest (>100 m from an edge), the amount of edge between older forest and other vegetation types, and showed a quadratic (convex) relationship to the distance between patches of older forest. Reproductive output was negatively and non-linearly associated with the amount of interior older forest, had a quadratic (concave) relationship to the number of older forest patches, and was positively associated with the amount of edge between older forest and other vegetation types. Thus, there appeared to be a trade-off between the benefits to survival conferred by interior older forest and benefits to reproduction conferred by less interior older forest and more convoluted edge between the two habitat categories. Estimates of λ_H ranged from 0.438 to 1.178 (mean = 1.075). Based on 95% confidences intervals, 69% of owl territories had estimates of $\lambda_H > 1$, indicating owls at these territories more than replaced themselves. Franklin et al. (2000) suggested that habitat quality may determine the magnitude of λ (finite rate of population growth) and recruitment may determine variation around λ. In addition, owls in territories of higher habitat quality (i.e., $\lambda_H > 1$) had greater survival during inclement weather than those in poorer quality habitat, suggesting that habitat quality buffered individuals from the negative effects of weather.

Three additional studies estimated the effects of weather and habitat on Spotted Owl survival and reproduction in the Oregon Coast Range *(Olson et al. 2004),* central Cascades, (*Anthony et al. 2002a*), and southern Cascades (*Anthony et al. 2002b*). Long-term Spotted Owl demographic data were available from each of the study areas. Modeling generally followed the methods of

Franklin et al. (2000). *Olson et al. (2004)* and *Anthony et al.* (*2002a*) used three scales of analysis: 600, 1500 and 2400 m radius circles, corresponding to 113, 707, and 1810 ha. Vegetation was classified as late-seral conifer, mid-seral conifer, non-habitat, and broadleaf (Coast Range only).

In the central Oregon Coast Range, survival had a quadratic (convex) relationship to the amount of mid- and late-seral forest within 1500 m of owl site centers (707 ha circles; *Olson et al. 2004*). The best model explained only 16% of the variation in the data. Of the variation explained by the model, habitat accounted for 85%. Reproductive output was positively related to the amount of edge between mid- and late-seral forests and other habitat classes. The best model explained 84% of the total variability; however, the habitat variable accounted for only 3% of the variation explained by the model. Consitsent with results from the Klamath Province in California (Franklin et al. 2000), a mixture of older forests with younger forests and nonforested areas appeared to benefit owl life history traits. Estimates of λ_H ranged from 0.74 to 1.15 (mean = 1.05, variance = 0.005), with 95% confidence intervals around λ_H for all but one territory overlapping 1, indicating a potentially stable population based on habitat pattern *(Olson et al. 2004).*

In the western Cascades, owl survival had a quadratic (concave) relationship to the amount of non-habitat within 1500 m of owl site centers. The best model of survival explained 58% of total variance, and habitat accounted for 32% of the variance explained by the model. Owl productivity showed a negative linear relationship to the largest patch size of old conifer (> 50 cm dbh) forest within 1500 m of owl site centers (*Anthony et al. 2002a*). The best model explained 77% of the variation in owl productivity; however, 99.6% of this variation was accounted for by owl age, 0.4% by climate, and an immeasurable amount by habitat.

In the southern Cascades, two nested circles (167 and 1565 ha) and the ring between the circles (1388 ha) were used to characterize habitat at owl sites (*Anthony et al. 2002b*). The best model of owl survival indicated that survival increased non-linearly with the amount of mature and old growth forest within 167 ha around site centers and had a quadratic (convex) relationship to the amount of non-habitat in the 1388 ha ring. These two habitat covariates explained 54% of the spatial variation in survival; temporal variation was essentially zero (*Anthony et al. 2002b*). Owl productivity was positively related to the proportion of mature and old-growth forest within 600 m of owl site centers. However, the best model accounted for 25% of the total variance in reproductive output and the habitat variable only accounted for 7% of the model variance. Seventy-four percent of the model variance was explained by a biannual pattern in reproduction ("even-odd year effect") and the experience of male owls on a territory (*Anthony et al. 2002b*).

5.2 WEATHER

In the four studies described above (section 5.1), weather variables used in analyses included temperature and precipitation during various life history periods: winter stress, early nesting, late nesting, dispersal, and heat stress period.

In the California Klamath Province, annual survival was negatively associated with precipitation and positively associated with temperature during the early nesting period (Franklin et al. 2000).

Reproductive output was negatively related to precipitation during the late nesting period. This model explained essentially all of the estimable temporal process variation in reproductive output (Franklin et al. 2000).

In the central Oregon Coast Range, survival was negatively related to early nesting season precipitation and positively related to late nesting season precipitation *(Olson et al. 2004).* The best model explained only 16% of the variation in the data, and most of the variation was spatial; the precipitation covariates explained 15% of the model variation. Reproductive output was positively related to late nesting season precipitation. The best model explained 84% of the total variability; 38% of the model variation was explained by weather covariates.

In the western Cascades, owl survival was positively related to temperature during the winter stress period. The best model of survival explained 58% of total variance, and the weather covariate accounted for 68% of the variance explained by the model (*Anthony et al. 2002a*). Owl productivity was positively related to winter temperature and, to a lesser extent, negatively related to winter precipitation. The best model explained 77% of the variation in owl productivity; however < 1% of the variation was explained by weather and the remainder by owl age.

In the southern Cascades, the best model of survival did not include any effects of weather (*Anthony et al. 2002b*). Owl productivity was negatively related to precipitation during winter. The best model accounted for 25% of the total variance in reproductive output, with the weather variable accounting for 19% of the variance in the model.

Two additional studies found associations between precipitation and fecundity of Northern Spotted Owls: Precipitation during the nesting season was negatively associated with and accounted for 85-86% of variation in fecundity on two study areas in southwest Oregon (Zabel et al. 1996). In the southern Cascades and Siskiyou mountains, Oregon, fecundity was negatively associated with the amount of precipitation during September-April (Wagner et al. 1996).

5.3 BARRED OWLS

Barred Owls were recognized as a possible threat at the time of listing as stated in the federal register:

> "The barred owl's adaptability and aggressive nature appear to allow it to take advantage of habitat perturbations, such as those that result from habitat fragmentation, and to expand its range where it may compete with the spotted owl for available resources. The long-term impact to the spotted owl is unknown, but of considerable concern. Continued examination is warranted of the role and impact of the barred owl as a congeneric intruder in historical spotted owl range and its relationship to habitat fragmentation. The potential for interbreeding of the two species also merits concern and monitoring."
>
> Federal Register 26191

> "The 1989 Status Review Supplement did not reach a conclusion regarding the impact of the barred owl on the distribution, reproductive success, abundance, or survival of the spotted owl. Rather, the Status Review Supplement indicated that the long-term impact of the expansion of the barred owl into the range of the spotted owl was unknown, but of concern. The issue remains unresolved (USDI 1990)."
>
> Federal Register 26173

The effects of Barred Owls on Spotted Owl occupancy, persistence and reproductive success have been addressed by several authors (see chapter 7). On the Olympic peninsula, Gremel (2003 presentation, 2004 pers.comm) has been unable to demonstrate an effect on reproductive success, although the power of his tests is insufficient at this point to draw firm conclusions (the data are in the right direction and border on significance). In the western Cascades, Washington, Iverson (2004) found no difference in reproductive success of Spotted Owls with and without Barred Owls present within 2.5 km of Spotted Owl activity centers. However, the methodology of this paper is flawed in several ways, notably the small sample size and absence of adequate statistical power for the tests employed (Type 2 error), and the compounding of data across years.

In addition to modeling effects of weather and habitat (see above), *Olson et al. (2004)* modeled the effects of Barred Owl presence on Spotted Owl survival and reproduction in the Oregon Coast Range. Barred owl presence was negatively related to owl productivity. However, the Barred Owl covariate accounted for only 2% of the variation in the model, or roughly 1% of the total variation in reproductive output.

As discussed above, the number of territories in which Barred Owls were observed was negatively related to survival of Spotted Owls in two of fourteen study areas (Anthony et al. 2004) and showed only weak relationships to Spotted Owl reproduction. However, the Barred Owl covariate used in the meta-analysis was a post-hoc and compromise measure; it may have been at too coarse of a scale to reveal suspected effects (Anthony et al. 2004). Hence failing to detect an effect in the meta-analysis cannot be ascribed to the absence of an effect in the field. Further study of the demographic consequences of Barred Owl presence or competition are sorely needed (see chapter 12), including mining of existing data at demographic study areas.

5.4 PREY

The following information was available at the time of listing:

> "In some years most pairs may nest, whereas in other years very few pairs even attempt to breed. For example, Gutiérrez *et al.* (1984) noted a broad failure in reproduction from northern California through Washington in 1982. It has been suggested that fluctuations in reproduction and numbers of pairs breeding may be related to fluctuations in prey availability (Forsman *et al.* 1984, Barrows 1985, Gutiérrez 1985)."
>
> Federal Register 26115

Three studies since 1990 evaluated effects of prey abundance and/or diet on Spotted Owl reproductive success (White 1996, Ward et al. 1998, Rosenberg et al. 2003). In the western Cascades, Oregon, Rosenberg et al. (2003) measured three Spotted Owl reproductive parameters (proportion of female owls that nested, number of young fledged per female, and number of young fledged per nesting attempt) as a function of prey abundance and owl diet. Rosenberg et al. (2003) estimated prey abundance by trapping small mammals and estimated diet based on the composition of spotted owl pellets (egested prey remains). The sample unit was an individual territory in a given year (1987-1996). Flying Squirrels (*Glaucomys sabrinus*) were the primary prey consumed by spotted owls (mean = 49% of biomass, SE = 3.9); however, owl reproductive parameters were only weakly associated with both Flying Squirrel abundance ($r^2 \leq 0.26$) and the proportion of Flying Squirrels in the diet ($r^2 \leq 0.19$; Rosenberg et al. 2003). Although Deer Mice (*Peromyscus maniculatus*) comprised a small portion of the diet (mean = 2% of biomass, SE = 0.5), Deer Mouse abundance was strongly associated with the number of young fledged per female ($r^2 = 0.68$) and less strongly with the proportion of females that attempted to nest ($r^2 = 0.39$) and the number of young fledged per nesting attempt ($r^2 = 0.12$; Rosenberg et al. 2003). However, the proportion of Deer Mice in the diet was weakly associated with all reproductive parameters ($r^2 \leq 0.12$; Rosenberg et al. 2003).

The positive association between Deer Mouse abundance and Spotted Owl reproduction was also noted in the Mexican Spotted Owl (Ward and Block 1995, Ward 2001, cited in Rosenberg et al. 2003). Possible explanations for this phenomenon include: (1) Deer Mouse abundance may provide a critical level of nutrients or energy required for owl reproduction, (2) high density of Deer Mice may act as a cue to stimulate Spotted Owl courtship, and (3) Spotted Owls and Deer Mice respond similarly to weather patterns (Rosenberg et al. 2003).

In the Klamath province, California, White (1996) compared the diets of Northern Spotted Owls relative to fledging success based on composition of owl pellets. Pellets were combined across years (1987-1995) and sites (n = 63) for both reproductively successful (≥ 1 young produced) and unsuccessful owl territories. Prey were classified as small (e.g., Deer Mice and Voles [*Arborimus longicaudus*], medium (e.g., Flying Squirrels), or large (e.g., dusky-footed woodrats [*Neotoma fuscipes*]; White 1996). Pellets from successful owl territories contained more large prey (34% of items and 72% of biomass) than those from unsuccessful territories (23% of items and 55% of biomass).

In an analysis similar to that of White et al. (1996), Ward et al. (1998) compared the proportion of large prey (> 100 g) consumed at reproductively successful and unsucessful Spotted Owl territories (1987-1988, n = 9 owl territories). Dusky-footed woodrats comprised 39% of prey items and 71% of prey biomass; however, there was no difference in the proportion of prey > 100 g consumed by owls at reproductively successful and unsuccessful territories (Ward et al. 1998).

A more complete presentation of data on prey effects on Spotted Owl populations is found in chapter 4.

5.5 DENSITY-DEPENDENT FACTORS

The roles of density-dependent and density-independent factors is a long-standing debate in ecology. Density-dependent factors have the potential to stabilize populations at the 'carrying capacity' of the habitat or other equilibria points (e.g. those set by predators or parasites). Density-dependent factors include intra-specific competition, predation, parasitism, disease, etc. Note however that while density-dependent factors may be 'inherently' stabilizing, when the underlying factor itself changes (e.g. the carrying capacity of the habitat decreases) population numbers will also change.

In the case of the Northern Spotted Owl, while inter-specific competition, predation, disease etc all occur, the only significant density-dependent factor hypothesized to occur is intra-specific competition, as manifested in territoriality, and a maximum number of owls that may occupy an area. The presence of floaters (non-breeders who may seize opportunities to take over territories, and otherwise do not breed) argues that Northern Spotted Owl populations are at saturation or carrying capacity with respect to current habitat availability. Other potentially density-dependent factors (e.g. disease) are probably not linked directly to the densities of Northern Spotted Owls per se (but rather to those of overall susceptible avian hosts) so that no density-dependent effect on Northern Spotted Owls is likely.

Note that density-dependent and density-independent factors may interact, complicating interpretation of population dynamics. Franklin et al (2000) have discussed this issue with respect to Northern Spotted Owls, and shown that weather effects may act disproportionately on some 'low-quality' territory owners; hence weather can appear to act as a density-dependent factor because of such interactions.

Note also that a particular density-dependent factor – the Allee effect- may hold when population densities become so low that individuals have problems in, for instance, finding mates. While theoretically possible, such extreme low density effects have not yet been seen in Northern Spotted Owl populations, although the very low population levels in Canada are reaching the point where Allee effects might occur.

5.6 INTERACTIONS AMONG FACTORS

Franklin et al (2000) and Franklin (2003 presentation) have drawn attention to the fact that factors affecting demography do not operate alone, and may interact significantly. For instance, bad weather may have different effects on survival and reproduction, depending on territory 'quality'. In high quality habitat, owls may be buffered to an extent from environmental challenges such as bad weather. This may be understandable, in that, for instance, birds with reduced flight costs, higher prey availability and better thermal environments (all dependent on territory location) might be expected to both survive and reproduce more successfully. Similarly, prey and habitat are strongly linked factors (see chapters on habitat associations and prey, chapters 5 and 4); both are affected by weather, fire, forest management etc., and may be expected to influence owl demography in a complex manner.

Other important interactions include the effects of landscape pattern. As noted in chapter 5, spatial relationshps of different habitat types can have profound influences on prey abundance and availability, and are hypothesized to affect predation and competition. Finally, other chapters have documented strong geographic variation in forest composition, habitat associations, prey identity and abundance and other factors; climate (and weather) clearly correlates with many of these differences. In all these cases, our *a priori* assumption must be that demographic responses of Northern Spotted Owls will be complex, and are unlikely to be explicable in terms of just one driving factor.

Recognition of interactions among multiple factors (often with non-linear relationships) is a feature of the increasingly sophisticated understanding of Northern Spotted Owl demography. Use of information theoretic approaches, of maximum likelihood, and alternative model selection is one way to investigate such complexities. It is important to point out however that, a priori, multiple and interacting correlates reduce statistical power for demonstrating the effects of any one factor in a population. Also, it is appropriate to treat results on any one factor in any geographic area as limited in applicability to other areas, where many factors will be different.

6 EXPLANATIONS FOR REGIONAL AND SUBSPECIES TRENDS

As noted in the preceding section, there are many factors affecting Northern Spotted Owls. These factors are known to vary geographically, and to act in non-linear fashion, and there is evidence that the factors themselves interact in complex ways. Hence, it is a reasonable starting hypothesis that factors affecting populations in different areas will differ, and that it is unlikely that any one factor will explain observed data on demographic performance throughout the range. Given that there are only a total of 14 demographic studies (‘only’ being a relative term – this is the most comprehensive demographic study of any threatened species), there is almost no statistical power for a correlational study of the effect of any one factor, let alone for studies of interacting multiple factors. Hence we advocate considerable caution in attempts to ‘explain’ trends in Northern Spotted Owls, especially given the lack of a comprehensive, coordinated strategy to investigate the effects of correlates (e.g. prey density, weather, habitat change) on demographic parameters.

Nevertheless, we also recognize the need for policy-makers and others to understand the probable causative factors affecting regional or global populations. A Status Review must appropriately consider the current and future effects of different potential threats, even when the data are less than perfect. The following sections therefore evaluate such information as is available.

One pattern in the results from the meta-analysis is quite clear. The populations studied in Washington are performing less well than those in Oregon and California. All four Washington populations are in decline, with an ongoing decrease in survival rates that means the rate of decline is increasing. The authors of the meta-analysis identify five factors that may be contributing to this decline: Barred Owls, wildfire, logging on state and private lands, forest defoliation, and forest succession. Of these factors, some (wildfire, defoliation, succession) are more concentrated in particular biomes, and do not seem sufficient explanations for the general decline. Although the correlative analysis is limited, there is some evidence for Barred Owl effects on survival at three of these four study sites. (Note that northern populations are also more likely to experience deep or long-lasting snow cover, which may interact with factors such as food availability and competition). Essentially similar results are known for the population further north, in Canada. Although there is no formal demographic study in this area, populations are known to be declining rapidly. Timber harvest, fire, insect, and Barred Owl effects are all viable hypotheses for decline in Canada, but again, only timber harvest and Barred Owls appear sufficiently widespread to be a sufficient explanation.

Hence northern populations are in accelerating decline, apparently due to decreasing survivorship. While timber harvest, fire etc may be important and contributing factors, the only factor known to be both general and increasing in effect is the presence of Barred Owls. We emphasize that this is only circumstantial evidence, and that there may in fact be no single over-arching explanation for declines in the northern part of the range. Note also that the northern part of the subspecies range is also the extreme of the species' distribution. Hence it is to be expected that such populations 'at the edge of the range' may be more susceptible to negative factors. Populations in Washington may generally experience lower prey density (chapter 4), higher energy expenditures, more critical weather events, and more usually have lower demographic performance. It is unsurprising therefore that declines may be largest in this portion of the range.

A persistent issue of interest is the effect of timber harvest on population trends. Habitat loss was not addressed by the meta-analysis itself, although the report makes some reference to suggested effects. For instance, of the four declining populations in Washington, one (Cle Elum) had some timber harvest, one had some habitat loss to fire (Wenatchee), while two had little habitat loss – yet all four declined. Similarly one reason for the decline at the Warm Springs Reservation is held to be 'loss of habitat, as there has been continued logging of older forests over the last two decades, and there has been small wildfires in some territories. Similarly, the report calls for comparison of the Hoopa and North West California study sites, because they have different forest management practices. This parallels suggestions in the California Spotted Owl meta-analysis that differences in the demography of owls at one study site could be explained by the presence there of a different vegetation type (Giant Sequoia). These may all be reasonable and plausible explanations or hypotheses; however they must be treated with considerable caution - with such low sample sizes (n=1, 2, or 3), the power of inference is very small. We note that AFRC's preliminary study failed to show any obvious association of current harvest with demographic parameters in a limited sample of study areas. At this point, we feel that it is appropriate for further investigation of the effects of habitat loss on population trends, and that meaningful statements of the effects of timber harvest, fire and other habitat loss on demographic performance must await such a well-planned and systematic study.

7 SMALL POPULATIONS AND DEMOGRAPHIC ISOLATION

> "The central problem of subpopulation isolation is one of maintaining a critical population size level in the absence of genetic or demographic contributions from other subpopulations. The smaller a population or subpopulation and the greater its isolation

from other populations, the greater the risk of its elimination as a result of chance demographic and environmental events or genetic effects (Shaffer 1987).

The population of spotted owls on the Olympic Peninsula may be isolated demographically, and perhaps even genetically, from other owl populations, since there does not appear to be an effective, self-sustaining population in either southwestern Washington adjacent to the Olympic Peninsula or the northwestern Oregon Coast Ranges (Irwin *et al.* 1988, 1989d; A. Potter, Wash. Dept. of Wildlife, Olympia, WA, pers. comm.; Forsman *et al.* 1977; Forsman 1986; W. Logan, Bureau of Land Management, Salem, OR, pers. comm.). While the population in the Oregon Coast Ranges may not be currently isolated due to a tenuous connection to the Cascade populations at the southern part of the range provided by lands managed by the Bureau, the scale of habitat fragmentation throughout the range is of considerable concern (USDI 1989). As one moves north along the Oregon Coast Ranges, habitat ownership becomes fragmented because of checkerboarding of Bureau and private lands. Remaining old growth and mature forests become more fragmented as well. During the next 10 to 15 years, given the existing direction of land management, the current degree of isolation on the Olympic Peninsula and the potential for isolation of portions of the Oregon Coast Ranges province are likely to become exacerbated, as most intervening habitat is privately owned. Currently there are few pairs of owls in the northern part of the Oregon Coast Range and under current management trends, these may disappear as remaining suitable habitat is lost or becomes too isolated."

Federal Register 26182

The listing document (USFWS 1990) makes reference to the effects of small population size, and of demographic isolation of populations. Some populations of Northern Spotted Owls are undoubtedly at low densities (e.g. South West Washington, North Coast Oregon, Canada), while others may have greater or lesser degrees of demographic isolation, with reduced dispersal into and from neighboring areas (Olympics, Canada, Marin County). Recent genetic evidence suggests that gene-flow may indeed be reduced in the Marin County population of Northern Spotted Owls, but especially in some California Spotted Owl populations (Henke et al. in prep).

Small and isolated populations are widely recognized as being subject to unique effects, including inbreeding, demographic stochasticity, and catastrophic events. While such effects have been acknowledged as potentially important to Northern Spotted Owls, they have received relatively little study or emphasis. We have no new information to review here. However, it is perhaps worth pointing out that some emerging threats and trends are likely to have greater effects on small and/or isolated populations. For instance, hybridization with Barred Owls is usually now regarded as being of limited extent, and as posing only a minor threat (see chapters 7 and 10). This assumption may not hold true for extreme situations where Barred Owls greatly outnumber Spotted Owls, which may then have problems finding mates (i.e. currently in Canada, and perhaps in areas of Washington in the future). Similarly, we have largely discounted the idea that loss of genetic diversity will be a significant factor in the short term for Northern Spotted Owls (chapter 3). For the <30 pairs of remaining Canadian birds, this may not be correct. Once again, new threats, such as West Nile Virus (see below) could potentially eliminate all members of a small population.

Small and low density populations of Northern Spotted Owls may not contribute greatly to the overall numbers of the subspecies. However such populations may have disproportionate value in terms of geographic representation, and may be the kernel for recovery strategies.

8 POPULATION PROJECTIONS AND EXTINCTION RISKS

Evaluations on status of the Northern Spotted Owl, including final status under ESA, must address future probabilities of persistence, recovery or extinction. The listing decision (1990), Final Draft Recovery Plan (1992), NWFP (1994) and other documents have all considered these probabilities, and such assessments remain key to regulatory decision-making (e.g. jeopardy calls). However, there has been relatively little attention paid to formal risk assessments or population projections. The demographic studies described in earlier sections, and in the meta-analysis (Anthony et al 2004) have carefully and explicitly stated that such results are retrospective only, and should not be used for population projections, or assessment of extinction risks.

In the Appendices , Noon (2004) reviews the history of population projection models as applied to Northern Spotted Owls, and in particular the models underlying the listing decision and the NWFP (chapter 9 provides a complementary perspective on the NWFP). As Noon shows, the basic premises of these models remain as valid now as in 1990 or 1994. (Note that this appendix represents the work and opinion of Noon alone, but was commissioned as part of the SEI status review process).

As discussed elsewhere in this chapter, and in chapter 9, the NWFP adopted management options that were held to have a high likelihood of eventual recovery of Northern Spotted Owl habitat and Northern Spotted Owl populations. However, in the first phase of plan implementation (first 20 years) populations were predicted to decline (Raphael et al 1994 appendix to SEIS). Moreover, during this period population projections were extremely sensitive to starting conditions in the models, essentially rendering them useless as predictions of actual trends or as tools to assess the success of the NWFP in terms of owl recovery (Raphael et al. 1994).

Given this background and lack of a yardstick on which to judge population trends, we are unable to determine the current causes of demographic change in Northern Spotted Owl populations, or to predict future outcomes. We cannot, for instance, distinguish at this point between three outcomes discussed at the time of listing, and NWFP design:

1. A temporary decline and eventual recovery of Northern Spotted Owl populations, following regrowth of forest habitat
2. Temporary or other decline of Northern Spotted Owl populations due to climatic or other factors
3. Ongoing decline and extinction of Northern Spotted Owl populations that have passed ‘extinction thresholds’ (sensu Lande 1987)

Our inability to distinguish between such different outcomes is regrettable, but is a consequence of lack of explicit yardsticks and models. Noon (Appendix) argues that this is a fundamental gap in our ability to understand and manage Northern Spotted Owl populations. In chapter 12, we also argue that this would be a useful or critical need to be met by future work (however we feel that modeling should not be seen as a substitute for essential monitoring or experimental activities).

We note three additional issues with population projection or PVA modeling for Northern Spotted Owls. Firstly, to be effective, such models must address all major factors affecting owl populations, and not simply those affecting habitat. West Nile Virus, Barred Owls, and weather may all affect Northern Spotted Owls, and interact with habitat, prey, etc. to drive patterns of population persistence or extinction.

Secondly, some important factors will probably always be difficult to parameterize. A currently unresolved issue is the degree to which current declines in some owl populations reflect harvest of years or even decades past. Lacking any understanding of the extent and duration of such lag effects, models (at one and the same time) may be difficult to parameterize, and also more valuable as exploratory tools.

Thirdly, as noted by Noon (Appendix) and the panel (Chapter 12), models are often most useful when integrated with a well-designed experimental and monitoring program, by generating testable hypotheses. Such integrative and adaptive science and management programs would greatly advance understanding of Northern Spotted Owl populations, and our ability to predict population trends.

9 PREDATION

Predation was addressed in the Federal Register in the following passages:

> "The Status Review Supplement (USDI 1989) recounted both the observation of predation on spotted owls by great horned owls and the concern that such predation may increase with increasing habitat fragmentation. The Status Review Supplement did not make a judgment as to the impacts of great horned owl predation on the spotted owl population; the 1990 Status Review (USDI 1990) deals with the situation in a similar fashion (Sec. 3.5). The Service employs the best scientific information available and extrapolates where warranted and does not believe that unwarranted conclusions were drawn concerning the significance of predation or competition to the status of spotted owl populations."
>
> Federal Register 26174
>
> "Specific impacts of great horned owl predation on the overall spotted owl population are unknown, but this remains an issue of concern."
>
> Federal Register 26187

9.1 INCIDENCE OF PREDATION

Although practically all birds are subject to predation, it is not easy to assess its effects on population levels (Newton 1998). Most predators of birds are generalists, utilizing a wide variety of prey opportunistically. Predation is seldom distributed evenly in space and time and may be concentrated near predator breeding sites, where prey are unusually plentiful or vulnerable, or on particular age groups, social classes, or sexes (Newton 1998). Some long-term declines in bird populations have been associated with landscape level habitat changes that have resulted in the loss of a species primary habitat, which in turn has promoted an increase in predator abundance and prey vulnerability. It has been suggested that this may be the case of the Northern Spotted Owl (Dawson et al. 1985, Thomas et al. 1990, USDI 1990, USDI 1992).

Predation on Spotted Owls has been directly observed only infrequently (*R. Reynolds pers. comm. via E. Forsman*), but the examination of the remains of numerous corpses indicates that predation was the most likely cause of death in many cases. The majority of potential predators on Northern Spotted Owls are other large birds and include Great Horned Owls (*Bubo virginianus*, Forsman et al. 1984), Northern Goshawks (*Accipiter gentilis*, USDI 1992), Cooper's Hawk (*Accipiter cooperi*, Forsman et al. 1984), Red-tailed Hawks (*Buteo jamaicensis*, *E. Forsman, pers. comm.*), Barred Owls (*Strix varia*, Leskiw and Gutiérrez 1998), Ravens (*Corvus corax*, USDI 1992), and Golden Eagles (*Aquila chrysaetos*, *R. Reynolds pers. comm. via E. Forsman*). The lone potential mammalian predator is the Fisher (*Martes pennanti*) and is only a suspected predator because it has been observed climbing in Spotted Owl nest trees (Gutiérrez et al. 1995).

While a number of reports and publications provide some information on predation (*Meslow and Miller 1983*, *Meslow et al. 1984*, *Meslow and Miller 1984*, Forsman et al. 1984, *Meslow et al. 1985*, Gutiérrez et al 1985), the best quantitative data on predation is provided for adults and subadults in USDI (1992) and juveniles in USDI (1992) and Forsman et al. (2002). In these studies, 10% of the 344 radio-tagged adults and subadults, and 21% (N=85) and 18% (N=386), respectively, of radio-tagged juveniles died from predation (Table 8.6). The consensus of all of these works was that Great Horned Owls were responsible for most predation events on Spotted Owls. However in other parts of the range, Goshawks appear to be locally important (Blakesley, pers.ob.).

9.2 BIOLOGY OF PREDATORS

The Great Horned Owl (*Bubo virginianus*) can be found throughout North, South and Central America (Johnsgard 2002, Voous 1989). This species occupies a broad range of habitats from dense forests to essentially treeless areas. In the Pacific Northwest, this owl occupies a variety of habitats and coexists with the Northern Spotted Owl where there is a combination of older forest and natural or man-made clearings *(Johnson 1992).* While habitat composition of the landscapes where Great Horned and Northern Spotted Owls responded was variable and often similar, Great Horned Owl response locations tended to be less forested, in younger forests, and had greater linear edge-to-old forest ratio than sites where Northern Spotted Owls responded *(Johnson 1992).* This led *Johnson (1992)* to conclude that these two species were keying on opposite ends of the habitat spectrum. Ganey et al. (1997) found considerable overlap in home ranges between Great Horned Owls and Mexican Spotted Owls (*S. o. lucida*), but they noted that overlap within individual forest stands was limited.

Northern Goshawks (*Accipiter gentilis*) inhabit boreal and temperate forests within the Holarctic region (Squires and Reynolds 1997) and, where their ranges overlap, they use forests with features similar to those used by Northern Spotted Owls. While generalists at large spatial scales, goshawks consistently nest in mature trees set amid groups of codominant, close-canopy neighbors (Reynolds et al. 1982, Squires and Reynolds 1997, DeStefano 1998). This nest grove is situated within a larger (10-100ha) homogenous forest stand typified by deep, closed canopies and little shrub cover (Reynolds et al. 1992, Finn et al. 2002b). Goshawk post-fledging areas (100s of hectares) and home ranges (1000s of hectares) are dominated by mature sawtimber or mid- and late-seral, closed canopied forest (*Allison 1996*, *Daw 1997*, *Desimone 1997*, *McGrath 1997*, *Patla 1997*, Finn et al. 2002a). On the Olympic Peninsula, occupied goshawk sites tend to have a high proportion of late seral forest, reduced non-forest cover, and reduced landscape heterogeneity in areas ranging from tens to thousands of hectares around the nest site (Finn et al. 2002a). Goshawks consistently used nests in 40+ year old trees situated within mature (mean = 120 year old) forest stands of Douglas-fir and Western Hemlock. Canopy cover was nearly 80% in occupied stands and reproduction and occupancy were greatest where shrub cover was <20% (Finn et al. 2002b). Late seral forest was consistently >40% of the landscape (measured at tens to thousands of hectares) surrounding occupied sites at goshawk territories from Arizona to Washington (Reynolds et al. 1992, Finn et al 2002a).

Goshawks hunt a great diversity of avian and mammalian prey in a wide variety of forest types, including clearcuts, riparian forest, and moderately dense to open conifer forests (Beier and Drennan 1997, Watson et al. 1998, Bloxton 2002). But, they rarely occupy landscapes with <15% non-forest (naturally open areas and recent harvests; Finn et al. 2002a). Thinning to reduce fire risk may benefit goshawks. Deep tree crowns can be produced by thinning Olympic Peninsula forest stands at 20-50 years of age (Long et al. 1983). Heavy thinning may increase shrub cover to the detriment of goshawks (prey is reduced in availability), but moderate thinning (reduction to 57-73 trees per hectare; Finn et al. 2002b) can facilitate crown development while limiting understory growth because the canopy closes rapidly (Hayes et al. 1997).

Barred Owl predation on Spotted Owls is suspected, and could be locally important in small Spotted Owl populations which are outnumbered by Barred Owls (e.g. Canada). Barred Owl-Spotted Owl interactions are discussed in chapter 7.

Forsman et al (2004) report one instance of a Northern Spotted Owl pellet containing Northern Spotted Owl remains.

9.3 EFFECTS OF PREDATORS ON SPOTTED OWLS

At a trivial level, predation must be important to Spotted Owl populations. All owls die, and the proximate cause of death is presumed to usually be biological: predation, disease, starvation, heat or cold stress, old-age, etc. By contrast, habitat loss is never the proximate causes of death, even though it is often the driving force behind population decline. In understanding the effect of factors on Spotted Owls, we must distinguish between the immediate agents of mortality (e.g. a predator) and the ultimate cause of vulnerability (e.g. lack of suitable habitat, food, competition etc.). Table 8.6. shows that predation on Northern Spotted Owls undoubtedly occurs, and at levels that could be important to populations.

There are no studies addressing whether predation levels affect Spotted Owl population trends. In the absence of such direct studies, we cannot fully evaluate the role of predators in Spotted Owl populations. However, there are several lines of indirect evidence that suggest that predation is not a major influence. For instance, numerous demographic studies (Forsman et al. 1996) have shown that annual survival is high for territorial owls and that these individuals are rapidly replaced upon death or disappearance. This implies that availability of territories is a limiting factor in such populations, rather than adult mortality. Predation does not seem to contribute towards a reduction in the breeding population (Newton 1998) of Northern Spotted Owls. If predation mortality is compensatory and not additive, it is of little concern to the long-term persistence of any population.

Additional indirect evidence for the lack of significant effects of some predators on Northern Spotted Owls is the work of Crozier et al. (in press) who showed experimentally that Northern Spotted Owls did not show any avoidance responses (reduced responses to conspecific calls) after hearing Great Horned Owls. Presumably if Great Horned Owls were major sources of mortality for *S. occidentalis*, they would have evolved anti-predator responses. This does not appear to be the case.

In summary, the majority of observations of predation are incidental to other studies, and there does not appear to be a strong case that predators are having major influences on Northern Spotted Owl dynamics. In their responses to the questionnaire, few panelists felt that predation was an important risk factor for Northern Spotted Owls (chapter 10). However, it should also be noted that there has been no systematic examination of predation, and that there is no effort to, for instance, assess predator numbers as a potential covariate in demographic studies. Since small increases in adult mortality could lead to decreased survivorship, and hence lower values for λ, the potential still exists that predation could affect population trends. However, at this point, a strong effect of predation is best regarded as an untested hypothesis which, while still possible, lacks any empirical support, and is not favored by circumstantial evidence.

9.4 INTERACTION OF PREDATION AND FRAGMENTATION

At the time of listing:

> "Predation by great horned owls (*Bubo virginianus*) has been identified as a major source of juvenile mortality in spotted owls (USDI 1987; Dawson *et al.* 1986; USDA 1986; Simberloff 1987; and USDA 1988). Concern has been expressed that increasing habitat fragmentation may be subjecting spotted owls to greater risks of predation as they move into or across more open terrain, or come into more frequent contact with forest edges where horned owls may be more numerous."
>
> Federal Register 26187

Fragmentation effects on Northern Spotted Owls have been discussed in other chapters. It is clear, for instance, that habitat heterogeneity is positively correlated with individual performance in some geographic areas (chapter 6), arguing against a simple, single effect throughout the range of fragmentation per se. Nevertheless, indirect effects of fragmentation through increased predation levels remains a possible effect – no evidence has contradicted the hypothesis. However, given the general lack of concern regarding predation effects (see previous section), and the absence of any corroborating evidence, there appears to be no reasonable basis for regarding an effect of fragmentation on predation levels as a primary or significant effect on Northern Spotted Owl populations. Absent new information, the indirect effects of fragmentation through predation remains an untested hypothesis.

9.5 INFORMATION NEEDS ON PREDATION

The panel did not regard new information on predators or their effects as a major information need (see chapter 12). Nevertheless there are significant issues that would repay further attention:

1. The data, as reported, does not allow time-specific analysis and interpretation for assessing annual influence of predation on Northern Spotted Owls (e.g. 20% predation mortality annually or over the 10 year period of study?).
2. Are radioed owls representative of the owl population in general?
3. Do radios influence predation risk?
4. Was habitat structure a contributing factor towards increasing vulnerability to predation of any owls, notably juveniles?

10 THE THREAT OF WEST NILE VIRUS TO NORTHERN SPOTTED OWLS

In an increasingly human-dominated world changes in land cover, land use, climatic regimes, and the ease with which we traverse our planet allow exotic species to thrive (Vitousek et al. 1996). Exotic species homogenize and reduce our distinct plant and animal life, often regardless of traditional plans to preserve or steward habitat (Vitousek et al. 1997). Introduced diseases often emerge as epizootics on native plants and animals that lack co-evolved immune responses. Not surprisingly, we often learn about exotic diseases challenging the population viability of native species. Recent examples include (a) plague challenging prairie dogs, (b) malaria and pox extinguishing Hawaiian birds, (c) rinderpest and distemper devastating African wildlife, and (d) fungi that defoliate and exterminate native trees (e.g., Dutch Elm Disease, Sudden Oak Death, Beech Bark Canker, Chestnut Blight; Daszak et al. 2000, Dobson and Foufopoulos 2001, Harvell et al. 2002). Most recently, West Nile virus (WNV) has killed millions of wild birds in North America since it arrived in 1999 (McLean et al. 2001, Caffrey and Peterson 2003, Marra et al. 2004).

10.1 THE BIOLOGY AND ECOLOGY OF WEST NILE VIRUS

West Nile virus was first isolated in 1937 in Uganda (Smithburn, et al. 1940). It was one of the earliest mosquito-borne viruses discovered by humans, but it was not considered significant because few people died from the resulting mild febrile disease. From 1996 to 1999, however, epidemics occurred in southern Romania, southern Russia, and the US (Hayes 2001). The resulting deaths of people in each outbreak was unexpected (over 300 died from 1999-2003 in the US), and led to close monitoring of the disease and its spread.

Like other flaviviruses within the Japanese encephalitis sero-complex, WNV is an arbovirus that is primarily transmitted by mosquito vectors (Fig. 1; Lanciotti et al. 1999; McLean et al. 2001). While the primary host species of WNV are avian, other vertebrate animals (humans included) may be infected incidentally and develop disease.

WNV appears to have come to New York City in 1999 from the Middle East. Analysis of E-protein gene fragments indicates two major strains of WNV. The United States strain is closely related to a strain isolated from a dead goose in Israel in 1998. Possibly an infected bird, mosquito, or person from this area entered NYC with the disease (Lanciotti et al. 1999, Hayes 2001). This strain has higher documented bird mortality than other strains (Turell et al. 2002). The disease spread across North America in four years after it was introduced in New York in 1999 (Fig. 2).

WNV is an enveloped virus roughly 50 nm in diameter (Fig. 3). It has an icosahedral nucleocapsid that is roughly 30-35nm in diameter. The WNV genome is a single-strand of positive-sense RNA, roughly 12Kb in length. The genome encodes 10 proteins (three structural and seven non-structural) organized 5’ to 3’ as: C (capsid), prM (protease and Maturation), E (envelope), NS1, NS2a, NS2b, NS3, NS4a, NS4b, NS5 (Lanciotti et al. 1999, Margue et al. 2002).

10.2 WEST NILE VIRUS AND NORTHERN SPOTTED OWLS

WNV transmission depends on numerous factors, including: presence of a competent reservoir of birds, presence of a competent vector, a susceptible population, mosquito abundance, species diversity, and habitat structure (Deubel et al. 2001,Petersen and Roehrig 2001). Some of these factors are not optimal at least in the northern portions of the range of the Northern Spotted Owl. WNV has not emerged in Washington or Oregon, although isolated cases have been reported. In California, WNV is confined to six counties in the southern portion of the State. At least 39 species of mosquitoes and possible hybrids are known to be WNV vectors in North America (Nowak et al. 2001, Turell et al. 2001a, Fonseca et al. 2004). We know that 17 of these are present within the range of the Northern Spotted Owl (Table 8.7; Turell et al. 2001a, Dohm et al. 2001, Washington Dept of Health 2003, Boyce et al. 2004), but we do not know if the cool temperatures, little contact with infected hosts, or short-term climatic fluctuations (recent summers have been drier than normal west of the Cascades) have limited the emergence of the disease. Health officials expect eventual emergence throughout California, Oregon, and Washington.

We know less about the behavior of vectors in the range of the Northern Spotted Owl than we do about the abundance and distribution of possible vectors. The exact distance mosquitoes will fly from their birthplaces is unknown, but most of the species identified as potential vectors are believed to travel only 1-1.5 km over their lifetimes (Turell et al. 2001a, Dohm et al. 2002. *Aedes vexans* may travel up to 30 km, and generally lay eggs on river flood plains (Dohm et al. 2002). Culex tarsalis may also travel tens of kilometers during a lifetime and up to 10 km in a single night (need a ref here from alan). Environmental temperature has been shown to effect experimental transmission of WNV to mosquitoes in the laboratory, and the rate at which infections are disseminated throughout the mosquito, with more effective transmission and more rapid dissemination occurring at 30ºC as compared to 18ºC (Dohm et al. 2001). Further, temperature has also been shown to play a potential role in diapausing of both WNV and a related virus, Saint Louis Encephalitis (SLE) virus in mosquito vectors during winter months (Reisen et al. 2002, Mostashari et al. 2003). Females infected and overwintered at higher temperatures retained their infections through winter and transmitted it readily. Feeding on a vertebrate host after diapause termination significantly increased the titer of SLE in previously infected females (Mostashari et al. 2003). Overwintering temperature has been demonstrated to affect the recoverability of WNV in *C. pipiens*. At wintering conditions of 26ºC, virus was recoverable from most mosquitoes, while at 10ºC no virus could be recovered. However, mosquitoes incubated at 10ºC that were subsequently transferred to 26ºC for 2-3 days had increased virus dissemination and recoverability (Reisen et al. 2002). Therefore, throughout the range of the Northern Spotted Owl, mosquitoes exist at temperatures where transmission of WNV during the summer is effective. In most of the owl's range, infected mosquitoes can also overwinter, thereby allowing rapid spread of the disease during favorable conditions. One species of mosquito, *Culex tarsalis*, may be an important vector of WNV to Northern Spotted Owls. This species is abundant across the owl's range, feeds primarily on birds, is an efficient vector of WNV, and breeds in a variety of habitats. Populations of *Culex tarsalis* seem to fluctuate markedly, depending on weather before and during the peak mosquito breeding season. For example, summer abundances of *Culex tarsalis* in Kern County, California were positively correlated with river runoff. Increases of *Culex tarsalis* during the wet years also coincided with the re-appearance of western equine encephalomyelitis virus, which was carried by this mosquito (Wegbreit and Reisen 2000).

West Nile Virus passes through a diversity of vertebrate hosts. Though infected reptiles and mammals suffer morbidity and occasional mortality, most are infected at relatively low rates and are understood to be incidental hosts largely irrelevant to maintaining WNV reservoirs or spreading the disease (Campbell et al 2001). An important exception is the possible role of mammalian prey to the spread of WNV among predators, like Northern Spotted Owls. For example, in a Pennsylvania study 60-70% of shrews and squirrels and 20-40% of deermice carried WNV (Larry Clark, National Wildlife Research Center, *personal communication*). Owls and other predators of mice can contract the disease by eating infected prey, thus spreading the disease (Garmendia et al. 2000, Komar et al. 2001). More commonly, birds are the key reservoir hosts of the virus and as such are vitally important to understanding both the disease's ecology and public health consequences. (Rappole et al 2000, Mostashari et al. 2003). Over 150 native birds are known to host WNV in North America (Bernard and Kramer 2001, Komar et al. 2001, Komar et al. 2003, Marra et al. 2004). The virus's effect on laboratory-infected species varies widely in terms of viremia, mortality, and competence (Komar et al. 2003) and the role of various birds as primary reservoir hosts versus secondary reservoir hosts or incidental hosts is poorly understood. Some highly competent species such as the House Finch, American Robin, Ring-billed Gull, Killdeer, and House Sparrow suffer relatively low morbidity/mortality, and are therefore considered likely candidates for virus-amplifying, primary reservoirs (Dobson and Foufopoulos 2001, Bernard and Kramer 2001, Komar et al. 2001). Species showing low WNV competence in the laboratory, for example Rock Pigeons, European Starlings, and most native songbirds, are presumed to play little role in the virus's spread. However, field evidence specifying ecological relationships between virus and host is lacking. The only firm conclusions we can draw are that, via mosquito and possibly contact infection, the virus is amplified and spread in an unpredictable pattern by unspecified avian hosts through indefinite ecological mechanisms (Rappole et al. 2000, Campbell et al. 2002).

A recent modeling exercise by scientists at the University of California, Davis combined information on the occurrence of vectors and competent hosts to predict where WNV is likely to affect California wildlife, including Northern Spotted Owls (*Boyce et al. 2004*). The highest risk area in California is the Central Valley, but the western Sierra Nevada, Pacific Coast and adjacent inland areas, as well as portions of southern California are also at risk (Figure 4). This exercise suggests that populations of Northern Spotted Owls in the coastal mountains of northwestern California are at the greatest risk of exposure to WNV. Owls in the Cascade Mountains of California are at moderate risk of exposure.

One of the unexpected aspects of the North American emergence of WNV has been the severity of bird mortality. Mortality has been large enough to qualify as an 'epizootic.' Epizootics did not occur in other recent, old world WNV epidemics. Another unexpected aspect of the WNV epizootic has been its selectivity. Bird species vary in their susceptibility to WNV. Why some bird species experience almost 100% mortality and others experience none is not clearly known. Corvids (crows, ravens, magpies, and jays) are especially susceptible to the disease, but raptors are also vulnerable. Susceptibility varies greatly, even within bird groups. In raptors treated at The Raptor Center in Minnesota, Dr. Pat Redig (*personal communication*) reports that Great-horned Owls, Red-tailed Hawks, Cooper's Hawks, and Northern Goshawks died in large numbers when WNV first (2002) appeared in the region. Barred Owls were diagnosed with WNV less frequently. In Ohio, Dr. Thomas Grubb (*personal communication*) recorded 100% mortality of breeding Screech Owls (n = 61) when they were first exposed to WNV. Redig discovered that owls differ from hawks in how they respond to WNV. Owls localize the virus in the brain and heart. Hawks localize it in their heart and kidney. Hawks often go blind, but owls retain their vision and show signs of neurological damage (twisted necks and bobbling heads), and extensive tissue lesions (including their heart, brain, liver, kidney, pancreas, lung, and gonads (Fitzgerald et al. 2003). It appears that owls are quite susceptible to WNV, but some level of innate resistance may occur (Fitzgerald et al. 2003). This might explain why both Redig (using owls recovered by the public) and Grubb (observing wild owls) observed markedly lower mortality in the second year of exposure to WNV, suggesting that local impacts may be intense, but short-lived. This reduction in effect of the disease was also seen in Red-tailed Hawks and Great-horned Owls in the Northeast (Caffrey and Peterson 2003). The short-term, nature of mortality, and the fact that it is usually not uniform across a region (Kevin McGowan, Cornell University, *personal communication*), may explain why effects at a regional scale on populations are not large, even for very susceptible species (Caffrey and Peterson 2003). However, an alternative explanation is that populations of the WNV mosquito vector were reduced in following years, resulting in lower observed mortalities. The disease may exhibit an irruptive behavior as was seen in Colorado in 2003 when human cases increased from 14 (0 deaths) in

2002 to 2947 (63 deaths) in 2003. This type of increase had not been observed in other states where the disease had been prevalent for a longer period of time and was attributed primarily to environmental conditions that promoted large populations of *Culex tarsalis* mosquitoes.

Wild birds develop resistance to WNV. Birds can develop antibodies that prevent WNV E-proteins from binding with receptors or that interfere with virus structure (Deubel et al. 2001). Even extremely susceptible species like crows do not continue to die at high rates each year following the occurrence of WNV. The mechanisms allowing this in North America are not well known, but elsewhere species congeneric to susceptible species in North America have evolved resistance. In Egypt, for example, as many as 87% of adult Hooded Crows have WNV antibodies (Work et al. 1955). Juvenile crows have lower rates, but apparently build antibodies during their first summer as they are exposed to the disease. Hooded Crows show that immunity can develop, but this Old World species has co-evolved with the disease for many generations. Moreover, the strain of WNV in Egypt is less virulent than that North America. Thus, while immunity will eventually develop, it is uncertain how quickly this will happen in North America and how effective it will be among New World raptors.

Of importance to Northern Spotted Owl conservation is an estimation of the impacts WNV will likely have on owls directly and their predators, prey, and competitors, indirectly. We know that spotted owls are susceptible to WNV. A single captive Northern Spotted Owl contracted the disease and died in 2002 at The Owl Foundation's facility in Ontario. Nearly half of the 235 raptors at The Foundation died. Dr. Bruce Hunter (*personal communication*) tested 85 raptors and concluded that even though all the owl species had an approximate 86% exposure rate to WNV, susceptibility varied greatly among species. Some of this variation may be due to the captive setting. Neither Eastern Screech Owls nor Great-horned Owls were very susceptible, yet we know from Redig's and Grubb's work in nature that they are susceptible. Hunter reports that susceptibility was markedly higher among northern species than southern ones. Owls most susceptible to WNV at The Foundation were Snowy Owls, Northern Hawk Owls, Great Gray Owls, Boreal Owls, and Northern Saw-whet Owls. Pygmy Owls, Short-eared Owls, Flammulated Owls, Long-eared Owls, Great-horned Owls, Eastern Screech Owls, and Barred Owls were least susceptible. Of eight Barred Owls at The Foundation, only one died and it showed no presence of WNV.

The known response of raptors and other birds to WNV allows cautious speculation about the effects of this emerging, exotic disease on Northern Spotted Owls. It is undeniable that WNV is a new threat to Northern Spotted Owls. WNV also has the potential to reduce population viability throughout the owl's range. But the degree to which this potential will be realized is quite uncertain. It is not certain: (1) what proportion of owls that are infected will die from WNV; (2) how uniform infection will be throughout the range of the owl; (3) when, or if, owls will develop some immunity to the disease and therefore limit the duration of expected mortality; and (4) how the potential indirect benefits of reduced predation (e.g., loss of Northern Goshawks), the potential indirect detriments of increased competition (e.g., relative increases of less susceptible Barred Owls), or reduction in nest site availability by reductions in facilitating species (e.g., Northern Goshawks in eastern Washington, Tracy Flemming, NCASI, *personal communication*) will balance. We offer two scenarios of the impact of WNV that span the range in uncertainty.

Scenario 1. Range-wide reduction in Northern Spotted Owl population viability is unlikely. Because the risk of contracting WNV is not uniform across a region (*http://earthobservatory.nasa.gov?Newsroom?NewImages/images.php3?img_id=10784*), we suspect some locales will experience high Northern Spotted Owl mortality, while others will not. Warmer and seasonally drier habitats, such as those east of the Washington and Oregon Cascade Mountains, are likely at greatest risk because mosquito populations interact with a variety of virus-amplifying hosts, grow rapidly, and spread the disease most effectively in such climates (Turell et al. 2001b, McLean 2003). Coastal areas in northern California may be at even higher risk (*Boyce et al. 2004*). Increased mortality is expected to last 1-2 years after WNV emerges in a region, as it has in the Eastern and Midwestern US (Caffrey and Peterson 2003). A sizeable proportion of adult owls should develop resistance to the disease during this time, as Hooded Crows appear to have done in Egypt, but juvenile mortality may continue to be high until the population evolves greater resistance or the disease evolves less virulence. Using this same reasoning, the indirect effects of WNV on Northern Spotted Owls are also expected to be spatially variable and of relatively short duration. The cumulative effects of indirect factors may be minimal. Competitive gains by Barred Owls and momentary losses of nest sites provided by goshawks will be balanced by reductions in Northern Spotted Owl predators, notably Great-horned Owls and Northern Goshawks. Therefore, as is apparently occurring with Eastern Screech Owls and Great-horned Owls in the Midwest, the duration of population impacts due to WNV is likely to be short and the direct, range-wide effects on viability may be minimal (Caffrey and Peterson 2003; Thomas Grubb, Ohio State University and Pat Redig, The Raptor Center, St. Paul, Minnesota, *personal communications*).

Scenario 2. Range-wide reduction in Northern Spotted Owl population viability is likely. We suspect that WNV will occur locally throughout the range of the Northern Spotted Owl and affect adult and juvenile mortality as in Scenario 1. But the presumed limited impacts on Northern Spotted Owls in Scenario 1 are based on observations of common, wide-spread species like Eastern Screech Owls, Red-tailed Hawks, and Great-horned Owls. Rare species, like Northern Spotted Owls may not be able to recover quickly or uniformly from another source of mortality because local populations are small, not particularly diverse in a genetic sense (Brinigar et al. *personal communication*), and often isolated. Populations of long-lived species with relatively low annual reproductive output like Northern Spotted Owls, are especially sensitive to changes in adult mortality (Noon and Biles 1990, Franklin et al. 2000). Therefore, even though adult mortality may only affect owls for a few years, this, and the persistent increase in juvenile mortality, may be a significant threat to population viability.

We consider either scenario likely. Where the Northern Spotted Owl co-occurs with large mosquito populations mortality may increase for a few years after WNV emerges in the region. This direct effect and possible indirect effects may eliminate Northern Spotted Owls in parts of their range, but range-wide reduction of population viability is unlikely because owl populations number in the several hundreds to thousands. Thus, severe, but short-term population reductions may be tolerated. Alternatively, the effects of the disease may exhibit annual fluctuations with occasional years of high mortality that could result in long-term declines that may lead to extinction in parts of the range. The problem is that the disease has only been in the United States for five years and no studies have been able to adequately assess the effects of the disease on avian populations for a sufficiently long period of time and under fluctuating environmental conditions.

The uncertainty in how Northern Spotted Owls will respond to WNV should encourage researchers to learn more about the disease in their study areas (Boyce et al. 2004). To do this requires monitoring of vectors and hosts, preferably before, during and after the emergence of WNV. In California, researchers are already sampling owl blood to determine owl exposure to the disease, and some are sampling small mammals for prevalence of the disease in owl territories and mosquitoes to document important vectors. Additional data may be available from county or state Health Departments who often monitor mosquitoes and visible, ineffective hosts like corvids to track the disease and the risk to people. Coordinating efforts with such ongoing work may allow owl researchers to better evaluate the effects of WNV. In areas remote from people, owl researchers will probably have to conduct their own sampling. We suggest sampling owl blood, as well as mosquitoes and potential amplifying hosts, like American Robins, House Finches, Killdeer, and other finch and thrush species. Annual sampling would allow researchers to document persistent effects on survival, reproduction, and population viability of owls and elucidate how the disease is maintained and spread within the owl's range.

11 SUMMARY

The wealth of information on the demography of the Northern Spotted owl is unique. For no other threatened or endangered species do we have such extensive information on population trends and the factors affecting them. The demographic studies reported here are among the most significant scientific achievements in conservation biology.

Yet the information is still far from complete, and inadequate to make critical assessments. While Northern Spotted Owl populations appear to be in decline, it is not possible to determine whether this decline is greater than that predicted at the time of completion of the NWFP (see chapter 9 for fuller discussion of this issue). It is also not possible to predict the final fate of the Northern Spotted Owl populations (e.g. whether extinction thresholds have been passed, or whether the population will rebound as habitat develops). Some critical uncertainties (e.g. on causes of demographic change at particular study areas; correlations of demographic change with timber harvest; the effects of Barred Owls) are amenable to analysis (including re-analysis of existing data) or experimentation. Other key uncertainties (e.g. the effects of past logging on current demographic trends; extinction thresholds) are much more difficult to evaluate, and may ultimately be impossible to resolve. Such difficulties are not unusual for threatened and endangered species management. As we have discussed elsewhere in this report (chapters 1, 10, 11), uncertainty is inevitable in the management of large complex systems, such as the forest habitats of the Northern Spotted Owl.

Median natal dispersal distance was 1.7 times greater for female than male Northern Spotted Owls (median 23-25 km for females and 14-15 km for males), which is typical among avian species. Only 9% of juveniles dispersed > 50 km (range 0.6 – 111.2 km). Over half of the owls of both sexes were not paired until at least two years of age, and 9% of owls banded as juveniles were first reobserved as territorial individuals at ≥ five years of age. Owls did not disperse across the large unforested valleys of Oregon but did disperse between the Coast Range and Cascades through forested foothills.

Breeding dispersal was rare (6% of occasions) and occurred more frequently among females, younger owls, owls without mates in the previous year and owls that lost their mates from the previous year. Breeding dispersal distance was greater subadult than adult owls but did not differ by sex (median = 3.5 km).

Northern Spotted Owls exhibited alternating years of high and low fecundity in most of their range, a decline over time in fecundity on five of fourteen study areas, and an increase in fecundity on two study areas. Average fecundity over fourteen study areas was 0.074 for one-year-old females (SE = 0.029), 0.208 for two-year-old females (SE = 0.032), and 0.372 for adult females (SE = 0.029). In the western Cascades, Oregon, where Flying Squirrels dominated the Spotted Owl diet, owl reproduction was positively associated with the abundance of Deer Mice. In the Klamath province, California, reproduction was positively associated with the proportion of larger prey in the diet. The geographic extent of these associations is unknown.

Apparent survival probability of adult female Spotted Owls ranged from 0.750 (SE = 0.026) to 0.886 (SE = 0.010). Apparent survival declined over the past 10-17 years on all four study areas in Washington and one study area in California. The number of Barred Owls detected on study areas annually was negatively associated with Spotted Owl survival on the Olympic Peninsula and the Wenatchee study area in the eastern Cascades, Washington.

Over the past 10-17 years, Northern Spotted Owl populations declined in portions of its range, with estimated $\lambda < 1.000$ on 13 of 14 study areas (range 0.896 [SE = 0.055] to 1.005 [SE = 0.019]). However, estimates of λ were different from $\lambda = 1$ on 6 of the 14 study areas based on 95% confidence intervals. The magnitude and evidence for decline varied among study areas, but all four study areas in Washington, three study areas in Oregon, and one study area in California showed moderate to strong evidence of population declines.

Meta-analyses of Northern Spotted Owl demographic rates have not included habitat, weather, or prey covariates. However, individual studies have demonstrated relationships between habitat amount and configuration, weather, and prey, and one or more demographic rates. In the Klamath Province, California, there appeared to be a trade-off between the benefits to Spotted Owl survival conferred by interior older forest and benefits to reproduction conferred by less interior older forest and more convoluted edge between older forest and other vegetation types. Survival was also negatively associated with precipitation and positively associated with temperature during the early nesting period, and reproduction was negatively associated with precipitation during the late nesting period. In addition, owls in territories of higher habitat quality had greater survival during inclement weather than those in poorer quality habitat. Franklin et al. (2000) suggested that habitat quality may determine the magnitude of λ and recruitment may determine variation around λ. Similar analyses on three study areas in Oregon revealed varying results, with one study in the Oregon Coast Range indicating that a mixture of older forests with younger forests and nonforested areas appeared to benefit Spotted Owl life history traits.

12 FUTURE INFORMATION NEEDS

We agree with researchers who carried out the most recent meta-analysis (Anthony et al. 2004) and other scientists (ESA 2004) that demographic meta-analyses would be more informative with the inclusion of habitat covariates, including rates of timber harvest. To date, the necessary spatially and temporally explicit habitat data corresponding to each demography study area do not exist. The American Forest Resource Council (AFRC) attempted to quantify rates of timber harvest on five Northern Spotted Owl demography study areas and found that although it was possible to estimate the area of harvest, it was not possible to estimate the area of suitable Spotted Owl habitat removed (AFRC 2004).

Future demographic meta-analyses should also incorporate weather covariates similar to those found by Franklin et al. (2000) and *Olson et al. (2004)* and others to affect reproduction and/or survival. Furthermore, the effects of Barred Owls on Spotted Owl site occupancy, reproduction and survival could be examined using finer-scale data than was used during the 2004 meta-analysis (Anthony et al. 2004). More generally, causative explanations for observed population trends are generally lacking. Existing data sets could be mined easily, with potentially important results. For instance, separate calculations of λ for different periods of the studies would be easy and useful.

There is no reason why further analyses of these data must wait five more years. Given that millions of dollars have been spent to collect Northern Spotted Owl demographic data, reanalyses of these data collected through 2003 (incorporating habitat and weather covariates) would be relatively inexpensive.

13 TABLES

Table 8.1. Mean estimated density of Northern Spotted Owls.

Province and forest type	Crude Density owls/ km^2	Crude Density SE	Ecological Density Owls/ km^2	Ecological Density SE	Method	Source
Oregon Coast Range					Empirical	*Thrailkill et al. 1998*
Lorane DSA (10%)[a]	0.027	--	0.269			
Wolf Creek DSA (25%)[a]	0.087	--	0.349			
Lake Creek DSA (44%)[a]	0.097	--	0.220			
Oregon Coast Range					Empirical	*Anthony et al. 2000*
North Coast Range	0.051	--				
Elliot State Forest	0.106	--				
CA Coastal redwood/Douglas fir	0.209	0.009			Mark-recapture	Diller and Thome 1999
Klamath subregion	0.092	0.000	0.373	0.015		
Korbel subregion	0.351	0.014	1.049	0.041		
Mad River subregion	0.313	0.014	0.581	0.026		
CA Coastal	0.376	--	0.808	--	Empirical	*Chow 2001*
Hardwood			1.111	--		
Douglas fir			0.884	--		
Redwood			0.729	--		
Bishop pine			0.650	--		
CA Coastal[b]	0.198	--			Empirical	*Deubel Timberland 2003*
CA Cascades[c]					Empirical	*Woodbridge and Cheyne 1995*
mixed conifer	0.078	--				
white fir, red fir, pine	0.021	--				

[a] Percent suitable Spotted Owl habitat on three Density Study Areas (DSAs) within the larger Eugene BLM demography study area in the Oregon Coast Range. DSAs were 186 - 425 km^2 and contained 10, 25, and 44% suitable Spotted Owl habitat.
[b] Entire study area not surveyed; therefore density may have been higher.
[c] Numbers reported are owl territories (occupied by pairs or single owls)/km^2.

Table 8.2. Northern Spotted Owl Demography study areas, 2004 (after Anthony et al. 2004, Appendix A).

Study Area	Start year[a]	λ_{RJS} Start year[b]	Land owner[c]	Region	Latitude
Washington					
Wenatchee	1990	1992	Mixed	WA Mixed conifer	46.996
Cle Elum	1989	1992	Mixed	WA Mixed conifer	47.195
Rainier	1992	1993	Mixed	WA Douglas fir	47.041
Olympic	1987	1990	Federal	WA Douglas fir	47.800
Oregon					
Coast Ranges	1990	1992	Mixed	OR Coastal Douglas fir	44.381
H. J. Andrews	1987	1990	Federal	OR Cascades Douglas fir	44.213
Warm Springs	1992	1993	Tribal	OR Cascades Douglas fir	44.938
Tyee	1985	1990	Mixed	OR Coastal Douglas fir	43.468
Klamath	1985	1991	Mixed	OR/CA Mixed conifer	42.736
South Cascades	1991	1992	Federal	OR Cascades Douglas fir	42.695
California					
NW California	1985	1985	Federal	OR/CA Mixed conifer	40.848
Hoopa	1992	1992	Tribal	OR/CA Mixed conifer	41.051
Simpson	1990	1993	Private	CA Coast	41.122
Marin	1998	1998	Federal	CA Coast	37.994

[a] Year that mark-recapture study was started.
[b] First year that data were used for analysis of λ_{RJS}.
[c] Federal = Forest Service, Bureau of Land Management, National Park Service; Mixed = Federal lands mixed with inclusions of private or State lands; Private and Tribal lands were lumped together for analyses of ownership.

Table 8.3. Estimated mean annual fecundity (female young produced per adult female), (ϕ), with standard error (SE) and trend in fecundity for adult (≥ 3 yrs old) Northern Spotted Owls (after Anthony et al. 2004, Tables 5 and 24).

Study Area	Mean	SE	Trend
Washington			
Wenatchee	0.491	0.058	Stable
Cle Elum	0.574	0.069	Declining?[a]
Rainier	0.253	0.061	Stable
Olympic	0.293	0.057	Stable
Oregon			
Coast Ranges	0.260	0.050	Declining?[a]
H. J. Andrews	0.321	0.045	Stable?[a]
Warm Springs	0.424	0.070	Stable
Tyee	0.319	0.040	Increasing
Klamath	0.445	0.040	Stable
South Cascades	0.377	0.059	Declining
California			
NW California	0.333	0.032	Declining
Hoopa	0.216	0.043	Increasing
Simpson	0.326	0.037	Declining?[a]
Marin	0.530	0.056	Stable

[a] Best model included age and even-odd year effects, but a competing model had a negative time trend.

Table 8.4. Estimated average apparent survival probability (ϕ), with standard error (SE) and trend in ϕ for adult (≥ 3 yrs old) Northern Spotted Owls (after Anthony et al. 2004, Tables 22 and 24).

Study Area	ϕ	SE	Trend
Washington			
Wenatchee	0.750	0.026	Declining
Cle Elum	0.860	0.017	Declining?[a]
Rainier	0.832	0.020	Declining
Olympic	0.855	0.011	Declining
Oregon			
Coast Ranges	0.886	0.010	Stable
H. J. Andrews	0.883	0.010	Stable
Warm Springs	0.823	0.015	Stable
Tyee	0.878	0.011	Stable
Klamath	0.849	0.009	Stable
South Cascades	0.854	0.014	Stable
California			
NW California	0.869	0.011	Declining
Hoopa	0.853	0.014	Stable
Simpson	0.850	0.010	Stable
Marin – females	0.824	0.045	Stable
Marin – males	0.913	0.035	Stable

[a] Variable among years, but with a declining trend.

Table 8.5. Estimated rate of population change (λ_{RJS}) for Northern Spotted Owls, with standard error and 95% confidence interval (after Anthony et al. 2004, Table 22).

			95% CI	
Study Area	λ_{RJS}	SE	Lower	Upper
Washington				
Wenatchee	0.917	0.018	0.882	0.952
Cle Elum	0.938	0.019	0.901	0.976
Rainier	0.896	0.055	0.788	1.003
Olympic	0.956	0.032	0.893	1.018
Oregon				
Coast Ranges	0.968	0.018	0.932	1.004
H. J. Andrews	0.978	0.014	0.950	1.005
Warm Springs	0.908	0.022	0.866	0.951
Tyee	1.005	0.019	0.967	1.043
Klamath	0.997	0.034	0.930	1.063
South Cascades	0.974	0.035	0.906	1.042
California				
NW California	0.985	0.013	0.959	1.011
Hoopa	0.980	0.019	0.943	1.017
Simpson	0.970	0.012	0.947	0.993

Table 8.6. Summary of the available data on predation of Northern Spotted Owls from radio-telemetry studies in the Pacific Northwest.

Age Group	Sample Size	Confirmed Deaths	Confirmed Predation
USDI 1992			
Adult/Subadult	344	91 (40%)	36 (10%)
Juveniles	85	60 (71%)	15 (18%)
Forsman et al. 2002			
Juveniles	386	188 (49%)	83 (21%)

Table 8.7. Mosquito vectors known to carry West Nile Virus in the range of the Northern Spotted Owl. Range data from Darsie and Ward 1981, *Boyce et al. 2004* and *Dr. Scott Meschke*, University of Washington, personal communication. Vector activity from Dr. Scott Meschke, and www.cdc.gov/ncidod/dvbid/westnile/mosquitoSpecies. X indicates presence of the vector, - indicates absence of the vector, ? indicates unknown occurrence.

Mosquito Species	Occurrence Confirmed in:		
	Washington	Oregon	California
Culex pipiens	X	X	X
Culex tarsalis	X	X	X
Culex restuans	X	?	?
Culex territans	X	X	X
Culex stigmatosoma	?	?	X
Culex erythrothorax	?	?	X
Ochlerotatus japonicus	X	?	?
Ochlerotatus canadensis	X	?	?
Orchlerotatus sticticus	X	?	?
Orchlerotatus dorsalis	X	X	X
Orchlerotatus fitchii	X	X	?
Aedes vexans	X	X	X
Aedes cinereus	X	?	-
Culiseta inornata	X	X	X
Coquillettidia perturbans	X	X	?
Anopheles punctipennis	X	X	X
Orthopodomyia signifera	-	?	?

14 FIGURES

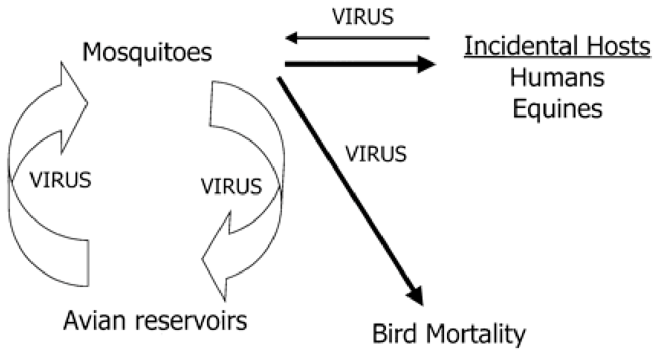

Figure 8.1. Schematic of the movement of WNV (virus) by vectors (mosquitoes) to variety of hosts. Arrows indicate how mosquitoes move the virus. The virus normally cycles among mosquitoes and an amplifying reservoir of bird hosts that carry the disease, but do not succumb to it. Occasionally the disease is passed to incidental hosts like people, horses, and susceptible birds that die or become sick. (After McLean et al. 2001).

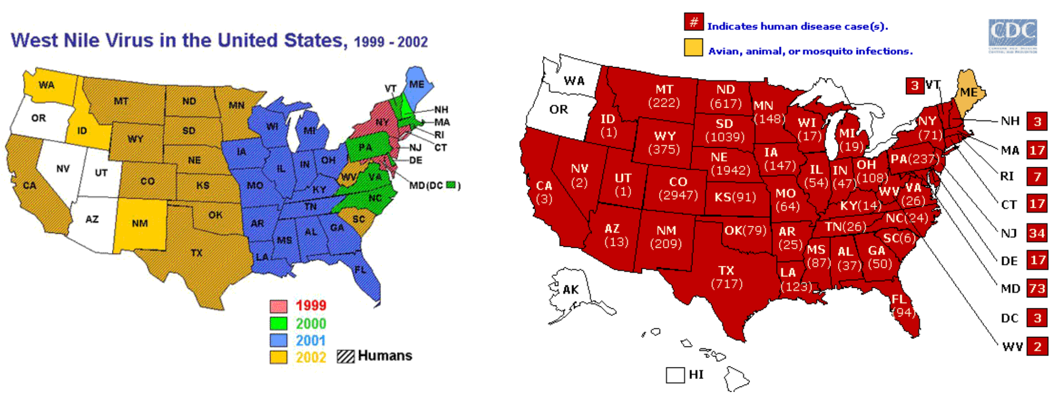

Figure 8.2. The spread of West Nile virus in the US after its introduction to New York City in 1999. States with occurrence of the disease from 1999-2002 are shown in the left map. States with occurrence of the disease in 2003 are shown in the right map (maps provided by the US Center for Disease Control).

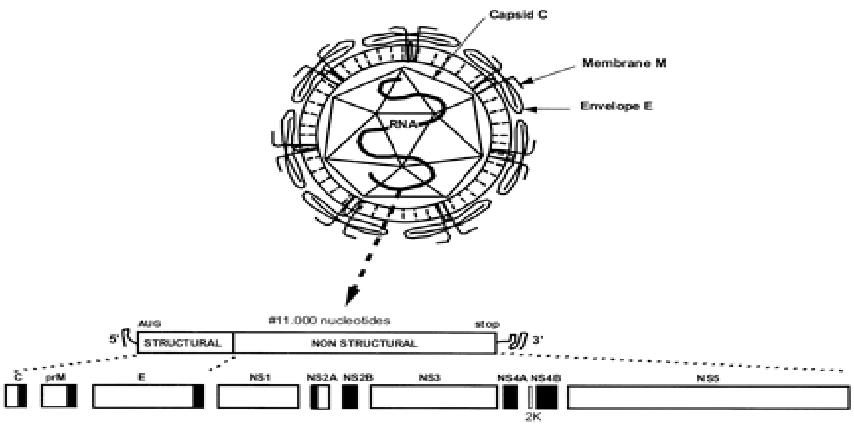

Figure 8.3. The structure of an individual West Nile virus. The spheroid protein-enveloped virus is shown above, and the detailed genomic map of the single RNA strand is shown below (After McLean et al. 2001).

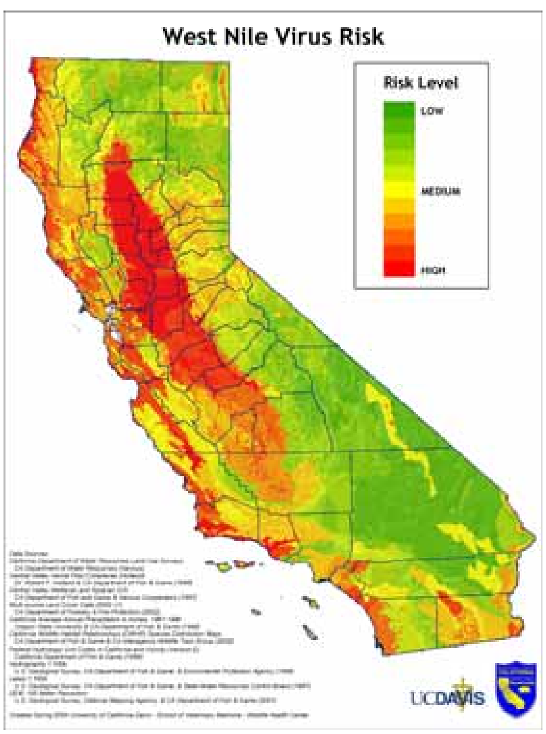

Figure 8.4. Modeled risk of West Nile virus in California as a function of mosquito and bird host abundance (from *Boyce et al. 2004*).

SCIENTIFIC EVALUATION OF THE STATUS OF THE NORTHERN SPOTTED OWL

CHAPTER NINE

Evolution and Effectiveness of Strategies for

Conservation of Northern Spotted Owl

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1 THE NORTHWEST FOREST PLAN

1.1 EVOLUTION OF THE NORTHWEST FOREST PLAN

The Northern Spotted Owl conservation strategy adopted as a part of the Northwest Forest Plan (NWFP) evolved through a series of scientific assessments and planning efforts between 1982 and 1994, when the NWFP was adopted. This sequence of activities commenced in 1982 with initiation of the development of a regional guide for management of the Northern Spotted Owl. The Forest Service plan was based on designation of relatively small (e.g., 600 ha) habitat areas for single and small clusters of NSO pairs—called Spotted Owl Management Areas (SOMAs) and Spotted Owl Habitat Areas (SOHAs) (USDA Forest Service 1989). Knowledgeable scientists considered this strategy to be flawed at the time it was proposed and so advised Forest Service leadership (Thomas et al., 1990).

The Forest Service' proposal for dealing with the NSO was subsequently rejected by Seattle Federal District Court Judge Dwyer (Yaffee 1994) on the basis that it lacked scientific credibility and, therefore, did not fulfill legal obligations under the National Forest Management Act of 1976. Specifically, the Record of Decision was rejected because it provided only a 50% likelihood of NSO subspecies persistence over the 100 year time frame of the strategy.

A series of independent scientific assessments followed rejection of this proposal over the next four years, all of which contributed to the ultimate development of the NWFP. Several of these were initiatives of the executive branch of government and one was a congressional initiative; as will be noted, some of the assessments were under development and consideration simultaneously.

The Interagency Scientific Committee to Address the Conservation of the Northern Spotted Owl (hereafter the ISC) was the second independent scientific teams to address conservation of the Northern Spotted Owl (following Dawson et al 1987). An initiative of USDA Forest Service Chief Dale Robertson, this team was chartered in 1989 by four federal agencies to *"Develop a scientifically credible conservation strategy for the northern spotted owl"* under the chairmanship of Dr. Jack Ward Thomas. This committee made its report in 1990 (Thomas et al., 1990).

A landmark scientific assessment throughout, the ISC's plan made two groundbreaking recommendations that subsequently were incorporated - in some form - into all further planning efforts (Thomas et al., 1990):

1. ***Delineation and conservation of large blocks of suitable habitat*** with each block capable of supporting multiple pairs of Northern Spotted Owl; and
2. ***Provision for dispersal habitat*** for Northern Spotted Owl in areas between habitat blocks.

The large habitat blocks--called ***Habitat Conservation Areas (HCAs)***--were selected so as to provide for a minimum of 20 pairs of owls and spaced at a maximum distance of 12 miles, parameters based on than current knowledge of Northern Spotted Owl biology. The *"**50-11-40***

rule" was adopted as the strategy for enhancing successful Northern Spotted Owl dispersal through areas between HCAs, called ***the Forest Matrix***; this "rule" required maintenance of at least 50% of the forest landbase between HCAs in stands of timber with an average dbh. of 11 inches or greater and at least 40% canopy cover. A corridor-based strategy for facilitating dispersal of Northern Spotted Owl was rejected because Northern Spotted Owls were suspected to disperse in a random manner. This was the first documented use of a matrix-based strategy for facilitating dispersal in conservation biology.

The ISC's plan was not adopted by the administration of President George H. W. Bush largely because it called for withdrawing 5,827,000 acres from the federal timberland base. Nearly two years later the Forest Service was allowed to formally adopt the plan as the basis for its planned management of the Northern Spotted Owl, but Judge Dwyer rejected the plan, sending the agency back to answer a series of questions. One important influence on Judge Dwyer was that in the intervening two years the Scientific Panel on Late Successional Forest Ecosystems (described in next paragraph) had provided a report to congress focused on old-growth forest and aquatic ecosystems and their constituent organisms and Dwyer wished to see these larger issues addressed. The Scientific Analysis Team (SAT) was created by the Forest Service to respond to Dwyer's questions and reported in early 1993 (Scientific Analysis Team 1993). The SAT activity was eclipsed by the election of President William Clinton and his chartering of the Forest Ecosystem Management Assessment Team (FEMAT) process; however, the SAT analysis contributed concepts to FEMAT, particularly with regards to the aquatic conservation strategy.

Lacking resolution of the timber owl issues, Congress intervened in the process in May 1991 by chartering the Scientific Committee on Late Successional Forests, known as the Gang of Four (Gof4). The Gof4 was chartered by two committees of the House of Representatives to: (1) Assess the state of old-growth forests and related organisms in the Pacific Northwest (including the Northern Spotted Owl and Marbled Murrelet); (2) Develop a plan for congressional action to deal with these issues; and (3) Assess economic costs and ecological benefits associated with the plan. The Gof4 delivered its report to congress in July 1991 *(Johnson et al. 1991).*

The Gof4 made several important contributions to Northern Spotted Owl conservation strategies. First, Gof4, with the help of over 120 federal agency staff scientists, mapped the late-successional forest habitat (i.e., mature and old forest) on federal lands within the range of the Northern Spotted Owl and characterized its quality based on a variety of criteria, including age and level of fragmentation. This produced a spatially-explicit data base of polygons - an area delineated on a GIS map) identifying the localities of major areas of Late Successional/Old Growth (LS/OG) forest and their quality (ranging from 'low quality' LS/OG1 to 'high quality' LS/OG3). The rating from poorest (LS/OG3) to best (LS/OG) old-growth forest was based on multiple criteria including forest age, site elevation and productivity, and level of landscape fragmentation *(Johnson et al. 1991).* The LS/OG polygons were than used as the foundation for creating an incremental series of 34 management alternatives that provided for increasing levels of habitat protection and modified management in the intervening areas (the matrix) *(Johnson et al. 1991).* Reserves were increased systematically beginning with reservation of the LS/OG1 polygons and progressing to inclusion of all polygons from LS/OG1 through LS/OG3 as well as some additional forest polygons (Owl Additions) necessary to meet the spatial criteria used in designing the HCAs. Costs and benefits of these management alternatives were analyzed using:

(1) Impacts on allowable timber harvest to index economic cost; and (2) Probabilities over 100 years of maintaining (a) old-growth ecosystems, (b) Northern Spotted Owl, (c) Marbled Murrelet habitat, (d) anadromous fish habitat, and (e) other old-growth dependent organisms to index benefits (*Johnson et al. 1991*, see also Franklin 1995).

The House Committees responsible for the oversight of this assessment process found the Gof4 report credible, but shocking in terms of impacts on timber harvest associated with achieving species and ecosystem conservation objectives. It was clear that no plans could provide for both high levels of timber harvest and associated old-growth forest ecosystems and organisms, including viable populations of Northern Spotted Owl. The three relevant committees of the House of Representatives agreed upon draft legislation based upon the Gof4 report but ultimately did not bring it to the floor of the House at the request of Speaker Tom Foley. Despite this lack of congressional action, the Gof4 effort made a substantial contribution to the FEMAT process, as will be seen, particularly in the form of the LS/OG polygon database.

During all of these processes a recovery plan for the Northern Spotted Owl had been under development by the US Department of Interior, which retained responsibility in the Secretaries Office rather than delegating it to US Fish and Wildlife Service. The final draft plan, which was never adopted, incorporated the HCA and Forest Matrix prescriptions from the ISC report (USDI 1992). HCAs were renamed Designated Conservation Areas (DCAs) in the DOI plan.

Management policy on federal forestlands within the range of the Northern Spotted Owl remained unresolved through 1992. Candidate William Clinton had committed to resolving the stalemate if elected and President Clinton initiated that resolution in April 1993. A timber summit was held in Portland to air public opinions on the various issues. President Clinton also initiated a scientific review leading to a environmental impact assessment (EIS) decision-making process as elements in resolving the conflict between timber and conservation objectives.

The Forest Ecosystem Management Assessment Team (FEMAT) was created to provide a review of scientific issues and provide plan alternatives (options) for the EIS process that would follow FEMAT. FEMAT dealt with multiple objectives and not just the Northern Spotted Owl, following the pattern of the Gof4. The Northern Spotted Owl and Marbled Murrelet were certainly key considerations, but maintaining viable old-growth ecosystems and all old forest associated species and sensitive fish stocks and aquatic ecosystems were also key objectives. FEMAT completed its work in three months (FEMAT 1993).

FEMAT produced 10 management alternatives or options (FEMAT 1993). All options were projected to provide for viable populations of Northern Spotted Owl over the long term with a high level of probability. All of the options were based upon establishment of extensive reserve systems—i.e., lands reserved from commercial timber harvest. The FEMAT team was unanimous that the primary emphasis in owl conservation should be on maintaining existing suitable habitat rather than attempting to create suitable habitat by forest management.

The reserve system involved several categories of federal land allocation or designation. It began with areas that had already been withdrawn from timber harvest by congress, such as wilderness areas and national parks, and administratively by the agencies themselves, such as

Research Natural Areas. However, significant new reserves--called Late Successional Reserves (LSRs)—were created to conserve much additional existing late-successional forest habitat. Areas representing these various categories of withdrawn lands were often contiguous resulting in large conservation units, such as where LSRs were adjacent to designated Wilderness. An additional new category of land allocation dedicated to restoration and maintenance of natural forest conditions were the unmapped Riparian Reserves, which were primarily to for conservation of aquatic organisms and processes but also contributed to terrestrial conservation objectives.

The LSRs were the major new withdrawal of land from the timber base under the NWFP. However, the various alternatives differed in the amount and basis for selection of these lands. The two alternative bases of construction of the reserve system represented in the FEMAT options were: (1) Reserves built primarily on the HCAs/DCAs developed by owl biologists; and (2) Reserves built primarily on the LS/OG polygons. These strategies differed significantly since the former focused on creating reserves for Northern Spotted Owl following a specific geographic design while the latter focused on conserving high-quality old-growth forests. As a consequence, the HCA/DCA system did not incorporate much of the best remaining old-growth forest (Franklin 1994).

FEMAT Option 9 was adopted as the preferred alternative in the EIS process that followed FEMAT (USDA Forest Service and USDI 1993). In this option the LSR system was based on integrating LS/OG polygons, which identified the best of the remaining old-growth forest habitat, along with the Key Watersheds (FEMAT 1993). The consequences of this choice were significant. More and generally better quality old-growth forest habitat was reserved than would have been the case with a HCA/DCA-based reserve system. As noted by Noon and McKelvey (1996), the selection of Option 9 resulted in creation of ". . . large reserve areas capable of supporting local populations of 40 to >170 owl pairs."

A key point is that the LSR network was designed to conserve existing late-successional forest conditions and all associated organisms (including Northern Spotted Owl), not exclusively as a conservation strategy for Northern Spotted Owl. However, the final ROD included "owl additions" to some LSRs where there were differences between the DCAs of the owl recovery plan and the LSRs.

The legal decision-making process involving draft and final supplemental environmental impact statements and a record-of-decision resulted in adoption of the NWFP (USDA Forest Service and USDI Bureau of Land Management 1994a, 1994b). The final alternative did include numerous modifications from Option 9 of FEMAT, however, particularly in regard to the width of the Riparian Reserves and adoption of the Survey and Manage provision. The land allocations within the NWFP included:

Congressionally Reserved Areas	7.3 million acres (30% of total area)
Late Successional Reserves	7.5 million acres (31%)
Riparian Reserves	2.2 million acres (11%)
Administratively Withdrawn Areas	1.5 million acres (6 %)
Matrix	4.0 million acres (16%)

Adaptive Management Areas 1.5 million acres (6%)

Judge Dwyer ruled positively on the acceptability of the plan and allowed the agencies to implement it in 1994.

The NWFP includes several important provisions for management of the LSRs that are relevant to creation and maintenance of Northern Spotted Owl habitat:

First, the NWFP allows for silvicultural treatment of young forests (<80 years of age) within LSRs for the purpose of accelerating development of late-successional forest habitat. This provision was included because the LSRs are relatively large blocks that include significant areas that have been logged, especially in the last 50 years. Since the development of large contiguous (unfragmented) blocks of late-successional forest is a key element of the Northern Spotted Owl strategy (ISC 1990) activities to accelerate restoration of simplified young stands were viewed as appropriate. Young forests have been treated under this provision of the NWFP.

Second, the NWFP allows for silvicultural treatments, including mechanical and prescribed fire methods, of old-growth forests on sites characterized by frequent, light to moderate intensity fire, such as pine and mixed-conifer dominated forests on the eastern slopes of the Cascade Range and in the Siskiyou-Klamath region. This provision was included because of the potential for uncharacteristically intense wildfire on sites where uncharacteristic fuel levels have accumulated. Such fires pose a high potential for temporary (and often long-term loss) of old-growth conditions, including habitat of Northern Spotted Owls. As noted elsewhere, such fires have occurred since the NWFP as adopted. This NWFP recommendation has not been widely implemented because such treatments often involve areas currently or potentially occupied by Northern Spotted Owls. Land management agencies appear not to have aggressively implemented such treatments even though the USDI FWS ultimately has approved any projects for which formal review was requested, even where “take” was involved, and sometimes has encouraged the development of such fuel treatment proposals.

1.2 EXPECTATIONS OF THE NWFP WITH REGARDS TO NORTHERN SPOTTED OWL CONSERVATION

1.2.1 HABITAT CONSERVATION

The NWFP has achieved several important goals for Northern Spotted Owl conservation. Foremost has been protecting the majority of existing suitable habitat of the Northern Spotted Owl from timber harvest on federal lands. Timber harvest levels on federal timberlands within the range of the Northern Spotted Owl during the last decade have been less than 5% of the area harvested on an annual basis during the 1980s. In fact, harvest in mature and old forests has been much less than the levels expected under the NWFP, for a variety of reasons, including law suits brought to challenge actions and provisions of the NWFP, particularly the Survey and Manage provision.

These provisions have made significant contributions to the maintenance of existing habitat, and accelerating the development of structurally simple forest into suitable habitat in the foreseeable future, hence contributing to owl recovery

By contrast, active management of late-successional forests on characteristically fire-frequent sites in the eastern and southern areas of the Northern Spotted Owl range has not been accomplished as envisaged under the NWFP. It was expected that significant areas of LSRs, which had uncharacteristic fuel accumulations, would be treated during the first decade of the plan; in fact, very few acres have been treated to reduce uncharacteristic fuels within LSRs and we are not aware of any that involved landscape-level plans for treatments within LSRs. Consequently, there has been limited progress in restoring characteristic structures and fuel conditions and reducing the potential for uncharacteristic stand-replacement fires on tens of thousands of LSR acres. The NWFP provides for such treatment but agencies have not implemented them despite the clear potential for significant loss of Northern Spotted Owl habitat. Factors probably include inadequate funding for this activity, other management priorities, potential public controversy, and risk aversion.

Thus far, the loss of Northern Spotted Owl habitat due to such uncharacteristic stand replacement fires has not been extensive range wide, although it has been locally extensive. However the failure to implement this provision of the NWFP is continuing to place high risk on existing owl habitat, and must be accounted as contributing to the risks of extinction of the species. This risk is sub-regional and not range wide; as we note elsewhere the issue of uncharacteristic fuel accumulation and potential stand-replacement fire is confined to the dry eastern and to a lesser extent the southern fringes of the NSO range (see chapters on habitat trends and questionnaire). Large fuel accumulations (i.e., stand structural complexity) and stand-replacement fires are characteristic within the bulk of the NSO range; any effort to modify these forests typified by the westside Douglas-fir/western hemlock type would, in fact, create totally unnatural habitat conditions for both NSO and their prey.

Failure to treat stands on characteristically fire-frequent sites also contributes to potential problems with insect pests, including loss of large veteran trees as a result of competition from densely growing young trees (see, e.g., McDowell, et al. 2003). For example, there has been significant loss of LSR forest and Northern Spotted Owl habitat due to spruce budworm epidemics on the Yakama Indian Reservation (WA) and Deschutes National Forest (OR). In the case of the Deschutes National Forest, dead trees created by the spruce budworm contributed significantly to the B&B Fire Complex that burned in 2003. As one example, the combination of Spruce Budworm and fire have impacted 18 out of 24 pairs of Northern Spotted Owls on the Sisters District of the Deschutes in 10 years; 15 of those pairs were affected by the B&B Fire Complex and habitat for 11 of those pairs is completely gone *(Helen Maffei, pers. comm.).*

The NWFP was always intended to have an adaptive component, so that new information could be incorporated into management. Some new information, such as that concerning the emergence of Sudden Oak Death (see Appendix), may constitute significant changes in our understanding of the threats to habitat (in the case of SOD, in a limited part of the subspecies' range). At the moment, SOD is an obvious threat but its ultimate impact on habitat is hard to assess at this stage. SOD does have the potential to have major impacts given the wide range of host tree species that are affected and its demonstrated virulence on several keystone tree species, such as tanoak, and the possibility that it may ultimately spread throughout the entire range of the Northern Spotted Owl.

In summary the NWFP has had considerable benefits to Northern Spotted Owls, by halting the removal by logging of occupied and future potential recovery habitat on federal lands, which would not have otherwise occurred. However failure to fully implement some of the provisions of NWFP has increased the risk that such habitat, occupied or future, will be lost in some portions of its range, moderately reducing the potential for Spotted Owl persistence and recovery. Note that in their individual responses to questions in the questionnaire, five of six panelists replied in response to Q.31 that habitat was at risk to fire in the Eastern Cascades, the Klamath region, and on federal lands generally. In response to Q.48, eight respondents all regarded fire as a risk to Northern Spotted Owls (2 high, 5 moderate and 1 low), ranking fire as the third greatest risk for owls (behind Barred Owls and timber harvest); in responses to Q.50, six panelists saw this risk as increasing.

1.2.2 CONSERVATION OF OWL POPULATIONS

The Reserve and Matrix strategy of the NWFP has been successful in that Northern Spotted Owl populations are persisting, and (largely) performing as predicted. Chapter 8 and Anthony et al (2004) discuss in detail the current and recent demographic performance of Northern Spotted Owls. Some owl populations have been stable over the past 14 years, some are declining, while on others the data do not allow us to determine whether the population is declining or not. As noted elsewhere in this chapter, declines over the past 14 years are expected under NWFP, and not immediate cause for concern. However lack of a firm predicted population trajectory makes such comparisons difficult.

However, in some regions, Northern Spotted Owl populations have declined faster than anticipated, including areas with little or no ongoing timber harvest (*AFRC 2004*). Given the *accelerating* downward trends in survival and reproduction on some federally managed study areas that have essentially no additional timber harvest since implementation of the NWFP, this suggest that something other than timber harvest is responsible for the decline and apparently has not been dealt with by implementation of the NWFP, at least not during its first 10 years of implementation.

Protection of suitable habitat for Northern Spotted Owl under the NWFP has not prevented invasion by the Barred Owl, a potential competitor (see chapter 7); i.e., the NWFP resulted in protection of the habitat but the Barred Owl may have rendered a significant amount of this habitat currently unavailable to Northern Spotted Owl (see chapter 6 and extensive debate therein). Continued cutting of suitable habitat of the Northern Spotted Owl (i.e., with no NWFP) might have accelerated the decline of he species and, possibly, facilitated more rapid displacement or occupation of vacated habitat by Barred Owl. Provision of suitable habitat for Northern Spotted Owl was an essential contribution of the NWFP but has not protected it from competition from Barred Owl.

In the same way, the imminent arrival of West Nile Virus constitutes a potential threat to Northern Spotted Owl populations that cannot be addressed simply by habitat protection under

NWFP (note that the extent and degree of threat posed by WNV is largely speculative at this point).

We emphasize that provision of habitat for owls remains an important contribution of NWFP but that, while provision of habitat is a necessary condition, it is not in itself a sufficient one to ensure conservation of Northern Spotted Owls or any other species. We also do not want to suggest that development of additional habitat and protection of existing habitat are not important conservation objectives.

1.2.3 ADAPTIVE MANAGEMENT PROVISIONS

Adaptive management activities have not been aggressively implemented under the NWFP, although adaptive management was supposed to be one of the major themes of the plan. Adaptive management was a strong element in FEMAT (1993) but has not been as strongly emphasized in the application of the final NWFP. There are many reasons for this lack of implementation, including the tendency of stakeholders of all stripes, managers, and courts to favor certainty rather than to emphasize uncertainty, which adaptive management does. The NWFP provided for 1.6 million acres in 10 Adaptive Management Areas but activities on AMA lands were actually more constrained than on the Matrix allocation, a circumstance that was definitely not intended by the FEMAT (1993) team. Lack of financing is also an important factor limiting learning-based adaptive approaches.

Adaptive management as envisaged under the Draft Recovery Plan, FEMAT and NWFP was expected to contribute to Northern Spotted Owl conservation, through the development of new management techniques, which would promote habitat development. The failure to take full advantage of the adaptive management provisions of the NWFP during its first 10 years is unfortunate for Northern Spotted Owl conservation.

1.2.4 RESEARCH AND MONITORING

There is a large scientific component to NWFP, including an extensive effectiveness monitoring program. Much has been achieved through science conducted under the framework of the NWFP (e.g. Lint et al 1999). For instance, the federal contribution to the coordinated demographic studies has been key, and has provided the majority of data currently available on owl population trends. Elsewhere (section 10 below, chapter on information needs), we have critiqued the lack of information on some important issues. A few of these information gaps pertain directly to NWFP (notably the lack of information on the amount and distribution of habitat); others (such as Barred Owl effects) are likely to be important across the range, including on NWFP lands. While some of these issues are pressing, we recognize that a constraint on research and monitoring under NWFP is that it must be relevant to plan implementation and success. We acknowledge that it is not a function of NWFP to answer all questions regarding Spotted Owl conservation.

1.3 THE SCIENTIFIC BASIS OF NWFP

As we have shown, the NWFP has been a major contributor to Northern Spotted Owl conservation. The huge efforts of scientists and managers in designing and implementing the plan to benefit owls have not been in vain. However we have also suggested that some expectations have not been met. In this section we address the successes and failures of the NWFP, regarding the scientific principles on which the Plan is based. We are particularly interested in determining whether the Plan's scientific premises regarding the NWFP are still defensible, or whether new information or hypotheses call into question either the overall strategy of the plan, or implementation of key features.

In the questionnaire section, the panel members were asked:

The federal conservation plan for NSO and other species (Northwest Forest Plan) depends upon the maintenance of populations, primarily in Late Successional Reserves, in a metapopulation structure, where each population has a high probability of survival. There have been changes in the implementation of the NWFP (lower harvest rates) and also in the impact of different threats. Based on the evidence available to the panel, and your evaluation of current threats, is this strategy based on premises that are currently well-founded, and supported by current information?

Of eight responses, none thought the NWFP was well supported on all issues, but none regarded the plan as 'not well supported'. Comments from panelists made clear that some felt that issues not fully considered under NWFP were emerging threats from Barred Owls and disease.

In the sections that follow, we address each of several main premises of NWFP in more detail.

1.3.1 A RESERVE NETWORK

All species require adequate habitat if they are to maintain themselves. This basic premise was at the core of the Northern Spotted Owl listing decision, and formed the heart of the NWFP (see above). Nothing has changed to alter this fundamental principle of conservation. Similarly, nothing has altered the general premise that the reserves for Northern Spotted Owl should be well-distributed throughout the range of the species, if reserves are to form the basis for range-wide recovery.

Similarly, it is a common principle of conservation biology that reserves should be large enough to allow persistence of local populations through demographic fluctuations, with an overall low expectation of local extirpation. While this principle is intact, the application of it to Northern Spotted Owl populations under the NWFP may be overly optimistic, in that new and emerging threats may reduce local populations of owls below levels anticipated, including in LSRs and despite the fact that the collective reserved areas under the NWFP are very large.

1.3.2 METAPOPULATION DYNAMICS, DISPERSAL AND MATRIX HABITAT

Allied to the concept of reserves, is the theory of metapopulation structure. When there are possibilities of local extirpation, or persistent 'sink' areas, core breeding reserves may allow the overall population to persist, and local habitat 'patches' to be recolonized if they lose owls. Again, this is a fundamental concept in conservation biology, which remains unchallenged.

The implications for Northern Spotted Owls of a metapopulation strategy are the need to have conditions in the matrix to allow for movement of dispersers from reserve to reserve, and perhaps to have some contribution of breeders in the matrix. Management of matrix habitat has been, if anything, of lower impact on Northern Spotted Owls than predicted. Owls are known to breed in substantial numbers in some matrix areas, and there is no evidence to suggest that dispersal habitat is currently limiting to the species in general (there remain local areas, e.g. Oregon Coast Ranges, where dispersal habitat has been identified as needed (see FDRP 1992)). Note however that dispersal remains a difficult topic to study (see chapter 6).

The general strategy under the NWFP was to replace earlier conservation strategies for dispersal habitat (the 50-11-40 rule of the ISC) with one based primarily on retention harvest requirements in the matrix and riparian reserves. Although the 50-11-40 rule was based on known information on habitat conditions for dispersal of juvenile owls *(Miller 1989)*, the riparian reserve strategy is thought to preserve more, better, and better-distributed dispersal habitat. More recent data on dispersal (Forsman et al. 2002) does not change this conclusion.

1.3.3 HABITAT DESCRIPTIONS

The NWFP focused on a strategy of conservation of late-successional forests, as these were regarded as prime habitat for Northern Spotted Owls throughout the subspecies' range (recognizing that in some areas, e.g. the coastal redwood region, structure could lead to owls using substantially younger habitat types). Notwithstanding the associations of owls with younger forests with complex structure in some areas (see chapter 5), there is still a strong association of owls with late-successional forests. Hence there is no reason to call into question this basic tenet of the plan.

As noted, some data from different parts of the range suggest that individual stand attributes and landscape configurations of habitat may hold more subtleties than at first recognized, which may complicate management effects.

1.3.4 PROTECTION OF HABITAT

A fundamental assumption of the NWFP was that habitat was adequately protected by reserve status or by management of reserves and matrix areas. This assumption would still appear to be warranted throughout most the Northern Spotted Owl's range along the crest and west of the Cascade Range, where large disturbance events are characteristic and to which the owl is presumably adapted. The FEMAT scientists knew that large disturbance event are to be expected in this region and designed the reserve system to accommodate such losses and appropriate recovery periods. However, in the driest portions of the Northern Spotted Owl's range—primarily east of the Cascade Range—proactive fuel measures have not been undertaken at the scale that was expected and there have been significant losses of habitat to uncharacteristic stand-replacement wildfire. The original intent of the NWFP was to treat these forests to reduce the potential for such fire. Such treatments need to be accelerated to assure continued existence of Northern Spotted Owl habitat in these areas.

1.3.5 POPULATION DECLINES

The NWFP predicted that Northern Spotted Owls would continue to decline for some time after plan implementation, as the consequence of lag effects at both individual and population levels, and the continued harvest of habitat (see Record of Decision). The most explicit treatment of expected population trends is given by *Raphael et al. (1994a,b)* who carried out simulation analysis of likely population trends in relation to alternatives being considered under FEMAT, based on earlier models developed by Lande (1987,1988), Thomas et al (1990), and Lamberson et al (1992). However these models were not intended to be benchmarks for considering plan success. Instead they were tools developed in order to qualitatively evaluate the alternatives under consideration. The models were extremely sensitive to both starting conditions, and to rule sets applied, so that they cannot in any way be held to represent predicted population trends:

> "Actual prediction of population levels during a transitional period is extremely unlikely to be reliable – even if the model were perfect- because these levels are very dependent on the start-up population and estimates of current population are still fairly crude."
>
> "Results of this analysis do not purport to represent actual population trends; rather its major purpose is to shed light on the sensitivity of owl population dynamics to varying degrees of habitat change over time and to compare the qualitative similarity of trends among alternatives. There are simply too many unknowns to be confident that any model will predict the actual population of a species many decades into the future."
>
> "Therefore, our results do not directly address the issue of whether owls will eventually achieve a stable equilibrium" *(Raphael et al. (1994a) pp 7-8).*

Note also that, while *Raphael et al.* are very wary about predicting 'decades into the future', they also state that initial model conditions swamp predictions of population trend early in the simulations. "Thus, the model results for the first decade or two are not as useful as those from later years"(p.5). *Raphael* go on to compare population trends only for years 20-30 of the simulations (corresponding to years 2014 to 2024) (see calculations of λ in Figure 6 of *Raphael et al. 1994a*). That is, *Raphael et al.* make essentially no predictions on owl trends over the period 1994 to 2004.

Hence no strong prediction of the magnitude of population decline was possible; indeed the results of *Raphael et al. (1994a,b,)* are largely qualitative and rank alternatives, but do not provide predicted owl numbers. There was however a clear expectation that populations would eventually rebound as more habitat developed *(Raphael et al. 1994b).* Models of habitat growth do indeed suggest that there is significant ingrowth and development of habitat throughout the federal landscape (see chapter 6 on habitat trends).

The observed pattern of demographic change of owl populations suggests a continuing range-wide decline (Anthony et al 2004). As mentioned above, the fact of such a decline is not in and of itself unexpected, or reason to doubt the effectiveness of the core NWFP strategy. Note also that for some areas studied in the demographic analyses there is significant ongoing timber harvest (such as on the Simpson Timber Company study area which is higher than on federal lands. The overall rate of loss over the whole population should not necessarily be the metric for examining NWFP success. Nevertheless, considering just populations on federal lands, there is a decline. The problem in assessing this decline is that we lack a strong benchmark to know whether this decline is greater or less than that predicted under NWFP.

Comparing geographic regions, there seems little doubt that populations in Washington are declining faster than elsewhere in the US (Anthony et al, 2004). This regionally greater decline is certainly not as predicted under NWFP. The reasons for these regional patterns are discussed in chapter 8. It is clear that there is no simple correlation with timber harvest patterns for instance (*AFRC 2004*), and Barred Owl invasion is certainly a viable hypothesis for this regional pattern (chapter 7).

Similarly, there is some evidence, that in some populations at least, there is a downward trend in patterns of survival and reproduction (Anthony et al, 2004) (i.e. the population is not simply declining in response to low values for survival and reproduction – these low parameter values are themselves declining). This is not predicted by the science underlying the NWFP. Again, Barred Owls are one factor that has been notably strengthening over the past few years, and may explain the observed pattern in demographic parameters. Climatic patterns (cyclic or directional) probably also need to be considered as a contributing factor.

One further concern about the continuing validity of NWFP science is that the Plan predicts a decline in owl populations until habitat begins to re-grow over a long time period. The current reserve system is designed to be large enough and close enough to maintain large populations in reserves, thus minimizing the risk of local extinction. This strategy of recovery from 'population lows' is predicted from theory, and there is no new information to suggest that the base principles are incorrect. However pressure from new threats (Barred Owls, WNV, SOD) may be such that the populations in reserves fall to lower levels (and at a faster rate) than anticipated under NWFP, thus increasing local extinction risks, and reducing the overall probability of owl recovery.

1.3.6 RECOVERY STRATEGIES

NWFP predicts that recovery of the Northern Spotted Owl will require provision of new habitat, through succession. There are no new data to suggest that this habitat strategy is incorrect or that it will be insufficient in the long term. Indeed, much of the habitat that is currently coming "on line" is the result of unsalvaged wildfires in the 19th and early 20th century that typically has significant biological legacies from the original old-growth stands and should, therefore, have attributes of suitable habitat. It is also assumed by the NWFP that recovery of owl populations in low population areas will require immigration of owls, from LSR and other reserve 'source' populations. There are no new data on, for instance, dispersal that suggest that this strategy is conceptually incorrect.

1.3.7 OVERALL ASSESSMENT OF SCIENTIFIC PRINCIPLES OF THE NWFP

The NWFP was extraordinarily ambitious in addressing conservation of a complex series of ecosystems over a large area. Many, but not all of the scientific building-blocks of this plan have been confirmed or validated in the decade since adoption. Largely the successes of NWFP are ascribable to good design and implementation. The inadequacies seem more to do with implementation – important provisions, such as fuels treatment and adaptive approaches have not been adequately applied.

One major limitation of the NWFP appears to be the inability of a reserve strategy to deal with invasive species. Not much will. Reserves are no protection against viruses, fungi or invasive owls. The reserve system was predicated upon redundancy of individual reserves in order to spread risk across the entire reserve system. The redundancy of the reserve strategy may yet prove a strong suite. However, nationally, there have been no ‘magic bullets’ for dealing with invasive species. Sometimes drastic measures and perpetual vigilance can prevent spread of the organism, as with the eradication of Medfly in Southern California, or the quarantine on Hawaii against spread of brown tree snakes. In other cases, nothing has proven successful (e.g. the spread of starlings). The NWFP cannot be held uniquely responsible for a general impossibility. Instead, we recognize that the NWFP has made important conservation contributions, and without the plan the situation of Northern Spotted Owls would be far bleaker. Indeed, one strength of the NWFP, its intended flexibility and adaptability, may yet prove key in responding to unexpected challenges.

Climate change is an additional threat to Northern Spotted Owls that was not explicitly addressed in the NWFP and, more generally, is not readily addressed by a reserve-based conservation strategy. Climate change is an additional uncertainty that could have both direct and indirect impacts on Northern Spotted Owls and their prey. However, the emphasis on maintenance of structural complexity and organismal diversity in the Matrix under the NWFP should contribute to the resilience of the federal forest landscapes to the impacts of climate change.

1.4 FUTURE DIRECTIONS FOR CONSERVATION OF NORTHERN SPOTTED OWLS ON FEDERAL FOREST LANDS

What inferences for Northern Spotted Owl conservation can we draw from the last 10 years of experience under the NWFP?

First, based on existing knowledge, ***large contiguous blocks of suitable habitat are still viewed as necessary for Northern Spotted Owl***, even if the habitat is not sufficient, by itself, to sustain Northern Spotted Owls in the face of a threat such as Barred Owl invasion. This science has not changed in the last 10 years. The details of the meta-population model on which it is based should probably be reexamined, however, since this model assumed that areas located between the large habitat blocks (the matrix) would be only partially suitable for dispersal (50-11-40 rule) and generally unsuitable for nesting and foraging. In actuality the NWFP provided for some protection of Northern Spotted Owl nesting and foraging habitat within the matrix (e.g., reserves around nest sites, although these reserves are very small and currently often unoccupied) as well as maintenance of general conditions within the matrix that would facilitate dispersal of Northern Spotted Owl and recovery of Northern Spotted Owl habitat following logging—e.g., variable retention harvesting. For these reasons, Northern Spotted Owl are using matrix habitat more than would be predicted with the meta-population model. Note however, that this is also a consequence of lack of management and harvest activity in the matrix. Owls currently live in a ‘matrix’ that has more habitat value than is designed for under the NWFP. The long-term suitability of matrix areas under a fully-implemented NWFP is impossible to assess at this point.

Second, **there are significant new uncertainties (i.e. new threats) for the Northern Spotted Owl that were not present at the time that the NWFP was adopted**. The level of competitive pressure on the Northern Spotted Owl from the Barred Owl is one of the most important of these uncertainties. However, Barred Owl intrusions do not negate the need for structurally complex forest to sustain Northern Spotted Owl. There is no clear indication at this point whether Barred Owls will render the reserve system less functional. Cutting habitat occupied by Barred Owl might simply result in further displacement of Northern Spotted Owl; furthermore, there is the possibility that Northern Spotted Owl may ultimately reoccupy some of the habitat currently occupied by Barred Owl. Major additional uncertainties for the Northern Spotted Owl arise from the potential impacts of West Nile Virus on Northern Spotted Owl and of Sudden Oak Death on Northern Spotted Owl habitat in the southern part of its range.

The NWFP was not designed to deal with invasive species and, given the new threats and uncertainties, realized population levels for the Northern Spotted Owl may be substantially lower than those predicted under the NWFP. At this point, it is possible that existing suitable habitat for Northern Spotted Owl eventually will prove important to the persistence of the subspecies. Very little late successional forest has been logged during the first 10 years of the NWFP on federal lands, so that additional options do exist for policy makers, such as protection of owl habitat outside of existing LSRs.

Third, **the hypothesis that Matrix is more effective as Northern Spotted Owl habitat than LSRs is neither proven nor necessarily relevant**. There is only limited evidence for such a phenomenon—e.g., a study on the upper Cispus River drainage near Mount Rainier. We are unsure whether this phenomenon is real and, if so, how widespread. In any case, within the Matrix allocation the Northern Spotted Owl is mainly using the patches of late-successional forest as nesting and roosting habitat (except within the Coast Redwood zone, and some young stands with LSOG components, in the Willamette Valley margin, and the Klamath region). There is also the possibility that Northern Spotted Owl and Barred Owl may partition some landscapes with Barred Owl favoring LS/OG forests found on highly productive sites along stream and river courses.

Fourth, ***we think that there is high potential for loss of significant Northern Spotted Owl habitat in the next few decades in the eastern and southern portions of its range.*** Significant acreages of suitable Northern Spotted Owl habitat are at risk of uncharacteristic stand-replacement fire, primarily on the eastern side of the Cascade Range and on localized sites in the Klamath Province. This will result in very long-term loss of suitable Northern Spotted Owl habitat on affected sites, which may also be locales where Northern Spotted Owl may have its best chance of resisting Barred Owls. The current dry phase of the Pacific Decadal Oscillation may also be contributing significantly to the increased size and intensity of fires within the range of the Northern Spotted Owl.

More aggressive active management will be necessary in late-successional forests and landscapes, which are at risk of uncharacteristic stand-replacement fires, if there is an intent to reduce the current potential for large losses of suitable Northern Spotted Owl habitat. Silvicultural treatments that involve both mechanical treatment and prescribed fire may be useful. Such treatments appear essential to avoid essentially permanent loss of Northern Spotted Owl habitat—as well as many other ecological values—on these sites, particularly on the eastern slopes of the Cascade Range. It is important to note that such fuel treatments are ***not*** appropriate on sites that are naturally characterized by heavy fuel accumulations and infrequent stand-replacement fire regimes, such as the moist Douglas-fir—western hemlock forests of western Oregon and Washington. Mechanical treatments if not properly applied can also reduce habitat quality or eliminate important habitat.

Developing guidelines for landscape-level treatments that are consistent with maintaining Spotted Owl habitat is an urgent research need on the eastern slopes of the Cascade Range. Immediate interim guidelines could be developed through expert panels. Maintenance of sufficient Northern Spotted Owl nesting and roosting habitat is a critical consideration as is maintenance of Northern Spotted Owl prey habitat. One hypothesis worthy of testing would be the value to Spotted Owls of maintaining islands of denser nesting and roosting habitat within a landscape matrix that has been treated to reduce the potential for stand-replacement fire. Some well-designed long-term research to test effectiveness of several alternative approaches is imperative; this research is going to have to address creation of heterogeneity at larger spatial scales. We believe that substantial progress in resolving questions could be accomplished in ten years. However, we also view it as imperative to avoid widespread application of untested ideas.

Finally, we note that that the LSRs were not created solely for nor justified exclusively by Northern Spotted Owl! The LSRs were designed to provide for the full array of organisms that utilize LS/OG habitat, including Marbled Murrelet and hundreds of other species. LSRs were located to provide for high-quality LS/OG terrestrial and aquatic habitat. The only aspect of the LSR design that was driven primarily by Northern Spotted Owl biology was the concept of creating large compact, contiguous blocks of habitat, which meant incorporating younger stands and recreating the late-successional integrity of the blocks over time. The LSR network was also designed to accommodate the large-scale disturbances that are characteristic of the region and to allow natural recovery processes when disturbances occur.

2 CONSERVATION MEASURES ON STATE AND PRIVATE LANDS (HABITAT CONSERVATION PLANS)

Conservation measures on non-federal lands are regulated under both the Endangered Species Act (ESA) and the Migratory Bird Treaty Act, as well as state laws (e.g. California ESA) and other regulations, including Forest Practices Rules. We do not intend to review all these regulatory mechanisms, which are appropriately dealt with by USFWS in their role of assessing regulatory sufficiency. In this section we will focus solely on Habitat Conservation Plans (HCPs), which are authorized under section 10 of ESA. Our goal is to examine whether the scientific principles used in development of such plans are well-founded, or invalidated by recent scientific results.

Essentially, HCPs allow management of non-federal lands where threatened or endangered species occur, including 'incidental take' – killing or otherwise harming of the species as a consequence of management activities. Incidental Take Permits are issued by USFWS in response to a conservation plan, on the basis of several criteria, including (most importantly):

1. The level of 'take' cannot cause jeopardy (an appreciable increase in the risk of extinction).
2. 'Take' is mitigated to the maximum extent practicable.

Typically (but not always) HCPs have stated objectives, an implementation plan, and reporting and monitoring requirements.

Managers and owners of non-federal lands are not obligated to prepare an HCP, nor are they obligated to make particular conservation proposals, or to follow guidelines set by an overall coordinating plan (e.g. Final Draft Recovery Plan). Each HCP is proposed by the applicant, under unique circumstances, and is then negotiated with USFWS. This applicant driven process determines a great deal of the idiosyncratic nature of HCPs, which are typically prepared and negotiated independently, often by different USFWS staff and USFWS offices in each case.

Currently there are 17 approved Northern Spotted Owl HCPs, with plans in each of the three states. HCPs range in size from 1,632,000 acres (Washington DNR) to 40 acres (Scofield Corp). Plan duration and mitigation measures also vary: from 100 year plans (West Fork Timber) to five year plans (Boise Cascade) to one-time partial harvest with permanent deed restrictions (Scofield Corp).

In this document we will not critique individual HCPs, address the likelihood of their success, or second-guess the USFWS decision on the appropriateness of approving the HCP and ITP, or the adequacy of the conservation and other measures in place. Nor will we comment on the desirability of approving HCPs or on policies applying to HCPs (e.g. 'no surprises'). Our goal is simply to assess the scientific principles used in plan development and implementation. Where policies have both a scientific and a value driven component, we will pass comment on the science, but make no judgment on the appropriateness of the overall regulatory decision, which (appropriately) addresses other issues in addition to science.

A case in point is the 'no-surprises' policy that is in place, and provides assurance to land-owners that HCPs and ITPs will rarely be withdrawn or modified by USFWS at additional cost to the landowner. An important issue in such situations is what constitutes 'unforeseen circumstances' that may cause plan modification. Typically an HCP, or Implementation Agreement may define such circumstances from a legal perspective. Scientific results that may, under some HCPs, qualify as such 'unforeseen circumstances' would be major new threats to the listed species that might affect HCP success. Biologically there are several emerging threats to Northern Spotted Owls (Barred Owls, West Nile Virus, Sudden Oak Death) and perhaps other new information (e.g. on habitat definitions) that might be relevant to individual plans. We make no recommendations on action regarding individual HCPs or on whether these new threats or new information should result in modifications to the plans.

We note an important fact concerning HCPs – they are voluntary and remain in place only at the permit owner's pleasure. In the event that Northern Spotted Owls and their habitat are no longer found on the lands in question, the permit-holder could withdraw from the HCP (but would be required to continue agreed mitigation for incidental take occurring to that point). While it is not our role to critique this aspect of HCPs, it is worth noting that threats that remove owls or their habitat (such as invasive species or large stand replacement fires) could eliminate the landowners need for a take permit.

2.1 CONSERVATION AND MANAGEMENT MEASURES UNDER HCPS

Because of the overall small number of HCPs, and their great variation, there is no one model or yardstick for plan design and implementation. Similarly the conservation objectives of individual plans vary greatly. In some HCPs, specified numbers of breeding owls, with specified levels of reproductive success are indicated. In other HCPs, habitat alone is the management objective. Habitat too can be of different types – nesting/roosting/foraging habitat or dispersal habitat only.

Monitoring and reporting requirements also vary greatly between HCPs, often in relation to the performance objectives. Some plans for instance require monitoring of owl reproductive success; others simply require reporting of habitat modifications (and even here there is variation in reporting – for some plans harvest levels are not reported separately for habitat and non-habitat). Some plans require annual reports on owl populations; others require only five year reporting of harvest levels. This lack of consistency across plans means that no meaningful critique on the overall scientific basis of monitoring is feasible.

2.2 CONSERVATION PRINCIPLES USED IN HCPS

2.2.1 RESERVES

A few HCPs establish no-take areas of different sizes, with reserve provisions for the length of the permit or other long-term periods (for instance on the Elliott State Forest, where long rotation periods on some river basins effectively function as reserves). As with our discussion under the NWFP above, we see no reason to question the utility or effectiveness of such reserve strategies (note that many HCPs are small, some even smaller than the home range of a single owl). Maintenance of breeding owls distributed across the landscape is consistent with the objectives of the FDRP, and remain supported as a conservation measure. However, we again recognize that reserves will not protect owls from invasive threats such as Barred Owls or WNV.

Note that in some HCPs there are reserves established for other species (e.g. Marbled Murrelet, salmonids) that may function as additional protection measures for Northern Spotted Owls, just as riparian reserves under NWFP may foster owl conservation.

2.2.2 SHIFTING MOSAIC PROVISIONS

Several plans protect either owls or owl habitat on a shifting basis, such that harvest is tied to the development of habitat and the movement of owls. Harvest then is allowed in some areas as owls move, or new habitat develops.

Such provisions are based on several aspects of Northern Spotted Owl biology. For instance, owls are known to shift nestsites (though rarely), and individual territories may be occupied only in some years. Moving harvest around such animals will minimize disturbance and take. Such strategies may be particularly useful in situations where owls are not strongly linked to foraging in late-successional habitats (i.e. southern ‘woodrat’ populations). Habitat will nevertheless be ‘taken’ under this approach, so that this sort of HCP may only delay ‘take’.

Shifting-mosaic models for owl persistence on the landscape are less well developed than reserve based models. There have been no analyses evaluating the efficacy of the shifting mosaic model. However we have no reason at this point to feel that scientific evidence negates this as plausible conservation strategy.

2.2.3 DISPERSAL HABITAT

Several HCPs have as their sole or major objective the development or maintenance of dispersal habitat. Given that, in some plans at least, this meets identified global objectives as set out in the FDRP, or represents an improvement from current conditions, such dispersal habitat may have a useful conservation function. We see no reason to challenge the proposition that dispersal habitat is an important and necessary objective, given the metapopulation conservation strategy in place for much of the subspecies’ range (see above section for NWFP). We also note that some HCPs are designed specifically to bolster dispersal opportunities for owls on adjacent federal landscapes; this should augment the federal NWFP strategy and should increase the probability of success of that plan. We note, however, that the standards for such dispersal habitat are not consistent across plans, nor are they consistent with the original federal provision (50-11-40) or current NWFP strategies (primarily riparian reserves).

2.2.4 DEVELOPMENT AND MAINTENANCE OF NESTING/ FORAGING/ ROOSTING HABITAT

Several plans aim to maintain or develop habitat for resident owls (although with no actual provision that such habitat must be occupied). As with the reserve strategy above, this appears to be a reasonable objective, and certainly would represent a contribution to conservation whenever Spotted Owls are maintained or recruited. As with the reserve strategy however, it is unclear whether this ‘habitat only’ strategy will be less likely to succeed than was originally planned in the face of new emergent threats.

Note that, as with dispersal habitat, there is no one definition of ‘nrf’ habitat used across HCPs. This may be justifiable and well supported on scientific grounds, to the extent that such variation may reflect regional differences in the habitat associations of Northern Spotted Owls (see chapter 5).

Some plans aim to develop habitat, often at some future point, following the harvest of existing habitat. This strategy may be appropriate given its generic resemblance to federal conservation strategies that envisage an owl population that declines initially, and then recovers as new habitat develops. However given additional challenges that threaten to further reduce owl populations (e.g. West Nile Virus), it may be that the survival of owls in such landscapes is now less assured.

2.2.5 MONITORING AND ADAPTIVE MANAGEMENT

As noted above, many HCPs have only limited monitoring requirements. While this may be appropriate and proportionate to the goals of the individual plan, it does mean that it is more difficult to make an overall assessment of the conservation success of HCPs. Some other HCPs have rigorous and statistically well-designed monitoring programs, with specified trigger points. These plans are easier to assess; currently no such plan is in serious default of its stated objectives.

The panel has discussed (section 6 above) the role of adaptive management in the NWFP. Few HCPs specifically state similar goals – adaptive management is unfortunately inimical to the regulatory certainty that is desired by most landowners. Nevertheless some HCPs have trigger points that can cause changes in management, and others have formal mechanisms for plan amendments and management changes. The panel is supportive of the proposition that relevant science be incorporated into HCPs on an ongoing basis.

2.3 CONCLUSIONS

The majority of scientific principles applied to HCPs remain valid, just as these same principles continue to underlie the NWFP. Application of these principles varies strongly across HCPs (as to be expected given the different management and conservation priorities for such lands). Similarly the standards imposed, e.g. for habitat definitions, vary greatly; there is less justification for this variation on a purely scientific basis.

Just as with the NWFP, there is reason for optimism in that most conservation measures appear well designed, from defensible scientific statements. However there is reason for the same global concern as for the federal plans – current conservation measures offer no protection against invasive species.

Finally it is worth noting that some, but not all, HCPs are nested within an overall conservation strategy that references local and regional contributions, and coordinates with the larger federal NWFP. Such landowners, who are contributing to an overall strategy, and may carry out significant monitoring and research, may provide a tangible conservation benefit.

3 CONSERVATION MEASURES IN CANADA

The Canadian population of the Northern Spotted Owl, although it falls under Canadian jurisdiction, is still listed under the US ESA. This small population is the subject of intense debate in Canada, and was the subject of a workshop held in early 2004 *(Zimmerman et al 2004).* The workshop proceedings summarized the particular circumstances faced by the owl in Canada, the conservation challenges that are posed, the problems with conservation and management, the uncertainties in information, and the role of science in the overall coordinated strategy. It is not our intent here to critique or report in detail the results of these efforts, which are appropriately understood from the primary source *(Zimmerman et al 2004).* Our goal here is simply to report on the main scientific principles in use, and to compare the two national strategies.

The Canadian population of the Northern Spotted Owl is very small, isolated and apparently in sharp decline *(Harestad et al 2004).* There are gaps in the Canadian distribution, and the species has not been found in large areas of apparently suitable habitat (however, some areas have not been adequately surveyed). The population(s) declined by an estimated 10.4% annually from 1992-2002, with a decline of 35% between 2001 and 2002. In 2002, the breeding population was estimated at fewer than 33 pairs. Reasons for decline are thought to include past and ongoing harvest, Barred Owls, weather, prey, and predation. However, data on these factors are relatively sparse.

The Canadian population has reached the point that it is now vulnerable to stochastic demographic events, that could cause further declines and perhaps extirpation. This high vulnerability is expected to last for a long period, because forest regrowth is unlikely to lead to major increases in habitat in the short term. Some factors, notably past and current harvest and Barred Owl populations may continue to act deleteriously on the Northern Spotted Owl population. Generally, there is some suggestion that, compared to US populations, Canadian Northern Spotted Owls have a more dispersed population, suffer higher mortality, have larger ranges, produce fewer young at longer intervals, and require higher quality habitat to reproduce successfully (Simpson 2004). Innes (2004) summarizes not only the information that is known about this small population, but also the many information gaps, and uncertainties.

Clearly, managers of the Canadian population are faced with significant challenges. There has been continuing debate among scientists, managers and interested parties over what conservation measures to enact. The 1997 Spotted Owl Management Plan had an estimated 60% chance of population stabilization, leading the first Canadian Spotted Owl Recovery Team not to endorse the plan. A new (2002) Spotted Owl Recovery Team has developed a recovery strategy that is deemed ecologically and technically feasible, but details on the plan are unavailable. Hence our comments on scientific strategies must necessarily be limited.

We feel that Canadian scientists have correctly identified that extremely small population size is a unique issue for their population. They are also correct in identifying demographic stochasticity and other random events as operating at these levels. The basic conservation principles that are being considered include reserves and matrix management, exactly as in the NWFP. Canadian scientists are also concerned about loss of habitat due to harvest and fire, and the spread of the potentially competing and hybridizing Barred Owl. Dispersal of owls is seen as a key to long-term recovery; a central plank in the Canadian strategy is that the owls exist in a metapopulation, and may be supplemented with owls dispersing from the US. Hence the Canadian strategy to a large extent relies upon the success of US plans such as the NWFP. Scientists and managers are also concerned about the ability of reserves and small populations to resist emerging threats such as Barred Owls and West Nile Virus. Just as in the US, adaptive management is advocated, but has not yet been widely implemented.

Overall, the Canadian population of Northern Spotted Owls is clearly at a critically endangered state. Some issues, mostly as a consequence of extremely low population size, are considered unique to Canada (viz. demographic stochasticity, risks from hybridization). Whether or not emergency or recent efforts to save the owl and its habitat succeed, Canadian biologists appear to be using the best available information and scientific knowledge to understand the situation, and draft their recovery strategies. We single out two issues for favorable comment. First, there is an attempt to integrate science and management into a comprehensive model of owl populations (there is no such model for the US). Secondly, there is a strongly coordinated process for cooperation among interested parties. This typically Canadian approach might be useful south of the border, where there is a need for a systemic and long-term coordinated program of research, monitoring and management.

SCIENTIFIC EVALUATION OF THE STATUS OF THE NORTHERN SPOTTED OWL

CHAPTER TEN

Questionnaire: assessment of data quality, uncertainty and risk

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1 INTRODUCTION

This chapter reports the results and responses to a questionnaire submitted to the panel in June 2004. The goal of the questionnaire was to provide detailed information on the individual opinions of panelists, while at the same time determining the degree of concordance between panelists. We were particularly interested in evaluating issues such as 'data quality', 'uncertainty', and 'relative risk', which may defy easy quantification, but which are of fundamental importance to decision-makers.

1.1 UNCERTAINTY AND THE SCIENTIFIC METHOD

Science involves uncertainty. The core of scientific knowledge develops through the testing of hypotheses or unproven ideas. Some hypotheses gradually become strengthened, through processes of experimentation, analysis and critique. Such hypotheses eventually become the dominant explanations accepted by workers in a particular discipline. Knowledge therefore proceeds from greater to lower uncertainty – there always remains a possibility that new information will change our understanding. This review of Spotted Owls has provided numerous examples where initial hypotheses have been rejected or modified by new data or studies.

The study of wild organisms is inherently complex. An individual interacts with other members of its own species and other species, as well as the many components of its environment. This complexity means that there are often multiple uncertainties when considering a species' requirements and status. In the case of long-lived species such as the Spotted Owl, these uncertainties may persist over many years, as data accumulate slowly and the generation time is long. This poses problems for managers and policy makers who often must make decisions with only partial and inconclusive information. Development of more conclusive information may take many years and a large detailed research program that challenges an agency's commitment to ongoing investigation.

Biologists have long recognized the difficulties of working with complex natural systems. Ecology makes extensive use of advanced statistical techniques, in order to tease out the important factors affecting a species. Studies often rely on such statistical inference, and must often be largely observational with inference based on correlation. Only occasionally are biologists able to manipulate natural systems on a scale large enough to provide direct experimental testing of hypotheses. Therefore, ecological studies by their very nature are usually less definitive than some studies in other scientific fields.

1.2 PEER REVIEW

Science as a process involves many steps in the progress of an idea from untested hypothesis to widespread acceptance. Perhaps the most important aspect of the scientific method is the open presentation of studies that allow methods to be criticized, results to be evaluated and replicated if necessary, and conclusions to be challenged. Over the years, 'peer review' has developed as the major form of scientific quality control. Ideally, peer review is the unbiased assessment of scientific work, usually as presented in a scientific document. Using peer review, findings are critically examined, and (we hope) mistakes are corrected, before they become accepted by the community.

A finding that has undergone peer review is more likely to be robust relative to a finding that has not undergone peer review. For those who must make decisions, whether or not a conclusion is based on peer-reviewed data and information may prove a useful indication of scientific quality. At the very least, the manager has confidence that someone with technical expertise has evaluated the findings.

Scientists make widespread use of peer review in many of their own decision-making processes. Hence peer review is used as the primary tool in determining whether a study was well carried out, and is sufficiently worthy of publication. Peer review is also a major tool that supports funding decisions, approving grants, awarding tenure, etc. Peer review is not just applied to materials for publication.

Published information has often (but not always) undergone peer review. Hence there is a tendency among many persons to assume that published work has been peer-reviewed, while unpublished reports, etc. have not, and are hence less reliable. This is an oversimplification and a mistake. For instance, some of the most heavily scrutinized science is undoubtedly to be found in graduate students' theses, which are unpublished and read by at most a few people. In studies of wildlife, many data are to be found in annual reports and other unpublished 'gray literature'; sometimes such reports have undergone (more or less) formal peer review, even though they are unpublished. An example from our review of the Northern Spotted Owl is the exhaustive meta-analysis of population trends, which is a massive and important scientific endeavor, reviewed by other scientists (Ecological Society of America), but is as yet unpublished. Conversely, all scientists are aware of publications that obviously received cursory or inadequate peer review, and are still replete with inappropriate statistical tests, mis-interpretations, etc. *Beier et al. (2003)* give an (un-peer reviewed) account of how peer review failed to prevent publication of incorrect inferences for one endangered species. Scientists also recognize that peer review does not automatically confer infallibility – it is simply one indication that a paper has been examined critically by experts in the field. The peer review that allows publication merely allows the paper to then be further evaluated on the international stage of scientific opinion.

The 'gray literature' and other forms of scientific communication (presentations, personal communications, etc.) may contain important information that has undergone challenge. Presentation at formal meetings before a panel of experts, as carried out in this status review, is another form of review. Indeed the level of scrutiny and argument in the SEI panel process may sometimes be uncomfortably incisive.

1.3 RISKS, UNCERTAINTY, ACCURACY AND DECISION-MAKING

An important issue for those considering the application of science to natural systems is the probability of error and the risks of being wrong. Managers and policy makers should recognize that science does not provide certainty, and that decision-making will always be carried out against that background of uncertainty. Peer–review may reduce these uncertainties, by de facto solicitation of scientific opinion. However, scientists and decision-makers both need to recognize the limits of science. Often the role of science is simply to delimit the 'decision space' for a manager or policy-maker.

It is useful to distinguish between risk and uncertainty. Uncertainty refers to whether an inference or conclusion is correct. Risk refers to the consequences of taking action with uncertain knowledge. There is always some level of uncertainty in a scientific conclusion. In systems such as natural ecosystems, this usually stems from inaccuracy, due in part to random factors, difficulties of observation, etc. In this status review it is important to recognize the differences between these independent criteria. For instance, we may characterize a study as having limited accuracy but little uncertainty. An example may be the attempts to track changes in habitat acreage over the past ten years. The review panel has characterized such estimates as inaccurate, but still believe that these estimates are good approximations to reality. There is low accuracy, but still little uncertainty, and decisions based on these data are unlikely to carry much risk from being wrong. Conversely, the panel reviewed many excellent and presumably accurate local studies, but are still uncertain about the degree that these can be extrapolated to other sites – that is there is good accuracy, but little certainty, and hence decisions based on such conclusions carry risks from the potential of being wrong. A well-known example of such a conclusion is the initial emphasis of Spotted Owl studies (in Washington and Oregon at least) on old-growth conditions; it is now clear that other components of habitat are also important in different parts of the range. Lastly, it is also useful to recognize that there may be some uncertainty over an issue, but that it still entails little risk. For instance, introgression of genes from Barred Owls may be entering the Spotted Owl population through hybridization – the degree of such gene flow is essentially unknown, but the panel has evaluated this as of little risk.

The SEI panel process attempts to lay bare these different criteria. Our intent is to show the degree to which different conclusions are supported by the evidence. This then allows us to evaluate remaining uncertainty over an issue, and to discuss the relative importance of different threats. Ultimately, information on uncertainty and risk is critical to decision-makers who must determine the listing status of Northern Spotted Owls.

1.4 THE QUESTIONNAIRE

The questionnaire was designed to make clear how information was used in the preparation of this status review. The results show the individual panelists' scientific opinions on the full range of topics. In some cases, the panelists agreed with their evaluation of studies and the conclusions to be drawn from them. For such issues and data, unanimity among the panel may be a measure of a relatively high degree of certainty. On other topics there was less agreement – this may be taken as indicating more uncertainty.

Each panel member was asked to respond to a set of 52 detailed questions. Some questions were more extensive, and more detailed than others, and each panelist was given the opportunity to comment or provide additional information on their response. The following sections of this report summarize the results of the eight questionnaires that were filled in. Full details of each panelist's responses are shown in the Record. Note that sometimes panelists checked more than one answer to a question, so that for some questions, there are more than eight responses recorded.

Initial sections of the questionnaire were focused on overall issues of data quality and of the comprehensiveness of the review process. Subsequent sections considered the data and conclusions in different subject areas. After these detailed questions, the questionnaire contained sections for evaluations of uncertainty and of risk, which ultimately led each individual to rate the threats now faced by Northern Spotted Owls. Finally, panelists were asked to compare our understanding of different subject areas, as well as the importance of developing new information to improve evaluations in the next status review. Thus, the questionnaire encapsulates in miniature the entire status review, including the degree of consensus among us.

2 SUMMARIZED RESULTS OF THE QUESTIONNAIRE

2.1 OVERALL RESPONSES

The panelists easily completed most sections of the questionnaire, and most made extensive comments. However in a few subject areas, not all panelists felt able to answer all the questions, indicating that they did not have sufficient information, or that they were not sufficiently familiar with the issue. In particular, sections dealing with models of habitat development were left blank by several panelists. In some other cases, panelists did not wish to express their personal opinions on issues which were very well explained elsewhere.

Two panelists (A. Franklin and Gutiérrez) declined to fill in sections of the questionnaire dealing with demography of Northern Spotted Owls. Their reasoning was that the meta-analysis report (Anthony et al 2004) is a much more complete analysis of demography than that the summary prepared for this review. They felt that the empirical data in the meta-analysis were available and more relevant than panel opinions on the summary provided. Also, as co-authors on the meta-analysis, it was difficult for them to comment on it. The rest of the panelists, while agreeing that the meta-analysis should be used directly by those interested in population trends, nevertheless felt able to summarize the data. It is necessary nevertheless to point out that A. Franklin and Gutiérrez are the two panelists with greatest experience with Spotted Owls, and hence that the answers on demography were provided only by non-Spotted Owl biologists.

Although all panelists provided additional comments throughout the questionnaire, there was (unsurprisingly) a tendency for panelists to comment most extensively on those subjects in their own area of particular expertise or where they had had primary authorship of a chapter within the status review. Therefore, in these sections below, we distinguish the comments of such ‘specialists’ from those of the other panelists.

The following sections summarize the responses of the panelists, including clarifying comments. An example of the actual questionnaire follows, with all scores and comments. Individual panelists’ responses are provided in the Appendix.

2.2 QUESTIONS ADDRESSING DATA QUALITY AND THE REVIEW PROCESS

Panelists were asked to rate the overall quality of information available to them during the review process (Q.1). There was considerable variation among panelists' responses, with some indicating general satisfaction, while others argued that there were major information gaps. However detailed examination of comments showed that most respondents recognized that, compared to other endangered species, the available data on Northern Spotted Owls are excellent, and represent the combined work of many biologists over an extensive period. The Northern Spotted Owl is "one of the best studied birds in the world" with "one of the largest information bases for any endangered species". Nevertheless all panelists thought that there was a need for more information on critical topics.

In general panelists expressed satisfaction with many of the individual studies and the data examined through the review process (Q.2,3). As noted, there was recognition that some subject areas were better treated than others. However for the most part, panelists were satisfied with the high quality of published papers, but more critical of unpublished reports or of presentations where data were not easily examined. There was no obvious tendency for panelists to be more or less critical of information in their particular specialty area.

The panelists reported using peer-reviewed data in nearly all or at least a majority of instances (Q.4). Bigley and Fleischer reported that in their particular subject areas (habitat trends and genetics) some of the information was relatively new, and had not yet been subjected to extensive peer review. When non peer-reviewed data were included, most panelists felt that appropriate care was used (Q.5), with some recognition that discussion by the panel constituted a form of peer review. However Gutiérrez felt that non-peer reviewed data had been used excessively, particularly with regard to Barred Owls and habitat trends, while A. Franklin was concerned that sometimes too much credence was placed on information from oral presentations at panel meetings because too many details were omitted for the panel to adequately review the information.

There was unanimity among the panelists that the status review had comprehensively considered all issues of importance (Q.6).

2.3 GENETICS AND TAXONOMY

There was no disagreement among the panel about the status of the Northern Spotted Owl relative to other subspecies (Q.7,8). All felt that the California and Northern Spotted Owls had separate evolutionary histories, warranting distinct subspecies status. When differences were noted among published papers, the panelists felt these were minor (Q.9), with some earlier studies being superceded by later studies.

The panel showed a diversity of opinion on the issue of boundaries between subspecies, half the responses indicating that the boundaries are well characterized, the other half disagreeing (Q.10), with some interest being expressed in additional studies. Introgression into the Northern subspecies was not currently thought to be a major threat, although most thought this was insufficiently known to assess (Q.11). Similarly, loss of genetic variation in small populations was not identified as a currently significant threat, but most thought that the data on this subject were insufficient to assess (Q.12). The geneticist on the panel (Fleischer) argued that there must eventually be some losses of genetic diversity, "but that how much and how significant a threat this will be is unpredictable".

2.4 PREY

Although the general patterns of prey use appear to be known (Q.13), some panelists were critical of gaps in knowledge. No panelist felt that the effects of variation in prey abundance, habitat use, and availability on Spotted Owl populations are well understood (Q.14) or that the population dynamics of prey themselves are well understood (Q.15). The fact that such studies had not been pursued or funded was singled out for comment by several panelists. Similarly, the panel unanimously felt that there was insufficient or inconclusive evidence as to whether Spotted Owls deplete their prey (Q.16). Biologists on the panel who study owls were as critical of the insufficiencies of prey studies as the other panelists. Generally, throughout the review process, panelists frequently commented on the irony of studying a predator without studying its prey.

2.5 HABITAT

Panelists commented on our current understanding of habitat associations of Northern Spotted Owls in different parts of the subspecies' range. With few exceptions, panelists felt that initial findings on habitat associations, as known at the time of listing, were confirmed and supported by more recent work (Q.17). An association with old-growth forest is still accepted, with demographic performance being linked to availability of such habitat (Q.18), and at least some evidence that late successional habitat may sometimes be limiting (although there is a diversity of opinion on the strength of such evidence) (Q.19).

Nevertheless, panelists acknowledged changes in our understanding of habitat since 1990. No panelist thought that there was significant support that, throughout the range, 'optimal' home ranges consists entirely of pristine old-growth (Q.20). As noted by those scientists studying owls, A. Franklin and Gutiérrez, this may be locally true, where flying squirrels are the primary prey. Similarly, panelists largely rejected the notion that forest fragmentation was synonymous with habitat fragmentation (Q.21) (with the same caveat from A. Franklin and Gutiérrez).

Local differences in habitat associations were acknowledged by all panelists. Most panelists accepted that in the Redwood zone, owls may use young, but still structurally complex forests (Q.22), and that hardwoods were sometimes an important component of habitat (Q.24). However there was a diversity of opinion on habitat associations in the Eastern Cascades (Q.23).

Similarly, all panelists believe that there is evidence that heterogeneous landscapes favor higher demographic performance in some circumstances, such as in the Klamath region (Q.25) although opinion is divided for other regions in California and southern Oregon (Q.26) and most panelists think that there is little or no supportive evidence in other regions such as the Cascades (Q.27). There were substantial differences of opinion on whether local variation in habitat associations was generally explicable in terms of differences in prey (Q.28). All panel members felt that there was some evidence for this proposition, but opinion divided sharply on the strength of such evidence.

The distribution and availability of habitat was addressed in a separate chapter of this review (6) and in the latter part of the questionnaire section on habitat. There was a wide diversity of opinion on the quality of the data made available to the panel. Three of eight respondents thought such data were generally good, but three others disagreed, and characterized the data as generally limited (Q.29). Two others registered an intermediate position. It is worth noting however that no panelist regarded the data on habitat distribution as excellent.

Local and ownership specific trends in habitat were addressed in the sections of Q.30. The wide diversity of responses to some of these specific questions suggests an overall low level of confidence and understanding. While most respondents thought that habitat trends in British Columbia or on state or tribal lands were probably or definitely declining, for other areas, such as areas in the western Cascades, and on federal land, there was a great diversity in responses, with several panelists feeling that habitat trends are positive, several suggesting the opposite, and others unsure. Given the acknowledged importance of habitat to Spotted Owls, the low level of agreement among panelists for this question suggests that there is a significant need for better and less ambiguous data (as indeed was suggested by respondents A. Franklin and Gutiérrez).

The causes of habitat loss were addressed by Q.31, again on a regional basis. For this question, there was more concordance. Although both biologists who study owls (A. Franklin and Gutiérrez) and Fleischer felt unable to answer this question, the other panelists clearly identified regional causes of habitat loss. In British Columbia, and western Washington and Oregon, timber harvest continues as a major cause of habitat loss, although fire also is regarded as important by some. By contrast, on the eastern slope of the Cascades and in the Klamath region, fire is regarded as the major cause of habitat loss, together with insect damage (eastern Cascades only). In the Redwood region, no clear pattern was apparent, although three respondents regarded timber harvest as important. Considered by ownership basis, panelists clearly distinguished federal lands from others. Only one respondent considered timber harvest to be a significant contributor to habitat loss on federal lands, as opposed to five who saw fire as important. On tribal and private lands, timber harvest is still regarded as the major cause of habitat loss, while state lands occupy an intermediate position in the opinion of panelists.

Habitat trends were modeled by the federal agencies, who presented results on habitat development (presentation of Cadwell). Questions regarding this model drew a poor response from panelists - four of eight felt able to comment at all, even to state that the performance of the model was uncertain (Q.32). Given this low rate of response, it is probably unwise to draw many conclusions on this model, or on the highly variable panel responses (Q.33-36). Note however that the panel specialist in this area, R. Bigley, gave a long and detailed response to these questions, including a critique of methods.

2.6 BARRED OWLS

No area of the review was more strongly debated among the panel than the quality of the data and studies on the effects of Barred Owls on Spotted Owls. This debate was reflected in responses to the questionnaire. Two panelists (A. Franklin and Gutiérrez) declined to fill out the tables in three Barred Owl questions that required detailed geographic knowledge, given what they saw as insufficient information to make such specific comments. However, they did provide comments concerning their general opinions on effects. By contrast the other panelists were unambiguous in their opinions: all six respondents felt that Barred Owls were currently having strong effects on Spotted Owls in British Columbia and Washington, with nearly as strong as effect in Oregon or on the whole subspecies (Q.37). These six respondents included panelists (Cody, Marzluff, Courtney) with extensive experience with inter-specific interactions. Similarly, all six respondents saw lower or no effects in the Klamath and Redwood zones, and no effects in the California Cascades and the Sierra Nevada.

A very similar response was shown to considerations of the long-term (>50 year) effects of Barred Owls on a regional basis (Q.38). A. Franklin and Gutiérrez again declined to fill out the table in this question, while other panelists saw the Barred Owl as having a negative effect in > 50 years everywhere except in the California Cascades and the Sierra Nevada where the future was unpredictable. Once more, predictions of the future trends of Barred Owl numbers followed the same pattern. The six respondents suggested lower rates of increase in the northern-most areas (British Columbia and Washington) where the population of Barred owls is already large, with greater predicted rates of increase in Oregon, and uncertainty regarding California (Q.39).

Detailed considerations of the spread and effects of Barred Owls drew somewhat mixed responses. Regarding Barred Owl use of more mesic habitats, five panelists predicted that this pattern would change (Q.40), but three were uncertain. However we note that no panelist predicted that a continued association of Barred Owls with mesic habitats was likely. A very similar pattern of responses was elicited to a question on whether Barred Owls would maintain a current association with late-successional habitat (Q.41). A majority of panelists predicted this pattern would change, but many were uncertain. There was however no clear response on whether forest harvest and fragmentation promoted spread of Barred Owls (Q.42). Finally, no panelist saw hybridization between Barred Owls and Spotted Owls as frequent (Q.43).

Despite the diversity of opinions and predictions about the effects of Barred Owls on Spotted Owls, there was agreement among the panel about the quality of the data on this issue: no panelist thought that the data were of high quality (Q.44). At best, panelists saw the data as of mixed quality, with several regarding the data as poor.

2.7 DEMOGRAPHY

The panelists were asked to consider the effects of West Nile Virus (Q.45). None thought that there was a compelling basis for extrapolation to predict effects on Spotted Owls, although the majority thought such an effect would be logically consistent.

Regional population status and trends were addressed in Q.46. As discussed above, the two most qualified panelists (A. Franklin and Gutiérrez) declined to fill in the table, in deference to results from the meta-analysis report. By contrast the other panelists, including those with a background in population approaches (Cody, Marzluff, Courtney) unanimously stated their opinions that Spotted Owl populations were in decline in British Columbia and most of western Washington.

The situation was regarded as probably negative elsewhere in Washington, but was regarded as less certain progressing further south, with mixed opinions for the Klamath, Redwoods, and California Cascades areas.

2.8 RISK AND UNCERTAINTY

One of the most important sections of the questionnaire asked panelists to assess the state of knowledge on different issues of Spotted Owl biology (Q.47). There was a great deal of unanimity among the panelists, especially considering the diversity of backgrounds of the panelists, and the healthy debate during the review process.

Panelists thought that the following topics were either well or adequately understood: taxonomy of spotted owls; population trends overall, and in different regions.

Panelists thought there was more uncertainty on the following topics, with some debate about whether the knowledge base was adequate: genetics, effects of Barred Owls, current harvest, fire, windthrow, insect damage, fragmentation, weather and demographic isolation.

Panelists agreed that the following subjects were inadequately understood: West Nile Virus and other diseases, synergism between and among factors.

On only two subjects were there significant differences among panelists. There was little agreement about the state of knowledge on the effects of past harvest, and of predation.

Many of these same factors were then evaluated in terms of the risk to Spotted Owls, if they were to occur (Q.48). Again there was a heartening unanimity among panelists.

Panelists agreed that the following issues, if they were to occur, would pose little risk to Spotted Owls: Genetics issues, including introgression and hybridization with other subspecies and species; windthrow; predation.

Significant risks were identified by panelists for the following issues: habitat loss to past and current harvest, fire, insect damage and Sudden Oak Death; the effects of fragmentation, weather, demographic isolation, and synergistic interactions.

The panelists were unanimous in stating that the risk posed by Barred Owls was high.

The last response was particularly interesting. Although there is disagreement among the panelists on the strength of evidence regarding the effects of Barred Owls (see section 2.f), there is no disagreement that such effects could pose high risks. This is a subtle but important point – the panelists clearly identify Barred Owls as a potential major threat.

Questions 49 and 50 directly address the issues of threats. The panelists were asked to evaluate the many different factors as current or future threats to Spotted Owl survival. All panelists regarded Barred Owls as a current and probably future threat. A majority of panelists also identified the lingering effects of past harvest, and synergistic interactions as current threats.

Current harvest and fire were regarded as current threats by 50% of the panelists. Genetic effects, Sudden Oak Death, West Nile Virus, and demographic isolation were largely regarded as future rather current threats. Introgression was regarded as a threat only by Fleischer, the panel geneticist. Insect damage and disease other than WNV were seen as threats only by a few panelists. Hybridization, windthrow, and predation were not regarded as significant current or future threats by any panelist (including those panelists with backgrounds in these study areas: Fleischer, J. Franklin, Bigley, Marzluff).

The panelists also compared these issues in terms of threat with the perceived threats from these same factors at the time of listing (Q.50). In general, panelists were in close agreement about the changes in threats over the past 14 years. All saw Barred Owls and West Nile Virus as increasing threats. Most also saw increased threats from fire, Sudden Oak Death, and synergistic interactions. Similarly there was general agreement that the threats posed by ongoing harvest had decreased significantly. On only two issues was there substantive disagreement: two panelists thought that the delayed effects of past harvest were decreasing - one panelist thought the opposite; five of seven respondents thought that the effects of fragmentation should be seen as a reduced threat now – two demurred.

In general, changes in perceived levels of threat came about due to a change in the factor itself rather than a change in our understanding of the issue. Barred Owls, West Nile Virus, and Sudden Oak Death are new, invasive threats, while the threat posed by fire is thought to be increasing due to the lack of pro-active management in fire-prone forests. Similarly the perceived threats from harvest and fragmentation have decreased greatly with the reduced harvest levels on federal lands following adoption of the Northwest Forest Plan. New information has contributed to these changed assessments of threats primarily for only two (related) issues: weather and synergistic effects. There is also some indication that new knowledge suggests that predation is less of a threat now than was thought at the time of listing.

2.9 CONSERVATION PLANS AND MANAGEMENT

The panelists were asked to re-evaluate the scientific premises of the Northwest Forest Plan, given the new information that has accumulated since Plan design (Q.51). No panelist thought that *all* the premises were currently well-supported (primarily because of the invasion of Barred Owls according to several responses). Two panelists thought that most important scientific premises were still supported, but five thought that only some such premises were still well-founded; this included the two panelists (J. Franklin and Bigley) with greatest experience with land management and the NWFP.

2.10 MONITORING AND RESEARCH

Given that the panelists had completed an analysis of scientific knowledge, and identified significant gaps in information, they were asked to evaluate whether further information would be useful to a future status review (Q.52). An important distinction was made between research (which would provide qualitatively new information, that could alter our understanding of Spotted Owl biology and status) and monitoring (which may not produce qualitatively new data, but will be essential to tracking , for example, population and habitat trends.

For only one subject area did the panelists generally feel that new information was unlikely to change understanding – the panel almost unanimously agreed that the taxonomy of Spotted Owls is robust, and unlikely to benefit from further investigation.
The panelists almost all favored a series of strong monitoring programs that would provide accurate information on owl population trends, habitat trends, and the incidence of Barred Owls, fire and West Nile Virus.

Many panelists also identified significant research needs: prey selection and dynamics, demographic performance in different habitats, genetic differentiation, regional differences in habitat selection and the extent and effects of ingrowth.

It is worth stressing that no panelist regarded the current knowledge base on Spotted Owls as adequate, or thought that monitoring programs should be curtailed.

Summary of responses
Sustainable Ecosystems Institute

Northern Spotted Owl Questionnaire

The NSO questionnaire addresses many of the important issues considered during the review process. The individual panelists' responses will show the degree of unanimity or uncertainty on different topics. They will also show which data are considered most reliable, and why panelists have reached their individual conclusions.

In filling out this questionnaire, please take the opportunity to expand on your answers. We have found that such 'explanations' can be very useful. It is also a way that you may address uncertainties, alternate hypotheses, etc. Use this also as an opportunity to comment on ambiguities or qualifications. If you are filling in an electronic copy, simply add space as necessary. If working from a hard copy, use a separate sheet for expanded responses.

Key to respondents:

AF	Alan Franklin
JF	Jerry Franklin
JM	John Marzluff
MC	Martin Cody
RB	Richard Bigley
RF	Rob Fleischer
RG	Rocky Gutiérrez
SPC	Steven Courtney

PART I. GENERAL QUESTIONS

1. Compared to other endangered species issues you have worked with, how would characterize the knowledge base for understanding the status of the Northern Spotted Owl?

XXMajor information gaps;
XX X Minor information gaps;
XXXWell understood

Additional comment:
SPC -While many areas have been well studied (e.g. demographic study areas), other essential topics have not been considered at all.
MC - Except for a) Barred Owl influence not at all well researched; b) prey base of NSO not much studied; c) demography analysis seems very limited compared with its potential, needs more insight and original, extended analysis.
RB - Compared to other species, we have very good information on Northern Spotted Owls; they are the best-studied owl in North America. Significant progress has been made in specifics concerning their population trends and habitat selection. Considerable information gaps remain, many relate to new possible risks to the species.
RG - The northern spotted owl has one of the largest if not the largest information base for an endangered species. The fact that some key information remains unknown or uncertain points to the difficulty of determining the causative factors related to a species decline.
Major information gaps: 1) the causative mechanisms that affect survival rates, fecundity rates, and population trends, 2) the effect of barred owls on spotted owls; 3) the relationship of habitat characteristics to occupancy and performance in that habitat; 4) trends in habitat on public land over time, 5) effect of regulation on mitigating negative effects of habitat loss or change, 6) trends in habitat on private land. Minor information gaps: 1) Genetic structure, variation, and gene flow among populations (introgression of barred and spotted owls). Well understood issues are habitat use, habitat selection patterns, food habitats, home range size, general dispersal patterns, basic genetic relationships.
RF- The NSO has been the subject of a tremendous amount of research, but gaps do remain in areas such as disease, genetics, and impacts of Barred Owls.
AF - There are very few wildlife species that could be characterized as "Well understood". The knowledge base for northern spotted owls is mixed. There are major information gaps for certain aspects, such as specific effects of barred owls on spotted owl life history parameters the causative mechanisms for observed variation in life history traits and population dynamics, and the effects of natural and anthropogenic disturbance on spotted owl population. There are minor gaps in other areas, such as genetics, and natural history.
JM - One of the best studied birds in the world

2. In your opinion the overall quality of the information available during the review process (across all subjects considered by the panel) was:

High quality, majority of conclusions strongly supported X
Generally high, most conclusions strongly supported XXXX
Mixed quality, some conclusions based on limited evidence XXX
Very mixed, some conclusions based on sparse evidence
Generally low, many conclusions based on weak evidence

Additional comment:
SPC - Barred owl, habitat trends and correlates of demographic changes are just 3 areas that were poorly known.
MC - Many of the regional reports are somewhat anecdotal in info reported, Probably as they are generated by field personnel with limited training and scientific expertise.

RB - There is an extensive body of peer reviewed literature on Northern Spotted Owls. Most important aspects of NSO ecology have been investigated over several years, often by multiple investigators at multiple locations. Additional data and years of observation are valuable. The future evaluation of remaining issues will add an increased level of specificity to our understanding and new aspects of NSO biology like Barred Owl interactions and the threat of West Nile Virus.
RG - Mixed quality. General population dynamics, natural history of owl, and genetics are very good, but we are lacking key information on causative mechanisms (see 1 above) which leads to a mixed quality assessment because we cannot distinguish (for example) barred owl effects from some other effect on spotted owls in the northern part of their range
AF - For the most part, the quality of the published literature is high. However, many of the reports and presentations were of mixed quality and it was often difficult to evaluate the methods used, especially in the presentations because of their short duration.

3. In your opinion the overall quality of the information available during the review process (in your subject areas, and for the documents you personally read) was:

High quality, majority of conclusions strongly supported X
Generally high, most conclusions strongly supportedXXX
Mixed quality, some conclusions based on limited evidence X X X
Very mixed, some conclusions based on sparse evidence
Generally low, many conclusions based on weak evidence

Additional comment:
MC - I.e. on BO influences, basic lack of studies directly addressing BO numbers and trends, and data collected incidentally to NSO survey work leaves much to be desired.
RB - There are still considerable uncertainty and conjecture, particularly related to regional trends in habitat development and loss.
RG - The barred owl information was very mixed for the numerous issues cited in the barred owl chapter, but the population and habitat data were very good.
AF - Quality of information on trends in populations and habitat associations was generally very high. The quality of information on the effects of barred owls on spotted owls tended to be more speculative and poorly analyzed.

4. The conclusions reached during the review process were based on peer-reviewed data and papers:

In nearly all subject areas XXX
In a majority of subject areas X X XXXX
In some subject areas but not others

Additional comment:
MC - and in those areas based more on regional reports, the data quality was high even tho not peer reviewed.

RB - For the traditional areas of owl biology (taxonomy, habitat use, demography) conclusions are solidly grounded in carefully reviewed data and interpretations. For emerging issues (Barred owl interactions, West Nile Virus) and some long-term issues (suitable habitat trends) the information is relatively new and has not benefited from the lengthy review and reexamination process of more traditional subjects.
RG - In nearly all subject areas, but was considered more heavily in the section on barred owls.
AF - See comment 5 below.
RF - There was a lot more "grey" literature in the aspects dealing with habitat and ecology of NSO, and only a handful of unpublished reports or manuscripts dealing with the areas in which I was primarily concerned (systematics, genetics, and BO/SO hybridization).

5. For some subject areas the panel relied on information that had not been peer-reviewed (reports, presentations, etc.), as noted by italicized citations throughout the report. In your opinion the degree of discussion and scrutiny by the panel assured that when such information was used, it was used appropriately.

X X XX Strongly agree
X X X X Agree with qualification
Disagree

Additional comment:
SPC - Some areas, e.g. Barred Owls, were well discussed. Other areas, such as habitat trends were not.
MC - Noting that is IS a role for field survey notes and comments, as these personnel generally know well NSO and what they are doing and saying.
RB - The panel process was essentially a peer review process.
RG - I think that non-peer reviewed information was used more than it was warranted in a few cases (e.g., barred owls and habitat relationships). I believe this was done because of the pressure to use non peer reviewed information. In one respect this was relevant in the form of panel meetings because it helped formulate the issues needed for discussion. But use of non-peer reviewed information is always suspect in my opinion because there is no way to evaluate the data (most of the time non peer reviewed papers have no data but only generalities and opinions of the authors).
AF - I think too much weight was sometimes placed on information presented in oral presentations. These presentations often were too brief and omitted too many details to be adequately reviewed by the panel.
RF - In some cases, unpublished material was given high credence because of our own "peer review". We can tell quality from not.

6. In your opinion, the SEI review process comprehensively addressed all major issues affecting NSO populations

XX XXX X X X Strongly agree
Agree with qualification

Disagree

Additional comment:
RB - A considerable time has passed since the last comprehensive synthesis of NSO ecology as related to potential population threats. I hope that one of the outcomes of this process is to refocus efforts to fill in the identified information gaps.
RG - I think the panel made a serious effort to uncover those areas that were essential to assessment.

PART II QUESTIONS RELATED TO GENETICS AND TAXONOMY

7. In your opinion the best available scientific evidence supports:

A significant evolutionary separation between California Spotted Owls and NSO
XXXXXXXX
Lack of significant evolutionary separation between California Spotted Owls and NSO
There is insufficient and/or contradictory evidence so that it is hard to form a strong conclusion.

Additional comment:
RB - There is consistent evidence that supports a solid subspecies separation between the Northern Spotted Owl and the California Spotted Owl. The preponderance of information suggests the subspecies have been separated, probably for on the order of ten thousand years.
AF - There seemed to be very strong evidence for a separation between California and Northern Spotted Owls.
RG - A significant evolutionary separation between California Spotted Owls and NSO **–** Clearly this is the case.
This should be a non issue from a scientific point of view. There is clear evidence that these subspecies have genetically differentiated
RF - There is no doubt that there has been, and at present is, a significant divergence between the two geographically defined taxa. Evidence of morphological divergence is mixed, but the mtDNA signal is strong and clear.

8. The differentiation between California Spotted Owls and NSO can best be characterized as that between:

Separate evolutionary species
Distinct subspecies XXXXXX
Poorly defined but biologically significant subspecies X
Distinct Populations with extensive gene flow
Clinal variation within one interbreeding population
Other:

Additional comment:

MC - Though undoubtedly there is clinal variation within each subspecies.
RB - There is consistent evidence that supports a solid subspecies separation between the Northern Spotted Owl and the California Spotted Owl. The preponderance of information suggests the subspecies have been separated, probably for on the order of ten thousand years.
AF - I felt this question was beyond my expertise to comment on with this level of detail.
RF - There is some question about how much introgression there is and will be in the future between the subspecies, but at present, they are well-diagnosed by 75% rule and other subspecies definitions.

9. In general the conclusions drawn by the panel from the different studies on taxonomic status showed that these studies were:

In agreement with each other XXXX
Different on minor points of technique and data analysis XXX
Different on minor points of interpretation and conclusionsXX
Significantly different from each other in conclusions
So different as to render interpretation difficult

Additional comment:
RB - Increasing sophistication is being used to analyze taxonomic data. At the rate in which new information is emerging, I anticipate increased clarity in the years to come. I think the more interesting studies will investigate the levels of introgression between the NSO and the CSO.
RG - I thought the first Haig et al. paper was seriously flawed by incorrect analysis and poor choice of a genetic system relative to the question being asked.
AF - My assessment here includes the recent work by Haig et al. that seemed to contradict their earlier paper.
RF - The studies differ in methods, some with better resolution than others (e.g. mtDNA and microsatellites versus RAPDS and allozymes). In addition, authors, to some extent, interpreted the results of the lower resolution markers with greater certainty than they were due.

10. The boundaries of NSO and CSO distributions are:

Well characterized XXXX
Not well characterized, and in need of clarification XX
Not well characterized, and unlikely to be easily clarified XX

Additional comment:
MC - Because subspecies ranges are contiguous and dispersal capacity in the owls is considerable.
RB - There appears to be directional introgression northward into the historic range of the NSO. The rate is unclear. Further investigations into this process would be very helpful.
RG - I think it is general true that the subspecies boundary is definable as a zone but not a strict boundary as is the case with most parapatric subspecies. Whether this zone can be more rigorously defined would depend on additional sampling within the zone of contact.

AF - The word "boundary" is a strong term. Rather, there are indications of a zone where the two subspecies are in contact with each other, the extent of this zone is still poorly understood.

11. The panel heard from presentations by Haig and others that there is evidence for introgression between CSO and NSO populations. Gene flow between NSO and CSO populations is:

Likely to have negative consequences for NSO fitness.
Unlikely to have negative consequences for NSO fitness. XXX
Insufficient evidence to evaluate XXXXX

Additional comment:
RB - The rate and consequences of introgression are unclear and should be monitored and reassessed in the future.
RG - Barrowclough et al. first found such introgression and it was subsequently verified by Haig et al. At this time the amount of introgression is small and it is unknown if this is recent or old gene flow at this time. The latter precludes any conclusions about whether this is good or bad or neutral in its impact or whether it will continue in the future.
RF - The data on this question are just not there. I imagine it not likely to impact fitness, but may impact listing status if the evidence of introgression is substantiated, and it continues in the future.

12. It is often held that small population sizes, and isolation of populations may result in reduced genetic variation and loss of evolutionary potential. In NSO it has been suggested that some populations may be vulnerable to such effects. Based on the evidence available to the panel, such effects:

Are significant and probably occurring
Are significant and while not yet occurring, may do so in the futureXX
Are likely insignificant XX
Are plausible, but there is insufficient evidence to determine if they are operating XXXXX

Additional comment:
RG - Small populations are vulnerable to these effects if there is no gene flow to maintain such genetic diversity. It appears that no populations are truly isolated in terms of gene flow. This is especially true in the short-term (100 years or so) when population dynamics issues will be more important to the continuance of spotted owls.
MC - Nb there have been only a couple of generations of owls since dramatic reductions of numbers and range; negative consequences might take a lot longer to show up than a couple of decades.
RB - It is unclear what effect increased fragmentation may have on effective population size and levels of inbreeding. It is likely that any additional isolation effect would have negative impacts on genetic variability. It is also likely that isolation effects will increase in the future.
AF - The hypothesis is plausible and needs to be examined further. However, the effect may be

unlikely because of the capability of juveniles to disperse long distances.
RF - There is evidence of reduced variation in CSO in Southern California, and probably on the Olympic Peninsula. As BO and habitat effects continue to fragment and marginalize the SO populations there will be some impact on genetic variation, inbreeding and loss of adaptability, but how much and how significant a threat this will be is unpredictable.

PART III. QUESTIONS RELATING TO PREY

13. The diet of NSO has been studied in several areas. In general, the diet of NSO can be characterized as (check as many as apply):

Well understood, with good information on geographic variation in dietXXXX
Well understood in some areas but not others XX
Understood in broad terms, but lacking information on seasonal and individual variation XXXXXX
Understood in broad terms, but lacking information on key issues XXX
Poorly understood

Additional comment:
MC - I am amazed that so few studies have addressed the breadth, numbers, density, and variation over time in the prey base. This is something that should have been incorporated into the heavily-funded demography studies many years ago.
RB - We have very little information on the influence of the ecology of most prey. Long-term studies of prey in relation to annual variations in weather and vegetation would make a valuable future contribution to our understanding of owl habitat associations.
RF - Owl pellets are a great benefit!

14. The effects of variation in prey abundance, habitat use, and availability on NSO populations are:

Well understood
Understood in broad terms, but not in detail XXX
Not well understood X XXXX

Additional comment:
SPC - Geographic variation in prey identity is correlated well with some aspects of owl biology. However there is no study adequately looking at prey abundance and availability across habitats and seasons
MC - For example, is the alternate-year breeding pattern largely, somewhat, or not at all attributable to local prey reduction and thus requires an interim year for prey recovery?
RB - More information on prey abundance and availability would help interpret patterns in NSO reproductive success and evaluate possible management in and around suitable habitat.
RG - Prey studies have not been funded to coincide with demographic studies even though this has long been thought to be critical to understanding spotted owl population dynamics.

AF - Mechanisms, such as the relationships between habitat-specific fluctuations in prey density and spotted owl population dynamics, are lacking.
RF - This appears to be a gap in the demography analyses, that these factors were not uniformly studied with respect to changes in lambda, or really to habitat structure, climate, etc

15. Population dynamics of major prey species are:

Well understood
Understood in broad termsX
Not well understood: XXXXXX

Additional comment:
RB - The factors that contribute to the long-term dynamics of prey is an area of considerable uncertainty.
RG - There are no long-term woodrat studies within the range of the spotted owl but I am not sure about other species. This is necessary to understand their natural variation and dynamics in the lower half of their range. However, this does not appear to be evident for long-term prey studies on spotted owl study areas
AF - Most information is based on short-term (<5 years) studies that have not captured long-term temporal variation and the relationship between this variation and external factors.

16. Carey and others have suggested that NSOs may depress populations of some prey species (e.g. flying squirrels). Such effects could have consequences for prey persistence, coexistence of competing predators, and NSO populations themselves. The available evidence on this hypothesis can be characterized as:

Extensive, supporting a significant effect
Extensive, not supporting a significant effect
Consistent with the hypothesis, but inconclusive XXXX
Insufficient to evaluate XXXX

Additional comment:
MC - See above; as far as I am aware, there is not substantial amount of data to evaluate this potential effect, although of course there should be by now.
RB - As previously stated, long-term studies of prey ecology would be very valuable in interpreting reproductive success and foraging behavior. More information on access to prey and the role of forest succession in the absence of fire on the East Side of the Cascade Range would be valuable
RG - Carey documented this prey depletion but his study did not continue long enough to provide causative information on its overall effect on spotted owl prey. It clearly demonstrated that there needs to a variety of habitats and forest patches to the owl because of potential prey depletion.

AF - This work was based primarily on an observational study and the link between prey and foraging owls was missing (i.e., cause and effect was lacking). This area needs more work.

PART IV. QUESTIONS RELATED TO NSO HABITAT

Initial studies of habitat showed an association of NSO with late successional habitat, at several scales. In the report, the panel considered recent information on habitat associations in different areas, and on trends in habitat. How would you evaluate the following statements:

17. Initial findings on habitat associations are generally confirmed by results published since 1990.

_XXXXXStrongly supported
_XX_ Supported
_X_Weakly Supported
__Not supported
__N/A

18. In general, demographic performance of NSO is related to availability of late successional forest habitat.

X_Strongly supported
XXXXX Supported
_X_Weakly Supported
__Not supported
_X_N/A

19. Late successional habitat is a limiting factor for NSO populations in significant parts of the subspecies' range

_XXX_XStrongly supported
_XX_ Supported
_X_XWeakly Supported
__Not supported
__N/A

20. Home ranges composed entirely of pristine old forest are optimal for spotted owls throughout the species' range.

__Strongly supported
__ Supported
__XWeakly Supported
XXXXXXX__Not supported
__N/A

Additional Comment:
RG - This question seems to be inappropriately worded. This statement is not supported for areas like the Klamath province but it is unknown for many other areas, and in fact my be strongly supported if such data were available for the Olympic Penn, Western Washington Cascades, Western Washington lowlands and other provinces where the primary prey is the flying squirrel.
AF - This is an ambiguous question and open to misinterpretation. My interpretation was that this may be operating in some portions of the owls range but not in other portions.

21. Forest fragmentation is equivalent to habitat fragmentation

__Strongly supported
_X_ Supported
__Weakly Supported
_XXXXXXX_Not supported
__N/A

Additional Comment:
RG - Same problem as the above question, it is likely to be a different answer in different parts of the range.
AF - See comment in question 20.

22. In the redwood zone, NSO use significantly younger forests, whose structure resembles old-growth forests elsewhere

__XXStrongly supported
__XXXX Supported
__Weakly Supported
__Not supported
_XX_N/A

23. In the eastern Cascades, NSO are associated with younger forests, whose structure may allow access to prey

__Strongly supported
_XX_ Supported
_X_XWeakly Supported
_XXX_Not supported
_X_N/A

Additional Comment:

AF - There is no support for the last portion of the statement.

24. In some areas, hardwoods are a significant component of habitat

X_XXXStrongly supported
__XXX Supported
_X_Weakly Supported
__Not supported
__N/A

25. In the Klamath region, heterogeneous landscapes may favor higher demographic performance

_XX_XStrongly supported
XXXX Supported
_X_Weakly Supported
__Not supported
__N/A

Additional Comment:
AF - The support is based on observational studies.

26. Elsewhere in California and southern Oregon, heterogeneous landscapes may favor higher demographic performance

_X_XStrongly supported
__X Supported
_XXWeakly Supported
_XXX_Not supported
__N/A

Additional Comment:
AF - I put "Not Supported" primarily because the work is not completely finished in this area and some studies suggest a weak effect, if any.

27. In other locations (e.g. Cascades) heterogeneous landscapes may favor higher demographic performance

__Strongly supported
__X Supported
__XXXWeakly Supported
_XXX_XNot supported

__N/A

Additional Comment:
AF - There is insufficient evidence to support this statement

28. Geographic differences in habitat use are generally explicable in terms of differences in prey availability and use

_X_Strongly supported
XXX Supported
_XXXX_Weakly Supported
__Not supported
__N/A

Additional Comment:
RG - Temperature can have a substantial effect on habitat selection.

29. Overall, the quality of data on current distribution and availability of NSO habitat as available to the review committee was:

Excellent
Generally good XXX
Mixed in quality XX
Generally limited XXX

30. NSO breeding habitat is affected negatively by timber harvest, fire, windthrow and disease, and positively by succession. Ingrowth may have both positive and negative consequences. In different regions and on different ownerships current trends can be described as:

	Positive	Possibly Positive	Neutral	Possibly Negative	Negative	Uncertain
British Columbia				**X**	**X XXX**	**X**

Western Cascades, Coast Ranges, Olympic Peninsula		**X**	**X**	**X**	**XX**	**X**
Eastern Cascades				**XXX**	**XX**	**X**
Klamath			**XXX**	**XX**		**X**
Coastal CA (Redwoods)			**XXX**	**XX**		**X**
Federal lands	**XX**			**XXX**		**X**
State lands				**XXX**	**X**	**XX**
Tribal lands				**XX**	**XXX**	**X**
Private lands			**X**	**XXX**	**X**	**X**

Additional comment:
RB - A "Possibly negative" designation provides considerable latitude to cover our uncertainty over the habitat trends data. We have little or no insight into habitat trends on other than Federal lands. On State, private and tribal lands we lack a baseline from which change can be calculated. On the California coast, there have been very small documented losses on Federal lands and we have more confidence that developing habitat is suitable for NSO breeding.
RG - I really have a difficult time explicitly answering this question because of the specificity of the questions and the special extent of the answers. That is there is much uncertainty about the effects of these factors and how they influence owls except at the very grossest level. Perhaps these tables could be used as a basis for the federal agencies providing specific numbers?
AF - I could not fill in the table. I do not have sufficient grasp of the details for all of the regions and different land bases to provide an informed opinion. This is too speculative a question for me. I would rather see empirical data used to provide this type of information.

31. In your opinion, major factors currently contributing to habitat loss/removal in different regions and on different ownerships are (check all that apply):

	Timber harvest	Fire	Insects	Disease	Windthrow
British Columbia	XXXXX	X			
Western Cascades, Coast Ranges, Olympic Peninsula	XXXXX	XXX			
Eastern Cascades	XX	XXXXX	XXXX	XX	
Klamath	X	XXXXX		X	
Coastal CA (Redwoods)	XXX			X	
Federal lands	X	XXXXX	XX	XX	X
State lands	XXX	XXX	X	X	X
Tribal lands	XXXXX	XX	X	X	
Private lands	XXXX				

Additional Comment:
RG - The data are not sufficient to answer this question, given what I have seen provided to the review panel.
AF - I could not fill in the table. I do not have sufficient grasp of the details for all of the regions and different land bases to provide an informed opinion. This is too speculative a question for me. I would rather see empirical data used to provide this type of information.

32 to 36. The federal agencies presented the panel with a model of forest development. Please evaluate the model:

RB - Estimates of habitat development were calculated by a modeled projection of stands at the regional scale. Stands that reach the age of 80 years are assumed to be habitat. The method used by the Federal Agencies to model forest development might be described as a rather straightforward, mechanistic approach. Net increases in late-successional forest (80 years or greater) were estimated by decade. A lack of more detailed stand condition information precluded alternative methods of habitat development assessment.

In reality, projecting the transition of a forests age and size classes to different levels of habitat function requires extensive field verification. It is recognized that the accuracy of both estimates are approximations to be used on range- wide scales. Habitat development certainly is not a mechanistic process and there is considerable variation in the rate of natural habitat development. The habitat complexity that most definitions project as suitable habitat develops over multiple decades and is not a threshold that is achieved with an average size class. Stand age or size does not account for the history, growing conditions, species composition, and other factors that determine the rate of habitat structure development. There is considerable uncertainty in the transition between mid-seral stage stands and suitable habitat. These uncertainties still exist with remote sensing information or inventory methods that are not specifically designed to sample the key components of suitable habitat.

Given the uncertainty about the rate of complex forest structure development in the 80+ year-old stands, habitat development was likely overestimated. The extent of overestimation can not be determined. However, since many of the stands that are projected to become habitat originated after natural disturbances, it is highly plausible that the majority of the projected new habitat would function as suitable habitat when predicted, and the remainder would follow within a couple additional projection periods

RG - This model needs to be evaluated by experts in the field, but at the level of model structure, assumptions, and function. Models are useful primarily as tools to ask questions and derive hypotheses because they are highly vulnerable to parameter input which may or may not realistic.

AF - I cannot answer these questions because I am not familiar enough with the structure and assumptions of the model. The presentation was not able to provide me with these details.

32. How well does this model of ingrowth and succession approximate to development of habitat?

Xwell
Poorly
XXXUncertain

33. This model is plausible and appropriately constructed

Strongly agree
X X XX Agree with qualification
Disagree
N/A

34. The data used in model development are sufficiently accurate for the task

Strongly agree
X X Agree with qualification
XX Disagree
N/A

35. The model is well supported by data on actual trends

XStrongly agree
X Agree with qualification
X Disagree
X N/A

36. If the model of forest development accurately represents habitat development, this would indicate a current net positive trend in habitat on federal lands. Does this agree with your best professional judgment on actual habitat trends.

XXStrongly agree
X Agree with qualification
X Disagree
N/A

Additional Comment:
MC - there has been no critical evaluation of the quality of the ingrowth as NSO habitat

PART V. QUESTIONS RELATING TO BARRED OWLS

37. In your opinion, are Barred Owls currently having negative effects (on occupancy, survival and reproduction) on NSO populations in :

	Strong effect	**Slight effect**	**No effect**	**Insufficient data**
British Columbia	XXXXXX			
Washington (all areas)	XXXXXX			
Oregon (Cascades and Coast ranges)	XXXX	XX		
Klamath Province		XXX	XXX	

California Redwood Zone		XXXX	XX	
California Cascades/Sierra			XXXXXX	
On the subspecies considered as a whole	XXXX	X		X

Additional comment:
MC - The most parsimonious and reasonable explanation for NSO declines in more northerly and more mesic habitat is its failure to withstand competition from BO
RB - We have yet to realize the full extent of the impacts from the Barred Owl invasion of the West Coast. Monitoring and investigations into the interactions of the Barred Owl and The NSO have only been conducted for several years. There is substantial circumstantial information on the negative effects of Barred owl presence on NSO occupancy in Washington State. The fact that the available evidence on the impact of Barred owls on NSO varies from area to area makes one hesitant to generalize about the interspecific interactions between these species and the ultimate impact on the NSO.
RG - (did not fill in box) Barred owls could easily be having an effect on spotted owls but we have no idea of its real magnitude across the range (at the level of this question).
AF - (did not fill in box) I was unable to fill in this table because I think Barred Owls may well be having an effect on spotted owls but we have no real estimate of the magnitude of this effect.

38. In your opinion, Barred Owls will in the long-term future (50 years+) have negative effects on NSO populations in :

	Strong effect	**Slight effect**	**No effect**	**Insufficient data**
British Columbia	XXXXXX			
Washington (all areas)	XXXXXX			
Oregon (Cascades and Coast ranges)	XXXXX	X		
Klamath Province	XXXX	X		X
California Redwood Zone	XXXX	X		X
California Cascades/Sierra	X	XX		XXX
On the subspecies considered as a	XXXXX	X		

whole				

Additional comment:
RB - Long-term trends are difficult to predict. I suspect that some kind of equilibrium will be reached. It will be interesting to see if the impact continues to show a strong attenuation to the south.
RG - (did not fill in box) See answer above in 37.
AF - (did not fill in box) I was unable to fill this table out because I predict the future poorly.

39. In my opinion, the probable population trends of Barred Owls in the near future (next 5 to 10 years) in the following areas are likely to be:

	Strongly increasing	**Slightly increasing**	**No effect**	**Decreasing**	**Unsure**
British Columbia	X	XXXX	X		
Washington Cascades	XXX	XXX			
Olympic Peninsula	XXX	XXX			
Oregon Cascades	XXXX	XX			
Oregon Coast Range	XXXXX				X
Klamath Province	XXX	X			XX
California Redwood Zone	XXX	X			XX
California Cascades/Sierra	X	XX	X		XX

Additional comment:
MC - It looks as if BO has peaked in density and distribution in BC, so expect no further increases. Expansion of BO into Sierra of CA seems inevitable, but the consequences for CSO are not predictable. NB even where BO is already common, we have not seen the yet seen its full effects on NSO reductions, that will surely take more time. Thus even with no further BO increases, there will likely to continued NSO reduction and displacement from traditional sites.
RB - It will be important in the short-term to gain a better insight into the theory that the Barred Owl invasion is a factor in depressing Spotted Owl survival and reproduction. Monitoring of the Barred Owl expansion in the Oregon Cascades would provide valuable information
RG - (did not fill in box) Barred owls will probably increase across the range but the rate and amount of increase I cannot speculate on without some basis or information
AF - (did not fill in box) I was unable to fill this table out because I think Barred Owls may well be having an effect on spotted owls but we have no real estimate of the magnitude of this effect. Thus, we have poor ability to predict the future trajectory of the effect.

RF - I think this will be a major problem for NSO and possibly CSO over the next decade and beyond.

40. Currently there is some evidence that Barred Owls in British Columbia, Washington and some parts of Oregon occupy more mesic and lower elevation habitats than do NSO. In your opinion, this pattern is likely:

To be maintained
To gradually change as Barred Owls slowly invade new areas XXXX
To rapidly change as Barred Owls rapidly invade new areas X
Too difficult to say XXX

Additional comment:
RG - Obviously the initial suggestions and patterns of relationship of Barred owls to mesic environments did not last, but I have no idea what the future pattern will be.
RF - But the data are a bit too limited to be certain at present.
MC - It has already changed on OLY Penin; clearly BO needs time to fill its preferred habitat before then progressing to less preferred habitat from which NSO will be similarly displaced
RB - Barred Owls have demonstrated that they are an adaptive species; there is no reason to think they will not expand their range to less than prime habitat as the population increases. Without monitoring we will never be able to answer this question.
AF - I don't think the there is sufficient data to support the statement.

41. Currently Barred Owls in the central Washington Cascades and some areas of Coastal California are more common in old-growth habitat and reserves than in some second growth and fragmented habitat. In your opinion, this pattern is likely:

To be maintained
To gradually change as Barred Owls slowly invade new areas XXXX
To rapidly change as Barred Owls rapidly invade new areas
Too difficult to say XX

Additional comment:
MC - BO is likely to remain most common in the OG and mature forests, but if earlier successional and less mature forest provide its resources, they too will be occupied in time. It appears that BO can do well in a mix of OG and earlier forest, more so than NSO.
RG - (did not check above) I disagree with the question. The question makes the assumption that this is a true statement. The problem is that it is not known. There have been no studies to determine if this is correct assumption or pattern.
AF - I would argue that there is no data to support the statement.
JF - Not persuaded that this is true in c WA Cascades
RF - But the data are a bit too limited to be certain at present.

42. In your opinion, the effects of forest harvest and fragmentation on Barred Owl invasion are best characterized as:

Forest harvest and fragmentation directly favors Barred Owls by creating favorable (early successional) habitat XXX
Forest harvest and fragmentation has no direct positive effect on Barred Owls X
Not possible to say at this point X XX
Other (explain)

Additional comment:
MC - however, if their effects have been to drastically reduce NSO populations and thus place it at risk to BO competition, the net effect on BO is positive
RB - Barred Owls are known to use a wide assortment of forest types as habitat. I think it is plausible that Barred Owls will thrive in a fragmented forest habitat, riparian reserves for example. Further investigation into Barred Owl habitat breadth will be useful in predicting Barred Owl expansion and perhaps the eventual equilibrium between the Barred and NSO.
RF - But the data are a bit too limited to be certain at present.
SC - There is strong evidence that BO invade old-growth and unfragmented habitat; however BO also use other habitats, so the population may be favoured indirectly

43. In my opinion, hybridization of NSO with Barred Owls is:

Common
Infrequent XX
Relatively rare X XXXXX
Other (explain)

Additional comment
MC - And not likely to be a critical factor in BO/NSO interactions
RB - The frequency of hybridization that was suggested early in the invasion has not increased despite a considerable expansion of the Barred Owl population. In my opinion, hybridization with Barred Owls is not as serious a threat to NSO as the interspecific interactions.
RF - But more genetic data need to be obtained using Sue Haig's new AFLP or microsatellite methods – introgression via backcrossing, and also via extra-pair mating, could be a relatively cryptic problem.

44. The overall quality of the data on Barred Owl populations and their effects on NSO can be characterized as

High quality, majority of conclusions strongly supported
Generally high, most conclusions strongly supported
Mixed quality, some conclusions based on limited evidence XXXXX

Very mixed, some conclusions based on sparse evidence X
Generally low, many conclusions based on weak evidence X X

Additional comment
MC - Some conclusions based on sparse or weak evidence, but even where circumstantial and correlational, evidence overwhelmingly supports the view that BO has a strong negative effect on NSO.
RB - Even though the negative effect of Barred Owls is clearly correlational, we are still operating with considerable circumstantial information.
JMM - The details are not well known, but the effects of, and increase in, Barred Owls are so great that poor data is sufficient to document the effects. A subtle effect would not be possible to detect with the data, but this effect is not subtle.

PART VI QUESTIONS RELATED TO DEMOGRAPHY AND POPULATIONS.

45. West Nile Virus is known to affect owls in other parts of North America. The evidence that this disease will affect NSO is:

Compelling and based on firm extrapolation to NSO
Logically consistent but essentially circumstantial XXXXXX
Speculative at this point XX

46. Please indicate your opinion on the probable status of NSO in the following areas

	Definitely declining	**Probably declining**	**May be stable**	**Probably stable**	**Uncertain**
British Columbia	**XXXXXX**				

Western Cascades	**XXXXX**	**X**			
Olympic Peninsula	**XXXXXX**				
Eastern Cascades	**XXX**	**XXX**			
Oregon Coast Range	**XX**	**XXX**	**X**		
Klamath		**XX**	**XXXX**		
Coastal CA (Redwoods)	**X**	**XX**	**XXX**		
CA Cascades and Sierra		**XX**	**X**	**X**	**XX**

Additional Comment:
RG - (did not fill in box) I feel it is most appropriate to defer this to the results of the meta analysis which represents the single largest data set on mark recapture of an endangered species in the world. In addition, the last category is mixing two very different regions, which may be very different. Populations in the Sierra are not equal in their trends.
AF - (did not fill in box) I did not fill out this table because the empirical evidence from the recent meta-analysis provides this information better than my opinion. The results from the meta-analysis should be considered above any opinions from panel members.

PART VII QUESTIONS RELATED TO RISK AND UNCERTAINTY

We may distinguish between uncertainty regarding whether a potential threat is present, and the degree of threat or risk it may pose if present. For instance, we may not know whether a potential factor is operating, but have reason to believe that if present it will pose only a low risk (high uncertainty and low risk). In the sections that follow, please attempt to distinguish between the relative uncertainty regarding a topic or factor, and the probable risk to NSO if the factor is present.

47. <u>Uncertainty</u>:
How would you rate our understanding and degree of uncertainty on the following topics?

	Very uncertain	Uncertain	Adequately understood	Well understood	No opinion

Taxonomy of Spotted Owls			***XXX***	***XXXXX***	
Genetics of NSO populations		***XX***	***XXX***	***XXX***	
Relationship to prey abundance and distribution		***XXXXXX***	***XX***		
Effects of Barred Owl competition where present		***XXXX***	***XXXX***		
Likely spread of Barred Owl in CA		***XXXXXX***	***XX***		
Effects and extent of past Habitat loss to harvest	***X***	***XXXX***	***XX***	***X***	
Effects and extent of current Habitat loss to harvest		***XX***	***XXXX***	***X***	***X***
Effects and extent of Habitat loss to fire		***XXXXX***	***X***	***X***	***X***
Effects and extent of Habitat loss to windthrow		***XXX***	***XX***	***XX***	***X***
Effects and extent of Habitat loss to insect damage		***XXXXX***	***XX***		***X***
Effects of fragmentation		***XXXX***	***XXXX***		
Likely effects of West Nile Virus	***XXXXXX***	***XX***			
Likely effects of other diseases	***XXXXXX***	***XX***			
Likely effects of predation (goshawk etc)	***XX***	***X***	***XXXX***	***X***	
Effects of weather on populations	***X***	***X***	***XXXXXX***		
Demographic isolation of populations	***X***	***XXXX***	***XXX***		
Synergistic interactions between factors	***XXX***	***XXXXX***			
Overall population trends			***XXXX***	***XXXX***	
Population Status and trends in British Columbia			***XXX***	***XXXX***	***X***
Population Status and trends in Washington			***XXXXX***	***XXX***	
Population Status and trends in Oregon			***XXXXX***	***XXX***	
Population Status and trends in California		***XX***	***XXX***	***XXX***	

Additional Comment:
RG - Causal mechanisms for effects of weather uncertain.

48. _Risk_: Now evaluate many of these same topics as risks to NSO populations. Here risk is regarded as significantly contributing to the probability of extinction at local or global scales.

	High Risk	Moderate risk	Little risk	No risk	Insufficient evidence
Genetic consequences of small population size		XX	XXXXX		X
Introgression from CSO		X	XXXXX		XX
Effects of Barred Owl competition where present	XXXXXX XX				
Likely spread of Barred Owl in CA	XXXX	XX	X		X
Hybridization with Barred Owls			XXXXX X	XX	
Effects and extent of past Habitat loss to harvest	XXX	XXXX			X
Effects and extent of current Habitat loss to harvest	XX	XXX	XXX		
Effects and extent of Habitat loss to fire	XX	XXXXX	X		
Effects and extent of Habitat loss to windthrow			XXXX	XXX	X
Effects and extent of Habitat loss to insect damage		XXX	XXX	X	X
Effects and extent of Habitat loss to Sudden Oak Death		XXX	XX		XXX
Effects of fragmentation		XXXX	XXX		
Likely effects of West Nile Virus	X	XXXXX			X
Likely effects of other diseases	X	XX	XX	X	XXX
Likely effects of predation (goshawk etc)			XXX	XXX	
Effects of weather on populations		XXXX	XXXX		
Demographic isolation of populations		XX	XXXX		XX
Synergistic interactions between factors	XX	XXXX			XX

Additional Comment:
AF - Barred owl competition : high risk at a local scale, if barred owls are actually competing with spotted owls. Past habitat loss – high risk at a local scale if past habitat loss lowered habitat quality sufficiently and habitat qualityinteracts with extreme weather events. Current habitat loss to harvest – low risk if it remains at current low levels on public lands Sudden Oak Death - Has

the potential to be High Risk. Other diseases – high risk - if other avian diseases are introduced into the range of the owl.
RG - I not exactly sure I understand exactly how to answer this question given the uncertainty of key information on some of these questions. So I am making the assumption that some things are true which may not be given lack of information (e.g., barred owl effects on spotted owls). Thus, I am somewhat confused as to the manner in which to evaluate and answer the question.

49. Based on your answer to the previous question, which factors are currently significant threats to NSO populations, or may pose such threats in the near-term future (5-10 years)

	Current Threat	***Probable future threat***
Genetic consequences of small population size		***XXXX***
Introgression from CSO	***X***	***X***
Effects of Barred Owl competition where present	***XXXXXX XX***	***XXXXX***
Hybridization with Barred Owls		
Effects and extent of past Habitat loss to harvest	***XXXXXX***	***X***
Effects and extent of current Habitat loss to harvest	***XXXX***	***XXXXX***
Effects and extent of Habitat loss to fire	***XXXX***	***XXXX***
Effects and extent of Habitat loss to windthrow		
Effects and extent of Habitat loss to insect damage	***XX***	***X***
Effects and extent of Habitat loss to Sudden Oak Death	***X***	***XXXXXX***
Effects of fragmentation	***XX***	***XX***
Likely effects of West Nile Virus	***XX***	***XXXXXX XX***
Likely effects of other diseases		***XX***
Likely effects of predation (goshawk etc)		
Effects of weather on populations	***X***	***XX***
Demographic isolation of populations		***XXXXXX***

Synergistic interactions between factors	***XXXXX***	***XXXXX***

Other (specify)

50. Many of these factors were considered at the time of listing. Please indicate whether, in your opinion, there has been a change in threat posed now, as compared to 1990 (and the direction of such change). Indicate whether such changes are due to a change in the factor itself (e.g. a new or a reduced threat) or due to a change in our understanding (new data)

	Change in level of threat (increase or decrease)	*Change in factor itself?*	*New information?*
Genetic consequences of small population size	***I, I, I, I***	***XXX***	
Introgression from CSO	***I***		***XX***
Effects of Barred Owl competition where present	***I,I,I,I,I,I,I,I***	***XXXXXXX***	***XXXX***
Hybridization with Barred Owls	***D,?***	***X***	***X***
Effects and extent of past Habitat loss to harvest	***D,D,I***	***XXX***	***X***
Effects and extent of current Habitat loss to harvest	***D,D,D,D,D,?***	***XXXXX***	***XXX***
Effects and extent of Habitat loss to fire	***I,I,I,I,I,I***	***XXXXX***	***X***
Effects and extent of Habitat loss to windthrow	***D,?***		***X***
Effects and extent of Habitat loss to insect damage	***I,I,?***	***XX***	***X***
Effects and extent of Habitat loss to Sudden Oak Death	***I,I,I,I,I,I***	***XXXX***	***XXX***
Effects of fragmentation	***D,I,D,D,D,D,I***	***XXXX***	***XXXX***
Likely effects of West Nile Virus	***I,I,I,I,I,I,I,I***	***XXXXXXX***	***XX***
Likely effects of other diseases	***I,?***	***X***	
Likely effects of predation (goshawk etc)	***D,D***		***XX***
Effects of weather on populations	***I,I,I,I***		***XXXX***
Demographic isolation of populations	***I,I,I***	***XX***	***X***
Synergistic interactions between factors	***I,I,I,I,I,I***	***XXXX***	***XXX***

Additional comment:
AF - Question is confusing.

PART VIII QUESTIONS RELATED TO CONSERVATION PLANS AND MANAGEMENT

51. The federal conservation plan for NSO and other species (Northwest Forest Plan) depends upon the maintenance of populations, primarily in Late Successional Reserves, in a metapopulation structure, where each population has a high probability of survival. There have been changes in the implementation of the NWFP (lower harvest rates) and also in the impact of different threats. Based on the evidence available to the panel, and your evaluation of current threats, is this strategy based on premises that are currently well-founded, and supported by current information?

Well supported for all important issues
Well supported for most important issues XX
Well supported for only some issues XXXXX
Not well supported
Insufficient information X

Explain your answer:
MC - Does not account for BO impact. NSO may be displaced from LSR by dint of their being preferred by BO, leaving "matrix" available for NSO over a longer period (ie until BO expansion reaches into the matrix
RB - I still believe the NWFP strategy is will supported, however our inability to explain the continued decline in NSO numbers is an area of great concern. The appearance and spread of the BO and the continued threat of catastrophic habitat loss from fire are the greatest threat to the NWFP strategy.
AF - The Plan still remains a hypothesis that needs to be tested. Analyses comparing demographic performance of spotted owls on LSR and Matrix lands are currently being conducted and the results were not yet available to the panel. This information would shed considerable light on this issue
JM - Disease and barred owls are not exluded by reserves, especially connected ones. Reserves are necessary for northern spotted owls, but not sufficient.
RF - Barred owl appears to be excluding NSO from LSRs in many areas, plus probable change in the assessment of optimal habitat based on new research (i.e., old growth, plus edge).
RG - meta-analysis did not evaluate this topic which is the appropriate forum for this analysis

PART IX QUESTIONS RELATED TO MONITORING AND RESEARCH

52. In five years the USFWS may conduct another status review. In the interim it is to be expected that there will be ongoing monitoring and research on NSO and its habitat.

Please indicate whether you expect the following data will be critical to a future review of NSO status. Please distinguish between issues where we already have a solid understanding, and those areas where new information may be expected to change our understanding or ability to evaluate status of NSO.

	Already well understood	New information may be valuable	Ongoing monitoring essential to understanding status	New information likely to alter understanding of status
Population trends of NSO		*XX*	*XXXXXX*	*XX*
Prey selection of NSO	*XX*	*XXXXXX*		*X*
Prey dynamics		*XXXXXX*	*XX*	*XX*
Relation between demographic parameters and habitat		*XXX*	*XXXX*	*XXX*
Taxonomy of Spotted Owls	*XXXXXX*	*X*	*X*	
Genetic differentiation of NSO populations	*XXX*	*XXXXX*		
Population trends of Barred Owls		*X*	*XXXXX*	*XXXXX*
Effects of competition from Barred Owls		*X*	*XXXXX*	*XXXXX*
Regional differences in habitat selection of NSO	*X*	*XXXXXX*	*X*	*X*
Regional and ownership patterns in habitat trends	*XX*	*XX*	*XXXXX*	*XX*
Amounts of ingrowth of habitat	*X*	*XXX*	*XXX*	*XXX*
Effects of fire	*XX*	*XXX*	*XXXXX*	*XX*
Prevalence of WNV		*XXXX*	*XXXXX*	*XXXX*
Others				

Additional comment:
RG - As above, these are difficult to partition. I think there are some very key things that need to be done to advance our understanding. I also think that some very good things have happened for owl conservation that do not seem to be captured in this report (like the PNWFP) and change in regulation that have had a very positive effect on the owls, while new things have emerged as potential threats. Pigeon holing them does not seem to capture these ideas to me.

SCIENTIFIC EVALUATION OF THE STATUS OF THE NORTHERN SPOTTED OWL

CHAPTER ELEVEN

Threats

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1 INTRODUCTION

In this chapter we summarize our findings in terms of operational and potential threats to the Northern Spotted Owl. We define an operational threat as one that we perceive is currently negatively influencing the status of the owl, whereas a potential threat is either a factor that could become an operational threat in the near (15-20 years) future or is a factor that may be threatening the owl currently but for which we are uncertain about the extent of the threat. Operational threats can be considered analogous to "imminent threats" in the Endangered Species Act. While the logic underpinning our summary here is shown in detail in previous chapters, we also briefly summarize the reasoning for our conclusions in this section. We also compare the information that was available for our review to that available at the time of the 1990 listing decision. In this context, we frame our discussion relative to abatement or increase in various threats as well as new threats that have emerged since the 1990 listing decision. Finally, we briefly discuss the quality of currently available information, and of the relative certainties and uncertainties of our findings. Collectively, we bring our findings together in our overall summary of population trends and threats. Finally, we emphasize to the reader that we defined the time period of our consideration for the impact of threats based on the approximate longevity for Northern Spotted Owls of 15-20 years, with the understanding that there is a great deal of geographic variation that influences the ecology and status of the owl. We chose a time of reference based on the bird's biology because evaluation of risks and status of species based on life history parameters is used throughout the world, particularly by the IUCN (IUCN 2001).

1.1 THE 1990 FINDING AND LISTING DECISION

The Northern Spotted Owl was listed as threatened on June 26 1990 (USDI 1990):

> "The U.S. Fish and Wildlife Service (Service) determines the northern spotted owl *(Strix occidentalis caurina)* to be a threatened species pursuant to the Endangered Species Act of 1973, as amended (Act). The present range of the subspecies is from southwestern British Columbia through western Washington, western Oregon, and the coast range area of northwestern California south to San Francisco Bay. The northern spotted owl is threatened throughout its range by the loss and adverse modification of suitable habitat as the result of timber harvesting and exacerbated by catastrophic events such as fire, volcanic eruption, and wind storms."
>
> Federal Register 55: 28114

As noted above, the U.S. Fish and Wildlife Service reviewed much information in making its determination, but emphasized both past and continuing loss of habitat. However, throughout the listing decision, many other factors were discussed. Under the terms of the ESA section4(a)(1) the USFWS makes decisions on listing status based on a finding whether there is an imminent or probable future risk of extinction due to any one of five factors:

A. The Present or Threatened Destruction, Modification, or Curtailment of Its Habitat or Range.

B. Over-utilization for Commercial, Recreational, Scientific, or Educational Purposes.
C. Disease or Predation
D. The Inadequacy of Existing Regulatory Mechanisms.
E. Other Natural or Man-Made Factors Affecting Its Continued Existence

The Service determined on each of these factors as follows:

Factor A: The Present or Threatened Destruction, Modification, or Curtailment of Its Habitat or Range.

"The dependence of northern spotted owls on older forest, the low probability that significant amounts of suitable habitat will persist outside of preserved areas, and the inability of the protected areas to support a viable population of northern spotted owls, all indicate that the northern spotted owl is likely to become endangered within the foreseeable future throughout all or a significant portion of its range."

Factor B. Over-utilization for Commercial, Recreational, Scientific, or Educational Purposes.

"Considerable research by Federal, State, and private groups is being conducted on this subspecies. This work is providing valuable information and is not having a negative impact on the subspecies. The spotted owl is not a game bird, nor is there any known commercial or sporting use"

Factor C. Disease or Predation

No clear determination of threat level was made although Great Horned Owl, *Bubo virginianus*, predation as well as the potential impact of parasites were noted.

Factor D. The Inadequacy of Existing Regulatory Mechanisms

"The cumulative impact of timber-cutting practices by land managing agencies increases and exacerbates the fragmentation of existing owl habitat. The proposed spotted owl management plans of the Forest Service and Bureau of Land Management are untested. Recent legal actions aside, there is no indication from the land management agencies that the current rate of change from old growth to young, even-aged forest management will diminish. Further, as agencies concentrate their clear cutting activities outside designated spotted owl habitat management areas, future habitat management options will be lost if currently planned habitat networks prove later to be deficient. Existing regulatory mechanisms are insufficient to protect either the northern spotted owl or its habitat."

E. Other Natural or Man-Made Factors Affecting Its Continued Existence

No formal determination of threat level was made for this factor, although Barred Owl competition, issues related to genetics (e.g. inbreeding), malicious taking, and extrinsic factors (fire, wind) were mentioned.

In summary, the 1990 listing decision found:

"Given the loss of a substantial amount (60 percent) of historical habitat from timber harvesting, and continuing reduction and fragmentation of a large portion of the remaining old-growth and mature habitat, the northern spotted owl population will continue to decline unless steps are taken to offset these losses"

1.2 5 YEAR STATUS REVIEW

Under the terms of the contract with USFWS, SEI committed to evaluate recent information on

1. Habitat Condition and Use

2. Over-utilization for Commercial, Recreational, Scientific, or Educational Purposes

3. Predation and Disease

4. Other Factors

   - Population trend and demographics
   - Barred owl (range expansion)
   - Genetic issues
   - Malicious taking (poaching)

The manner in which we approached this review was to first gather relevant literature written subsequent to the listing decision. This information was identified as peer-reviewed literature and non-peer reviewed ("gray") literature. We then held public forums to solicit relevant information that had not been published as well as to provide an opportunity to scientitsts, managers, and others to provide personal and professional insight regarding the status of the Northern Spotted Owl. These processes are discussed in detail elsewhere in this report. However, we note here that we relied primarily on peer-reviewed literature (i.e., we gave most weight in our deliberations to peer-reviewed data). We used "gray" literature and the public forums as mechanisms to derive insight about operational or potential threats to the owl and to direct our attention to areas that concerned parties felt were important issues to consider. Thus, our process was to 1) synthesize new information, 2) solicit insight into the status of the owl, and 3) evaluate past, present, and potential threats in the context of the new information and suggestions provided to us through "gray" literature and public input. Finally, we critically evaluated all issues in the context of availablity of data to support or refute the issue.

In our scientific evaluation, we have considered all the major factors known to potentially or actually affect the Northern Spotted Owl. Our chapters do not follow the order set out in the contract, but all major issues are addressed:

- Habitat Condition and Use is discussed in chapters on Prey, Habitat Associations, and Habitat Distribution (chapters 4, 5, 6)
- Predation and Disease are discussed in the chapter on Demography (chapter 8)
- Other Factors are discussed in chapters on Genetics, Barred Owls, and Demography (chapters 3, 7, 8).

We did not find any synthesis of new information pertaining to use for commercial, recreational, scientific, and educational purposes, and regard this as a minor issue, which was consistent with the 1990 listing decision. We note that, as per terms of our contract, we did not address one of the factors used by USFWS in listing decisions. Factor D, the adequacy/inadequacy of regulatory mechanisms, is more appropriately assessed by USFWS as the regulatory agency. Nevertheless, our chapter 9 (conservation science) contains information on the degree to which current conservation planning in the U.S. and Canada is based on sound scientific principles.

In the sections that follow, we will use the information developed in the preceding chapters and following the logical procedure outlined above to address the issues identified in the ESA as required for 5-year Status Reviews. Under the terms of our contract with USFWS we were to address:

- Whether existing (operational) threats are increasing, the same, reduced, or eliminated
- Whether there are any new (potential) threats
- Whether new information or analysis challenges or invalidates any of the conclusions in the original listing determination
- Whether new information suggests that populations are increasing, decreasing, or stable

2 ARE EXISTING THREATS INCREASING, THE SAME, REDUCED, OR ELIMINATED?

2.1 HABITAT

Operational Threats

Clearly, one of the primary threats indicated in the listing decision and in the 1990 status review was loss of habitat due to timber harvest. [We note for completeness that “adequacy of regulatory mechanisms” was the other primary threat discussed in the 1990 listing decision, but as stated above we will not discuss this issue further.] As shown in chapters 5 and 6, the listing of the Northern Spotted Owl and the subsequent conservation measures enacted to protect the owl has resulted in greatly reduced rates of habitat loss from timber harvest on federal lands. Thus, the threat posed by current and ongoing timber harvest on these lands has been greatly reduced since 1990 primarily because of the Pacific Northwest Forest Plan. In addition, protection measures invoked under the ESA have reduced harvest of habitat or mitigated the impact of timber harvest on some non-federal lands, although timber harvest on these lands continues.

Although the 1990 listing document did not parse the effects (in terms of predicted future effects on Northern Spotted Owl population trends) of past, current, and future timber harvest, we feel that it would be useful for scientists to attempt such an endeavor. Such an endeavor has not been attempted by scientists studying owls primarily because there is not a consistent or accurate habitat map across all physiographic provinces inhabited by the owl. Although timber harvest has been greatly reduced on federal lands, the effects of past harvest on Northern Spotted Owls may still persist because of time-lag effects (i.e., owls are long-lived and individuals may persist in disturbed habitats even if that habitat is unsuitable for future colonization by other Spotted Owls; or habitat could have been reduced in quality and may only marginally support owls). Although we are certain that current harvest effects are reduced, and that past harvest is also probably having a reduced effect now as compared to 1990, we are still unable to fully evaluate the current levels of threat posed by harvest because of the potential for lag effects, especially if they interact with other factors (e.g., if past harvest has reduced habitat quality it may lose its ability to buffer the owls against poor climatic conditions *sensu* Franklin et al. 2000). In their questionnaire responses (see chapter 10), 6 of 8 panel members identified past habitat loss due to timber harvest as a current threat, but only 4 viewed current harvest as a present threat.

Fragmentation of habitat was identified as a major issue in the 1990 listing decision. While there can be little doubt that in some parts of the range (particularly the north), fragmentation was and likely remains a cause of poor demographic performance, recent research has also shown that habitat heterogeneity in some parts of the southern range appears to have net positive effects. We note here the distinction between habitat fragmentation and habitat heterogeneity, where the former is loss of habitat and the latter is habitat diversity (Franklin et al. 2002). That is, the recent work by Franklin et al. (2000) shows positive effects of habitat heterogeneity on reproduction. This work could be misinterpreted to suggest that logging is positive for owls. Such interpretation is not correct; we simply know that the diversity of habitats within an owl's territory may be beneficial, some of which may or may not result from logging. Further, the results of this study are applicable only to the geographic province where the study occurred (i.e., these results may not be applicable to areas in the central or northern part of the Northern Spotted Owl's range). Thus, we conclude that the threat posed by fragmentation was not (and is not now) fully understood at the time of listing. However, we believe the concern about habitat fragmentation's effect on Northern Spotted Owls was reasonable given our knowledge in 1990 about spotted owl habitat relationships. Thus, the new research discussed above suggests that habitat diversity may be important to owls in some parts of their range (particularly the southern part of its range), but it is unknown what is the best mechanism to promote that diversity or whether such diversity would be uniformly beneficial in all parts of the Northern Spotted Owl's range. Regardless, timber harvest rates have decreased and this has been associated with a likely concomitant decline in fragmentation since 1990. Two panelists viewed habitat fragmentation as a current threat.

Losses of habitat to other factors have continued unabated. We note in chapters 6 and 9 that currently the primary source of habitat loss is catastrophic wildfire, although the total amount of habitat affected by wildfires has been small (a total of 2.3% of the range-wide habitat base over a

10-year period). It is logical to conclude that this will continue to be the case, particularly if the fuels reductions provisions of the NWFP continue to be under-applied. Five panelists regarded fire as a major source of habitat loss in the eastern Cascades and Klamath regions, and on federal lands (as opposed to 2, 1, and 1 panelists, respectively, who thought that timber harvest was a major source of loss for each these areas).

Potential Threats

Some biologists and managers have suggested that ingrowth due to vegetation succession (i.e. the regeneration of young trees under the established canopy of older trees, particularly of different species) may make suitable foraging areas unavailable to Spotted Owls, because of vegetation density. We acknowledge this possibility exists but found no data by which we could evaluate this process as a threat. In addition, other areas of potential concern voiced during our public forums and in other discussions with concerned individuals were loss of trees to insect damage and windthrow. However, based on the available information, only 2 panelists viewed insect damage as a current threat, while none viewed windthrow as a significant factor.

In the future, there exists a potential for habitat loss due to Sudden Oak Death. This is neither a present nor an immediate threat, but it poses a threat of uncertain proportions because of its potential impact on forest tree dynamics and alteration of key habitat components (e.g., hardwood trees) in the southern portion of the range. Six of 8 panel members saw Sudden Oak Death as a future threat, while 1 panelist viewed it as a current threat.

2.2 BARRED OWLS

The listing document and the 1990 status review provided limited assessment of Barred Owls and their potential impacts on Spotted Owls. As shown in chapter 7, Barred Owls have been invading the range of the Northern Spotted Owl since at least the 1960s. Although the panel had strong differences of opinion on the conclusiveness of some of the evidence suggesting Barred Owl displacement of Northern Spotted Owls, and the mechanisms by which this might be occurring, there was no disagreement that Barred Owls represented an operational threat. In the questionnaire, all 8 panel members identified Barred Owls as a current threat, and also expressed concern about future trends in Barred Owl populations.

We note that hybridization between Barred and Northern Spotted Owls was one of the concerns expressed in the listing decision. Hybridization has not materialized as a significant problem, and was not regarded by any panelist as a current major threat. We recognize that hybridization could exacerbate a decline if a population of Spotted Owls is extremely low. However, if this situation occurs it is likely that demographic processes will exert a greater influence on the persistence of such a population than will hybridization.

2.3 PREDATION

There is very little available evidence that predation on Spotted Owls is having an effect on its population dynamics (chapter 8). While predation on Northern Spotted Owls occurs (and may be numerically important as a cause of death), no panel member identified this as a significant operational or potential threat (0 of 8 respondents to the questionnaire). Hence, the concern expressed in the 1990 listing document may have been an over-estimate of the threat posed by predation (even though no clear determination of threat level was made). We base this conclusion on several lines of reasoning. First, there have been many radio telemetry studies of Spotted Owls, but no published study has identified predation as a primary source of mortality. Second, survival rates of Spotted Owls are high in the presence of Great Horned Owls (a known predator of Spotted Owls). Third, the abundance of Great Horned Owls and Spotted Owls may be more related to the presence of suitable habitat for each species rather than to each other. Thus, there does not appear to be compelling evidence that predation by Great Horned Owls is a risk to Northern Spotted Owl viability.

2.4 DISEASE

The panel did not identify disease as a current major operational threat. However, there was considerable concern among the panel members about the imminent arrival of West Nile Virus. While there is no way to predict the impact of West Nile Virus, the panel was unanimous in regarding this as a potential threat in the future. We base this conclusion on the following line of reasoning: the virus has spread rapidly across the United States, and is now within the range of the Northern Spotted Owl in northwestern California and Washington (*Alan Franklin, John Marzluff, pers. comm.*). It is known to be fatal to many species of birds including Spotted Owls. However, we do not know how this virus will ultimately affect populations.

2.5 GENETICS

The listing decision also mentions genetic concerns, although the 1990 Status Review regards these as minor. In general, we concur that the genetic effects often associated with small population size, for example, are unlikely to be as important as the effects attributable to purely demographic factors. While genetics issues are not an operational threat, some (4 of 8) panelists considered genetic problems as a potential threat in the future. We base this conclusion on the following line of reasoning: there is no empirical evidence that Spotted Owls are currently suffering from the effects, for example, of inbreeding depression which might manifest itself in declining reproductive rates. Based on the abundant information on reproductive output of Spotted Owls, no such negative genetic trends in reproductive output are apparent. We also note that in the very small Canadian population, genetic effects could be occurring, but we have no empirical evidence to support this possibility.

2.6 SMALL AND ISOLATED POPULATIONS

The listing decision makes reference to the problems faced by small and isolated populations. While we have no firm evidence of such effects, or of their relative importance, we note that the reduced populations in the northern part of the range must be at increased risk for demographic stochasticity, etc., simply because they are becoming smaller. We base this conclusion on the results of the 2004 meta-analysis which shows that some populations have shown high rates of decline over the past decade or more. Moreover, populations in some provinces (e.g., Western Washington Lowlands) that were exceedingly low at the time of listing continue to remain low.

3 ARE THERE ARE ANY NEW THREATS?

As noted above, emergent biological invasions (Barred Owls, West Nile Virus, Sudden Oak Death) are operational, imminent, or possible future threats.

Recent research suggests that a significant factor in demographic performance may be interaction among factors (chapter 8). While individual factors (such as habitat loss or fragmentation) were previously identified as threats, their relative importance and effect may depend on the interactions (synergisms) between and among factors. Five of 8 panel members regarded the results of such interaction as a significant current threat. Unfortunately, at this time, there is little information available to examine such interactions; this would require far more detailed and statistically robust data on the causes of population trends than are currently available. However, limited analysis of such interactions suggests that good quality habitat may buffer the owls against the negative effects of bad weather (Franklin et al. 2000). If interactions such as this one occur at different scales and with different factors, synergistic effects could be very important.

4 DOES NEW SCIENTIFIC INFORMATION OR ANALYSIS CHALLENGE OR INVALIDATE ANY OF THE CONCLUSIONS IN THE ORIGINAL LISTING DETERMINATION?

Our review provides a comparison of our current knowedge with that existing at the time of listing. To a large extent, many of the broad conclusions made in 1990 are supported or confirmed, for habitat associations, habitat trends, disease, genetics, etc. Some small differences in scientific opinion have emerged; for instance, the effects of fragmentation, which are incompletely understood and may vary geographically in their effect, which led us to a conclusion that this issue may not be as great as originally perceived or that the threat has been reduced as a consequence of lower logging rates. Predation also appears to have been over-emphasized, but this appears by our reading of the listing decision to have been a minor part of the listing rationale.

Perhaps the most difficult task for the panel was to evaluate the relative importance of the three identified major operational threats: timber harvest, catastrophic wildfire, and Barred Owls. We regard all as currently important. In 1990, timber harvest was regarded as one of the two primary threats. The 1990 listing decision may have under-estimated the importance of potential threats other than harvest, but the evidence at that time (e.g. for Barred Owl effects) was weak or absent. This was certainly true when compared to the extensive knowledge and history of habitat loss across the range of the Northern Spotted Owl.

5 DOES NEW SCIENTIFIC INFORMATION SUGGEST THAT THE SPECIES POPULATION IS INCREASING, DECREASING, OR STABLE?

Chapter 8 reports on the most recent information on population status and trends throughout the range of the Nortern Spotted Owl. Although we have summarized all available information for a number of factors, and on population trends, the panel feels strongly that the most appropriate summary of population trends of the Northern Spotted Owl *per se* is the meta-analysis prepared by Anthony et al. (2004). The panel defers to that group in terms of findings on population trends because we feel that this is a state-of-the-art analysis based on one of the most rigorously gathered and largest data sets on a species population status in the world.

The best available information indicates that some population of the Northern Spotted Owl are declining with different trends in demographic performance among the different provinces (Anthony et al. 2004). Anthony et al. (2004) demonstrated variation in demographic performance at both local and regional scales and across different ownerships. Of the 13 demographic study areas for which rates of population change (λ) were estimated by Anthony et al. (2004), 12 had point estimates of $\lambda < 1$ over the study period (approximately 1985 – 2003) (i.e., $\lambda = 1$ indicates a stable population, $\lambda < 1$ indicates a declining population, $\lambda > 1$ indicates an increase population, but see below). However, only 4 of these 13 sites had a rate of decline where the evidence for a decline was especially strong (see Figure 9 of Anthony et al 2004), which suggested that demographic performance was variable across the range. The rate of decline averaged across all 13 study areas was about 4.1% per year.

Hence, the best available evidence suggests a decline in Northern Spotted Owl populations in portions of their range from 1985 through 2003. However, it is not easy, for a variety of reasons, to partition data pre- and post-listing, or pre- and post-adoption of the NWFP, and then to compare demographic performance under each of these circumstances. Thus, we cannot determine, absent extensive further analysis, whether overall negative population trends are currently changing relative to previous negative trends. *A priori*, the predicted effects of adoption of the NWFP should have been to reduce population decline. However, no analyses have formally compared data pre-and post adoption of this plan, so we cannot determine whether population trends are getting worse or better. Earlier concerns about strongly decreasing populations and decreasing reproductive and survival rates appear to have abated (except perhaps in Washington state), perhaps suggesting that some improvement has taken place in parts of the Northern Spotted Owl range. We do note that the meta-anlysis shows no trends (increasing or decreasing) in reproductive success, but that there were negative time trends in survival in 4 populations (including 3 of the 4 study populations in Washington).

We note that the NWFP predicted a continuing decline of Northern Spotted Owls until such time as new habitat developed (over a course of decades) (Appendix J of FSEIS). Hence, declining populations are not necessarily alarming, and could be following the trend predicted in the NWFP. However, the NWFP did not provide specific (quantitative) predictions for population trends. Thus, we cannot determine whether the observed rates of decline are greater or less than those predicted under the NWFP. In addition, regional differences (significantly greater rates of decline in Washington), and declining survival rates (once again in Washington), were not explicitly predicted by the NWFP.

Although there were no Canadian populations represented in the meta-analysis, Canadian populations are listed under the United States ESA and more importantly under Canada's Species at Risk Act. These populations appear to be in serious decline and could face imminent extinction. We note that Factor A in the listing decision criteria includes "*Curtailment of Its*

Habitat or Range." Thus, we conclude that the Northern Spotted Owl's range will be curtailed if the Canadian population becomes extinct; whether this will be followed by loss of some parts of the Washington range is currently unknown.

6 UNCERTAINTIES

In the individual chapters (2 to 9) we discussed the information available on the biology of the Northern Spotted Owl relative to key issues and threats. We have presented this information critically, with careful examination of the evidence, and discussion of alternative hypotheses and data adequacy. In chapter 10 we have elaborated in more detail on this issue, using individual panelists' opinions as a subjective measure of the relative strength of extant data and information, and of the uncertainties associated with our findings. While we found that there were many excellent sources of information on Northern Spotted Owls, and that a great deal of information has been collected since 1990, there were still key uncertainties that prevented an unambiguous evaluation of the trends and threats affecting Northern Spotted Owls. Moreover, this uncertainty is increased because of the geographic variability of owl habitat, environmental, conditions, and responses. Panel responses to questions 48 - 51 in particular illustrated many of the difficulties faced by the panel in evaluating the threats posed to the subspecies. Nevertheless, there were some clear patterns of panel responses. Three major current threats to Northern Spotted Owls, as identified by all the panelists in their responses to questions 48 and 49, were habitat loss due to timber harvest, habitat loss due to wildfire, and Barred Owls.

7 SUMMARY OF TRENDS AND THREATS, AND OVERALL EVALUATION OF POPULATION STATUS

We find that there are significant threats to the Northern Spotted Owl at this time. Table 1 shows a summary of our main findings. Overall the population of this subspecies appears to be declining, but this varies by physiographic province.

As discussed in chapter 8 (demography), one approach to evaluating threats is to make explicit estimates of risks using modeling approaches. PVAs and other sorts of models may have value both in assessing overall extinction probabilities, and in evaluating the relative importance of different threats. No such model is available for Northern Spotted Owls. In Chapter 8 we discuss the relative strengths and weaknesses of such an approach, and (following the discussion in the Appendix by B.Noon) the value that may or may not be derived from developing such a model (as an aid to synthesis and planning). However, for our present purposes, there is no currently accepted overall framework for quantifying extinction risks for Northern Spotted Owls, or the relative importance of different threats. Hence we have focused instead on the more tractable issue of how perceived threats have changed from 1990 to the present.

Loss of habitat due to timber harvest appears to have been generally reduced, and current timber harvest is now primarily occurring on non-federal lands. We base this conclusion on the protection of millions of acres of suitable habitat by the NWFP following the 1990 listing decision. In addition, rates of logging allowed under the NWFP have not been realized, which has further reduced the loss of habitat due to logging. As timber harvest rates decline, other potential threats are becoming relatively more important (e.g., loss of habitat to catastrophic wildfire). We base this conclusion not only on the known areas lost to catastrophic wildfire, but the continued accumulation of surface fuels and ladder fuels. In addition, very little management has been conducted to reduce risk of wildfire by removing these surface and ladder fuels forests. However, we also are concerned that widespread thinning to reduce the risk of catastrophic wildfire without understanding its effects on Northern Spotted Owl habitat may itself pose a threat. We concur with the 1990 listing decision that some factors (genetics, disease, scientific disturbance) are probably unimportant at this time. Our concurrence is based on the lack of information that would support such conclusions. Further, the relatively high rates of survival, relatively few owl mortalities resulting from handling by scientists and no declining rates in reproductive output (which might be a manifestation of disturbance because much work occurs during the nesting cycle) suggest that scientific disturbance has not been a factor in the owl's decline (although there have been no explicit studies of this issue). We believe that predation and fragmentation effects were not understood well enough to draw firm conclusions on their importance in 1990. However, we note that the 1990 listing decision did not place much emphasis on these factors. Barred Owl expansion was beginning to occur prior to the listing decision, but while recognized in the decision as a potential factor, the implications or extent of the Barred Owl invasion was not well known relative to today (although Barred Owl effects on Spotted Owls are still being debated). Some factors (demographic and genetic consequences of small population size) may become more important in those parts of the range where populations beome small and do not receive immigrants. This last conclusion is based on theoretical and empirical observations of small populations.

Given that some populations of Northern Spotted Owls are relatively numerous, and that some populations cannot be shown to be declining, there appears to be little risk of extinction in the short-term (15-20 years; the approximate longevity of a Northern Spotted Owl) of the entire Northern Spotted Owl subspecies. Conversely, some regions or populations are precarious (e.g., Canada and perhaps Washington state), and the trends in a number of the populations for the subspecies appear negative. We believe that one of the primary reasons (habitat loss due to logging) for listing has been significantly reduced, which has enhanced the prospect of persistence of the owl in the short-term. Certainly, had the NWFP not been formulated to conserve the owl and its habitat, the species' situation would be much more serious than it is today despite our continued concern for the status of Northern Spotted Owl populations. Nevertheless, it is unknown if there are lag effects or synergistic relationships related to past habitat loss that may still be affecting the owl's demographic performance since listing.

In addition, new operational or potential threats have arisen since the 1990 listing decision, which promote a high level of concern over their effect on the owl. Most notably among these is the impact of Barred Owls and the potential threats of West Nile virus and Sudden Oak Death. At least at this time, the effect of Barred Owls appears to vary geographically, with greater potential effects in the northern part of the owl's range. Close monitoring and research of this situation will be needed to elucidate these effects as well as to formulate a response if necessary. Hence, while we believe there is no reason to conclude that the Northern Spotted Owl is at high risk of extinction in the short term, it is equally clear that, with several increasing threats, there is a distinct possibility that the species may become at high risk of extirpation (particularly in northern parts of its range).

In 1990, the USFWS determined that the risks and threats faced by the Northern Spotted Owl warranted threatened status under ESA. It is not our role either to re-evaluate that decision, or to make recommendations on future status or regulatory decisions. We have instead focused on determining whether the effects of different threats have increased or decreased since 1990. As shown, some threats have decreased and others have increased or are new. It is not possible (for reasons discussed above) to provide quantitative estimates of the overall risk faced by Northern Spotted Owl, or to provide exact estimates showing whether this overall risk is numerically greater or lesser than at the time of listing. Nevertheless it is our firm and unanimous conclusion that the risks currently faced by Northern Spotted Owls are significant; our qualitative evaluation is that these risks are comparable in magnitude to those faced by the species in 1990. Based on the best scientific information, as shown throughout this report, we believe that there are significant threats to the species at this time, and that these threats have the potential to increase.

8 TABLE 1: SUMMARY OF MAIN FINDINGS OF THIS REVIEW

Issue / Threat	Chapter	Information quality	Findings
Genetics	3	Well understood	Northern subspecies confirmed as distinct Reduced genetic diversity not a current threat Hybridization and introgression occurs but at low levels
Prey	4	Poorly understood	Undoubtedly drives some aspects of NSO biology (e.g., habitat associations, population dynamics)
Habitat Associations	5	Well understood	Association with forest structure broadly confirmed Other forest components locally important Heterogeneity in some areas favors demographic performance
Habitat Trends	6	Data of mixed quality	Major cause of listing in 1990 Major achievement by 2004 was reduction of habitat loss to harvest (federal lands) Past habitat loss could still be having effect Current habitat loss to harvest mostly on non-federal lands, but harvest subject to review and consultation Habitat Conservation Plans are important and valuable factors in owl

			conservation Continuing/ Increasing threat from catastrophic wildfires Monitoring data relatively weak Modeling projections uncertain
Barred Owls	7	Poorly understood	Identified as issue in listing document Major threat in 2004 Diversity of panel opinion related to strength of causal link No evidence that fragmentation increases probability of invasion Some evidence for displacement of Spotted Owls Some evidence that Barred Owls use older forests and LSRs as well as young forest
Demography	8	Well understood with data gaps	14 demographic studies are a major achievement in wildlife/conservation biology Predation (fragmentation effects) probably unimportant (change from 1990) West Nile Virus imminent arrival, but risk unknown Trends are down, but it is unclear how these relate to NWFP projections Decline in Washington state of high concern Causes of trends poorly understood

			Lack of causation in meta-analysis. We know trends but not mechanisms causing those trends.
Conservation Science	9		Core concepts of NWFP unchallenged Harvest levels under NWFP less than predicted, therefore, hard to determine future impact of NWFP on NSO persistence Fuels treatments not applied as predicted
Threats	11		1990: Habitat loss to timber harvest pre-eminent threat 2004: Threats have changed both quantitatively and qualitatively Rate of harvest (federal lands) greatly reduced Risk of catastrophic wildfire continuing or increasing Barred Owl increasing Disease risks imminent

SCIENTIFIC EVALUATION OF THE STATUS OF THE NORTHERN SPOTTED OWL

CHAPTER TWELVE

Information needs

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1 INTRODUCTION

The Northern Spotted Owl is arguably among the best-known birds in the world; it is certainly one of the most intensively studied species that is listed under the Endangered Species Act (Noon and Franklin 2002). Over the past 20+ years, the Northern Spotted Owl has sparked intensive efforts in monitoring of habitat and populations. Many innovative and large-scale studies have been completed on diverse aspects of the species ecology, as reviewed in the pages of this status review. For instance, the current 14 demographic studies form a unique and coherent coordinated effort by applying similar techniques over a significant proportion of the species range. Also unprecedented is the degree of scientific cooperation among a diverse set of stakeholders – for no other threatened or endangered species have so many researchers agreed on common methodologies and objectives.

Spotted Owl research has also been innovative. For instance, new analytical techniques, now applied elsewhere in endangered species management, were pioneered with Spotted Owls (e.g., application of new methods for calculating population rates of change (λ) and the use of information theoretic approaches). At the same time, other biologists have continued traditional natural historical observations, discovering new facts about the species. Of course, Spotted Owl conservation was also the catalyst for a concerted ecosystem management approach under the Northwest Forest Plan (NWFP). In addition, coordination and integration of previous large-scale management plans such as the ISC report (Thomas et al 1990), the Final Draft Recovery Plan, and FEMAT/NWFP has required unprecedented cooperation.

In preparing this Status Review, the SEI panel was still unable to provide definitive evaluations of a number of critical issues. Many, sometimes crucial, data have not been collected, and critical areas of Spotted Owl biology are relatively unexplored. It is not the purpose of this Status Review to discuss the many contributing reasons that may have led to these gaps in information. However, it is important to recognize that such gaps still exist.

In the following sections, we first review earlier summaries of information needs, notably those in the Recovery Plan, and then show which of these previously identified needs have been met. We then provide a discussion of which gaps in information were most problematic in our review. In preparing this section on information needs, we will not make recommendations on whether new or existing research and monitoring should be funded and carried out. Our goal is simply to show which areas of knowledge are the most or least complete. We will also indicate which of these areas, if studied, are likely to enhance or change our understanding of Spotted Owl biology in the near future.

Our overall goal is to show which data will be most useful to the Service and others who will carry out the next Status Review for this species. In essence we are asking: what will we need to know in five years time? Hence, our purpose is subtly different from others who have made recommendations on monitoring and research. For instance, the Recovery Team made a long list of recommendations, primarily aimed at 'recovering' the species, aiding silvicultural management, and ultimately at de-listing. Similarly, the FEMAT/NWFP has a significant monitoring component driven by the needs of management and regulatory agencies to assess the effectiveness of that plan, as well as a large adaptive management effort. These differing objectives are understandable and mandated by the role of the organizations involved. Our goals are less value, policy or management driven – we are indicating which missing information prevented us from providing clearer assessments. However, there is considerable overlap between our identified information gaps, and previously stated needs. That these same needs were often stated ten or more years ago illustrates the difficulties in carrying out and funding long-term complex studies.

A critical distinction needs to be made at the outset of this chapter. Some data can be collected once, through a research project, and may then more or less definitively answer a simple question. Other data need to be collected continuously to be useful. For instance, monitoring of Northern Spotted Owl populations is essential to estimate population trends, which are important for conservation, management, recovery and eventually delisting. Some data also need to be collected over long periods of time to capture the effect of natural variation such the effects of weather on survival and reproduction. It is critical to note that without such efforts, the next Status Review team will know less than we know now.

2 PREVIOUSLY IDENTIFIED INFORMATION NEEDS

Throughout this Status Review we have indicated issues that remain unresolved, or questions that remain unanswered. The questionnaire responses (Chapter 10), both in the individual subject sections and in the final section on information needs, indicate repeatedly that, for many areas, important data are unavailable. For instance, all panelists identified a need for better data on Barred Owl ecology, on habitat trends, and emerging threats such as West Nile Virus. It is instructive to compare these identified gaps with earlier proposals and recommendations.

2.1 1990 STATUS REVIEW

The 1990 Status Review (Anderson et al. 1990) was a comprehensive summary of available information on Northern Spotted Owls. The authors of that report provided many details of relevant studies and assessments. In large part, the Status Review team saw the data at that time as excellent:

> "We have been impressed with the quality and quantity of information available on habitat relationships, population dynamics, and regulatory mechanisms which affect northern spotted owls. Never before has so much been known about a species considered for threatened or endangered status. It is fortunate that ample information exists to reach a decision…" (Anderson et al. 1990:59).

The 1990 Status Review did not indicate areas where information was incomplete, or where further research or monitoring was needed. This may have been seen as a task better suited to the Recovery Team.

2.2. LISTING DOCUMENT

The listing document (Federal Register) does not discuss research and monitoring needs in any detail, beyond discussing whether further research was necessary before making a listing decision. Again, the overall tone of the document is that sufficient information was available in 1990 to make a listing decision:

- *"if future research and management actions provide for conserving and recovering the spotted owl, it can be considered by the Service for delisting"*
- *"Although the Service acknowledges that on-going and future research efforts are likely to provide additional insight into the biology of the spotted owl, it is the Services' conclusion that the information currently available is more than sufficient to reach a determination on the proposed listing."*
- *"The Service agrees that information is needed on silvicultural methods to manage for high quality timber harvest and still assure long-term viability of the owl."*
- *"The Service agrees that determination of true dependency [of spotted owls on old-growth] requires a well-designed experiment, but maintains that the evidence overwhelmingly demonstrates strong association."*

2.3. ISC REPORT

The ISC proposed an integrated monitoring and research effort, focused primarily on assessing the success of proposed management strategies, or on information needed to enact these strategies, including data obtained through adaptive management. The plan document emphasized the need for a long-term, large-scale commitment to obtaining information:

> "We believe the spotted owl population response to implementing the conservation strategy will be manifest only over broad scales of space and time …. Also, the basic biological processes involved (for example: juvenile dispersal, habitat selection, and population regulation) require detailed research investment. Therefore, we must achieve an understanding of spotted owl responses to the landscape pattern, as well as to the dynamics of forest stands…"

Recommendations were for the most part focused on directly addressing hypotheses related to plan implementation and success (see Murphy and Noon 1992):

> "In active adaptive management, research blends with monitoring. While monitoring tests hypotheses specific to the conservation strategy, research will compare predictions and assumptions of hypotheses stemming from the conservation strategy and alternative landscape options and stand treatments."

Specific recommendations included:

- **Owl population trends** – Northern Spotted Owls should be studied in existing demographic studies and in each physiographic province, with important measures including juvenile survival and dispersal.
- **Additional inventory/surveys of owls** - Uncertainty over owl presence and numbers suggested the need for additional survey work
- **Habitat trends –** Such monitoring should include "*measures of the proportion of suitable habitat, the area of each suitable stand, indices showing forest fragmentation (Forman and Godron*

1986, O'Neil et al. 1988, Tumor 1989), and distances to the nearest adjacent HCA and patch (>25 acres) of suitable habitat (that is, a node or area occupied by one or more pairs). For nodes and pair-areas in the matrix, habitat measures might include indices to fragmentation and amounts of suitable habitat".

- **Relationship of immigration to maintenance of genetic diversity**
- **Dispersal success and recruitment rates –** Such measures should include effects of distance, size of reserves, degree of fragmentation
- **Habitat selection/association –** These studies should include the effects of stand condition, snags, patch size, fragmentation, etc. and include stand features that influence habitat use in each physiographic province.
- **Effects of forest conditions on demographic performance -** Studies are needed on how forest age and condition support reproduction and also to consider landscape studies of the effects of fragmentation on demographic performance.
- **Effects of timber harvest on demographic performance** - *"What rate and amount of timber harvesting can occur without impacting owl reproduction or survival? What factors influence owl recolonization of forests that have been harvested and regenerated?"*
- **Effectiveness of silvicultural treatments on occupancy and reproduction**. - *"We emphasize strong attempts to gather research information from owl pairs that will be influenced by timber harvesting in the forest matrix between HCAs"*.
- **Studies of prey –** These studies should include: effects of prey size on owl abundance and reproduction; effects of mistletoe on prey; silvicultural options, and effects of forest fertilization
- **Studies of owl biology –** These studies should examine specific aspects of Northern Spotted Owl biology such as responses to disturbance and displacement; effects of social facilitation; energetic costs of foraging in different habitats; factors causing elevational and latitudinal limits; and imprinting of young
- **Predation by Great Horned Owls, and influence of fragmentation on predation rates**
- **Effects of competition with Barred Owls**
- **Development of models that integrates owl and habitat dynamics over time and space to predict persistence under the conservation strategy**
- **Forest-growth models addressing Spotted owl habitat**
- **Spatially explicit models of landscapes linked to a habitat-relationships model that predicts stand conditions.**

2.4 DRAFT RECOVERY PLAN

The Draft Recovery Plan attempted to provide leadership in maintaining and recovering the Northern Spotted Owl, while minimizing the social costs of conservation measures. As part of the proposed suite of actions, the Recovery Team proposed a large monitoring and research effort that also examined silvicultural and other aspects of forest management:

> "Support for and implementation of a strong monitoring and research program are essential to the success of the recovery effort. Monitoring and research are intended to help achieve stabilization and recovery of the northern spotted owl population with the lowest possible economic and social costs."

The overall focus of the Recovery Plan was to provide proactive steps, including conservation and adaptive management, which ultimately would lead to recovery and delisting. The major research and monitoring actions proposed can be summarized as follows:

- **Owl population trends –** The plan suggested continuing and expanding the network of demographic studies to monitor population trends. In addition, the plan proposed that monitoring and research should provide the basis for predicting future trends with data from demographic studies; habitat association information, including performance related to habitat conditions; habitat trend data and projections.
- **Habitat monitoring** - Requires monitoring of habitat at several scales. The plan provides some criteria for a comprehensive monitoring program: *"The habitat monitoring program should include the collection of basic vegetative information about all stands, and should not simply be a classification of stands into suitable and unsuitable areas."*
- **Studies of Northern Spotted Owl habitat use** - This included examining variation (within and between physiographic provinces) by nesting, roosting and foraging owls, for home range size, habitat use, etc. Another important need was to characterize habitat use by dispersing juveniles. Finally, the amount and pattern of habitat on a landscape was to be related to owl distribution, abundance and vital rates.
- **Studies of silvicultural methods to create or maintain stand conditions suitable for owls, and use of those stands by owls and prey.**
- **Studies of diet and prey** - This was to include the relationship of diet to prey abundance, and influences on survival and reproduction. Other needed information included the abundance, distribution and dynamics of prey species and the factors affecting those species.
- **Studies on predation in relation to landscape composition**
- **Studies on competition in relation to landscape composition**
- **Integrative models of population and habitat dynamics**
- **Monitoring and research needed for adaptive management** - These experiments were to focus on behavioral and demographic responses to harvest activities.

The Recovery Plan also identified coordination of monitoring and research as a major need.

2.5 FEMAT/NWFP

The FEMAT report provided a comprehensive management plan for many species, including the Northern Spotted Owl, and proposed a programmatic response to the need for new information through monitoring and research. The ecosystem approach to management of the forest was acknowledged to require a major increase in scientific effort on lands in the range of the Northern Spotted Owl. Central to this effort was a commitment to adaptive management, and the integration of scientific studies with dynamic management approaches.

In regards to identified Northern Spotted Owl research needs, FEMAT largely deferred to the Draft Recovery Plan:

> "Research needs for the spotted owl have been summarized by several sources (e.g., Thomas et al. 1990; USDI 1992c). The Final Draft Recovery Plan for the Northern Spotted Owl (USDI 1"2c.-233-252) provided a particularly detailed listing of the types of research and monitoring needed by geographic province. Priorities included better information on population size and trends, habitat requirements, factors affecting prey populations, dynamics of dispersal, and landscape level factors that influence numbers or distribution of owls. Other items identified as research priorities included the development and testing of silvicultural methods for creating spotted owl habitat and the development of more realistic population viability models that can be used to investigate population response to different management approaches."

Implementation of the NWFP also expressed a strong commitment to monitoring, through the Effectiveness Monitoring program (Lint et al. 1999). Monitoring has included eight demographic studies of Northern Spotted Owls, and a habitat monitoring and modeling component: "*The cornerstones of the monitoring strategy are population and habitat assessments. The integration of data from population and habitat monitoring through predictive models should lead to further monitoring efficiencies*". The initial intent was that the first phase of effectiveness monitoring would explore the possibility of shifting effort from the (expensive) demographic studies to a habitat-only monitoring approach. Currently, there is on-going discussion of this option.

3 INFORMATION NEEDS IDENTIFIED IN THIS STATUS REVIEW

As stated above, our purpose in setting out information gaps/needs in this Status Review are different from the purposes of previous documents and plans, which have concentrated on conservation and management. We are primarily concerned with information that is needed to address the status of the Northern Spotted Owl. Hence, information of particular relevance to status (e.g., taxonomic identity, lag effects, effects of threats) is given more prominence here. In our identification of research needs, we did not include research that is currently ongoing, such as linking Northern Spotted Owl demographics with weather and habitat. We also did not provide a litany of specific questions that need to be addressed. Rather we proposed what we felt were the large-scale topics that needed to be addressed and which could be further refined by a subsequent panel of experts.

3. 1 GENETICS AND SYSTEMATICS

The panel is unanimous in regarding the subspecific status of S. o. caurina as well established, and unlikely to be revised with further research. However, the panel has identified several aspects of genetics that deserve further study:

- **Zone of contact between *S. o. occidentalis* and *S. o. caurina*** - this zone appears less well characterized than previously described (see also Gutiérrez and Barrowclough, in review). Individuals with genetic characteristics of one subspecies are found in the geographic range of the other subspecies. While such introgression is expected between subspecies, the exact amount of introgression, the center of the contact zone between taxa, the effects of introgression, the viability of 'hybrids', and the antiquity of the contact zone are all issues that may affect our understanding of the distribution and status of Northern Spotted Owls.

- **Loss of genetic diversity** - While there is currently little concern over loss of genetic diversity in Northern Spotted Owls, this issue may become a concern in the future (as identified in "Future Threats" chapter). Hence, a survey and monitoring program of genetic diversity and differentiation may be valuable as a benchmark for future studies. Isolated populations may also have reduced genetic diversity. Dispersal studies suggest large areas of unsuitable-habitat (e.g., agricultural valleys and large rivers) are deterrents to dispersal, and may prove important barriers to gene flow. Targeted studies of population genetics would determine whether currently isolated or semi-isolated populations (e.g. Olympic Peninsula, Marin County) show differentiation, and whether potential barriers (e.g., Columbia River, Willamette Valley, Puget Sound Trough) restrict gene flow.

These studies could be coupled with current existing studies by sampling captured birds for genetic material when possible. However, defining the limits of the zone of contact will require sampling beyond the boundaries of existing studies.

3.2 INTERACTIONS WITH PREY AND PREY BIOLOGY

The panel was unanimous in identifying the relative paucity of data on prey. While much relevant and important information has been collected (see Chapter 4), research on the relationship of Northern Spotted Owls to their common prey species has been fundamentally neglected. The panel is well aware that this is not the fault or responsibility of researchers who have long recognized the need for the systematic study of prey. Instead, we acknowledge that understanding the prey base would entail long-term research that would require a commitment from administrators and managers. While traditional prey studies can be expensive, recently developed analytical techniques based on distance sampling have made estimation of prey abundance more efficient and less costly (e.g., Lukacs et al. 2004). Information on prey relations and dynamics is a key component to understanding the temporal and spatial variation in Northern Spotted Owl population dynamics and for understanding the mechanistic process under which Northern Spotted Owl habitat should be managed. To this end, the panel felt critical studies should be initiated on Northern Spotted Owl prey to provide further insights into how changes in habitat and weather effect Northern Spotted Owl populations through their interactions with prey:

- **Habitat associations of primary prey species** - The basic diets of Northern Spotted Owls in different ecological provinces are relatively well-known. However, further information on habitat associations of prey species, and of individual prey behavior at ecotones may be useful in understanding and defining Northern Spotted Owl habitat, how individuals use the different components of their habitat, and how home range size or configuration is controlled by prey abundance in different forest types and seral stages.
- **Relationship of prey abundance, availability and dynamics to the demographic performance of Northern Spotted Owls** - The general lack of explanatory power on the

causes of demographic change (see below) is particularly noticeable in terms of prey effects. Prey abundance and availability is well-known to affect the demography and behavior of owls (e.g., Southern 1970). Reproductive success of Northern Spotted Owls may be related to availability of prey species in complex ways. For example, abundant populations of Peromyscus spp., while not important in terms of diet composition, may nevertheless be important for sustaining reproduction in Northern Spotted Owls (Rosenberg et al. 2003). It may be particularly important to establish whether there is widespread depletion of prey by Northern Spotted Owls (Carey et al. 1992), which would provide a mechanism for explaining shifts in territory locations, abandonment and re-occupation by Northern Spotted Owls.

- **Effects of fire and silvicultural treatments on prey species** - There is some limited information on response of prey species to fire, and silvicultural treatments; more information would be useful in developing active management strategies for thinning and prescribed burning that would maintain or improve Northern Spotted Owl habitat quality.

We recognize that the simultaneous study of several prey species in a single area, together with studies of individual performance of owls, may constitute a significant logistical and funding challenge. Nevertheless, we feel that our understanding of the ecology of the Northern Spotted Owl will remain incomplete without more information on how this predator exploits and depends on its prey.

3.3 HABITAT ASSOCIATIONS

A great deal of research effort has addressed habitat associations of Northern Spotted Owls in different parts of the range. We currently have a good understanding of the regional differences in habitat use, and how these operate at different spatial scales. However, we still lack a clear understanding of why Northern Spotted Owls use the habitats they do use. Thus, we believe the following research topics should be addressed further:

- **Better understanding of Northern Spotted Owl habitat –** Important questions that need to be addressed include 1) why are there provincial differences in habitat use?, 2) how do these provincial differences relate to prey?, and 3) Are there unifying characteristics of Spotted Owl habitat across the range? Some additional study of particular regions (such as the Eastern Cascades province) might be valuable in order to address these questions. All studies outside the Eastern Cascades and Redwood zone found that Spotted Owl core areas contained greater proportions of mature/old forest than random or non-use areas. In the Eastern Cascades, this trend was reversed; further research should examine putative causes of these regional differences and whether the differences in use of mature/old forest are related to regional differences in population trend. Some of these questions could be examined using retrospective meta-analyses of data from existing studies.
- **Examination of hypotheses as to why Spotted Owls use mature/old growth forest –** Gutiérrez (1985) proposed five key hypotheses (nest site availability, thermal regulation, prey availability, predator protection, and synergistic factors) as to why spotted owls used mature and old-growth forests. Thus far, only the hypothesis that these forests offer

protection from thermal extremes has been tested. All of these hypotheses could be tested using key experiments in the larger design of the existing demography studies.

- **Responses of Spotted Owls to habitat changes –** In particular, we need further understanding of how habitat changes affect occupancy, survival and reproduction in Northern Spotted Owls. Important issues at multiple scales include: 1) the effects of fragmentation and heterogeneity, 2) compatibility of maintaining high quality Northern Spotted Owl habitat with different silvicultural prescriptions, and 3) understanding how past natural disturbance regimes shaped spotted owl habitat and how current silvicultural prescriptions and activities could be developed to mimic past disturbance regimes. Clearly, one high priority is research on appropriate treatments for forests that are at risk of uncharacteristic stand-replacement fire. Such treatments have to be assessed experimentally. We are unanimously opposed to application of untested silvicultural approaches over large areas of Northern Spotted Owl habitat.

It should be noted that changes to habitat around existing territories may allow investigation of effects of treatments on owls that are already being studied.

3.4 HABITAT TRENDS

Our current understanding of Northern Spotted Owl habitat amount and distribution is limited by data quality that will remain as long as the assessments are done on a project by project basis. We encourage developing a coordinated effort to validate all aspects of habitat trends across the range of the Northern Spotted Owl, to help validate options to encourage the coexistence of forest management and Northern Spotted owl. This approach would be particularly valuable in interpreting habitat trends on lands managed intentionally for habitat as in the case of some areas under Habitat Conservation Plans. What is needed to track changes in Northern Spotted Owl habitat over the range of the subspecies and provide information that can be linked with existing and future studies is:

- **Range-wide, spatially explicit database –** This is necessary to track changes in forest condition due to individual management activities and natural disturbance. Because existing databases are not spatially referenced, calculations of habitat fragmentation were not possible from the available habitat trends analysis (nor was this information available for the most recent meta-analysis). With increased understanding of the complexities of Northern Spotted Owl habitat, efforts to document habitat fragmentation would aid current demography studies in assessing the effects of fragmentation on Northern Spotted Owl population dynamics. It would be desirable to integrate this database into the existing monitoring efforts.
- **Monitor habitat on private lands** - New generations of remote sensing, such as the Interagency Vegetation Mapping Project, has considerable promise to allow reliable, consistent tracking of habitat trends across the entire range of the Northern Spotted Owl. We remain poorly informed concerning habitat trends on non-Federal lands. Most information available from private entities as well as information contained in Habitat Conservation Plans and associated reports are not sufficient to calculate a rate of change on non-Federal lands. The panel recognizes that this information is usually maintained by private landowners and may be proprietary. Future habitat trends analysis using

remote sensing of all forested lands within the range of the Northern Spotted Owl could provide valuable insight to the continued role of non-Federal lands in supporting conservation of owl habitat.

- **Effective monitoring of developing habitat** - It will be important to develop an improved ability to track and validate the suitability of newly developed habitat. An important part of the validation of habitat development is validating current management approaches designed to accelerate habitat improvement. Research should begin to quantify: (1) Relationship between level of structural of stand complexity and probability of NSO usage for various activities, (2) Effect of mode of disturbance origin on rate at which suitable habitat will develop (e.g., unsalvaged fire vs. clearcut vs. retention harvest); and (3) Effects of intermediate silvicultural treatments on rate of development of suitable habitat (i.e., addressing issue of appropriate young stand restoration treatments).
- **Differentiate different types of disturbance** - Assessments of fire and insect damage are particularly problematic in terms of defining the effect on owl habitat. There appear to be considerable inaccuracies in estimates of habitat impact by fire. Assessments made soon after a fire may misrepresent the eventual habitat effects. It is often difficult to determine how much habitat was removed by fire, particularly regarding whether habitat affected by moderate intensity fire was sufficiently damaged to be unusable by Spotted Owls. New approaches that integrate with remote sensing to assess natural disturbances at various scales would be valuable in future habitat trends analyses.

3.5 BARRED OWLS

Perhaps no area of study received more discussion from the panel, with the unanimous conclusion that the threat posed by Barred Owls is potentially large and certainly imminent – and yet there are insufficient data to unequivocally demonstrate the effects, and no way currently to predict the consequences of this invasion. This was a major source of uncertainty in the Status Review, and will remain so in future reviews without a concerted effort to collect pertinent data. We have tried here to concentrate primarily on the larger issues that need to be addressed immediately to determine the effects of Barred Owls on Spotted Owls. These include:

- **Basic natural history of Barred Owls in the Pacific Northwest** – More complete information is needed on basic aspects of Barred Owl natural history in different ecological provinces to determine the extent that Barred Owls overlap with Spotted Owls in terms of diet and habitat use. Such studies should examine 1) habitat preferences and use by Barred Owls, 2) diet of Barred Owls in different habitats and geographic areas, 3) home range size and movement patterns of Barred Owls in different geographic areas, and 4) behavioral influences of Barred Owls on Spotted Owls, such as levels of aggression, effects of Barred Owl vocalizations on Spotted Owl vocal behavior, etc.
- **Development of an appropriate Barred Owl covariate –** Although this appears to be a minor point, development of some measure of Barred Owl presence in Spotted Owl territories is critical for assessing the effects of Barred Owls on parameter estimates such as occupancy, survival, and reproduction, which are being estimated on the existing demographic studies. There is a critical need for better causative explanations of demographic performance in monitoring areas, including the use of Barred Owl

covariates in future meta-analyses. Currently there is no agreement on how Barred Owl presence should be used as a covariate in the analysis of Northern Spotted Owl data. For example, such a covariate needs to differentiate between a Barred Owl heard once on a Spotted Owl site versus a pair of Barred Owls occupying a Spotted Owl site. The lack of an adequate Barred Owl covariate was problematic in the last Northern Spotted Owl demography meta-analysis (Anthony et al. 2004). Inclusion of an appropriate Barred Owl covariate into analysis of existing data from the Northern Spotted Owl demography studies would provide preliminary information on: 1) how Barred Owls affect Spotted Owl occupancy, reproduction and survival, and 2) whether Barred Owl presence is correlated with Spotted Owl abandonment and re-occupation of territories.

- **Population levels of Barred Owls on LSRs and Matrix lands -** The effects of Barred Owls may have serious conservation consequences. There are currently some indications that Barred Owls are more abundant in LSRs (Late Successional Reserves) than in the surrounding matrix (e.g., in the Washington Cascades, and California Redwoods). However, the affected LSRs are primarily in National Parks and riparian areas. Early observations suggest an initial invasion into riparian areas, which receive a disproportionate level of conservation in the Northwest Forest Plan. A key issue that needs to be resolved is whether LSRs in general have disproportionately higher populations of Barred Owls, whether LSRs with certain characteristics (e.g., more mesic) have higher population levels, or whether differential survey effort is responsible for the perceived differences. This issue can be resolved with current data using recently developed occupancy estimators (Mackenzie et al. 2003), and will be important for assessing the effectiveness of the NWFP.
- **Understanding the magnitude and mechanism of competition between Barred and Spotted Owls –** Clearly, a critical question is: *To what degree do Barred Owls compete with Spotted Owls?* In addressing this question, critical features are understanding the magnitude of competition and what type of competition is operating (e.g., interference versus exploitation). The panel discussed the need for experimental approaches that might unequivocally establish the effects of Barred Owls. Some panelists advocated the use of controlled experimental removal of Barred Owls in parts of existing demographic study areas, where Barred Owls are present. If done correctly (e.g., an interrupted time series with treatments and controls), such an experiment would determine whether Barred Owls are the cause of declines in Spotted Owl populations in portions of their range (one hypothesis) or whether some other factor is causing Spotted Owl declines and Barred Owls are merely replacing Spotted Owls that have disappeared (an alternative hypothesis). Such an experiment would need to be conducted at a large scale, over a long (5-10 years) time frame, and would require cooperation between different demography studies. Without some sort of experimentation, the question will always remain open as to which of the two hypotheses presented above are operating. In addition, large-scale experimentation would answer questions on whether Spotted Owls re-colonize sites after Barred Owl removal and whether active management (removal) can prevent Barred Owl invasions into critical Spotted Owl reserves. Some panelists were concerned about whether such an experiment could be designed appropriately, and whether unequivocal results would be available in time to halt the possible effects of Barred Owls. Given the diversity of opinion among panelists, and the possible urgency of making decisions (on both management and research), the panel suggests that 1) a group of scientists be

convened to conduct a meta-analysis of existing data to examine the effects of Barred Owls on Northern Spotted Owls and 2) a workshop be developed to develop a future Barred Owl research program, which would include observational and experimental approaches. Ideally, the meta-analysis would include development of an appropriate covariate to describe Barred Owl presence and would use advanced analytical approaches, such as recently developed occupancy estimators MacKenzie et al. (2003).

3.6 WEST NILE VIRUS

West Nile virus is a new threat that unexpectedly emerged. It is critical that the effects of this disease are monitored throughout the range of the Northern Spotted Owl. Fortunately, the existing demography studies offer a unique opportunity to examine the effects of this disease on survival and reproduction because estimates of survival and reproduction are available before the disease appears in Northern Spotted Owl populations. We recommend that a range-wide monitoring program be established on the existing demography studies. Such monitoring can be as simple as taking blood samples for testing from captured owls during routine banding operations to more complex monitoring of the prevalence of the disease and the mosquito vectors at Spotted Owl sites.

3.7 DEMOGRAPHY

There can be no doubt that the coordinated, replicated demographic analyses at 14 study sites are a major achievement and a critical base from which to develop other studies on Northern Spotted Owls. These investigations represent an enormous investment, the benefits from which should be maximized. Currently there is discussion of curtailing some of these studies. We regard the current number (14) of studies as adequate; reducing the number of studies will have several consequences:

1. Reducing the number of studies will reduce inference on a regional scale. For instance, there are currently four studies in Washington; all these are in decline. Eliminating some of these studies would mean that we would not be able to determine whether declines were regional (as currently appears to be the case) or were unique to the individual study areas. This could have significant consequences for understanding status. A single average estimate of population rates of change across the range of the owl is not very informative. It is the spatial differences that provide clues as to causative factors (if they are analyzed in that respect).
2. Most of the previous information needs that we have outlined are explicitly linked to the demography studies. For example, experiments involving Barred Owl effects will require a number of different demography studies to serve as spatial replicates and as treatment and controls.
3. Elimination of any demography study at this point would forestall options in designing large-scale meta-analyses and experiments that could provide crucial information for management. In this context, each study area serves as a replicate.

A significant problem will also arise in deciding which studies to continue, and which to stop, given the uniqueness of each site, and known histories of change. As noted in our introduction, without continued monitoring at the 14 demographic study areas, future Status Reviews will have less information than we now do. We have the following recommendations concerning additional information requirements for demography:

- **Emphasize processes rather than just trends on the demographic studies** - Given the investments in demographic studies, it is important to capitalize on them, and to maximize their data for additional information and insight. In particular there is a great need for efforts to provide explanations for observed demographic trends. A number of the demography studies have conducted, or in the process of conducting, research on factors such as weather and habitat quality that may affect population trends and individual demographic performance. However, the lack of correlational studies on other demographic studies with factors such as prey, weather, habitat changes or Barred Owls, is a major omission that should no longer continue. Clearly, the preceding sections would provide covariates that could be used to develop explicit hypotheses on patterns in demographic traits and rates of population change. We understand that funding may be an important constraint on studies of some factors (e.g., prey dynamics, and development of vegetation maps). However, without such data we will be left with only gross trends and untested hypotheses about the causes of such trends. This would be a major impediment to future understanding of status.

- **Strive to understand determinants and limiting factors** - There are important opportunities in linking habitat features to individual demographic performance. Such studies would test an important assumption of Spotted Owl conservation, that protection of habitat will be sufficient to maintain the species. It will also provide information on the amounts and distribution of high quality habitat necessary for survival and reproduction. Although a number of demographic studies have already linked habitat with demography, some of this work needs further refinement and more work still needs to be done on integrating the interactions of prey and weather with habitat and the effects of these interactions on demographic parameters.

4 COMPARISON OF PREVIOUSLY AND CURRENTLY IDENTIFIED INFORMATION NEEDS

We have identified the crucial information that will be important to any future Status Review. We have identified many gaps in information that are a matter of an analytical response (i.e., the data are available but the analysis has not been done). Table 12.1 summarizes these information needs, and compares them to previously identified needs.

It should be acknowledged that the objectives of the various groups (drafters of the ISC, FRDP, and NWFP, and ourselves) were different. We were primarily concerned with evaluating status, so that some issues (e.g. taxonomic identity, effects of past harvest on demography/lag effects) were important for this Status Review that were not so important for those focused on conservation, management, and recovery.

Several patterns emerge from Table 12.1. First, there are some activities that are ongoing, and need to be continued if status is to be understood. Owl population trends (on demographic study areas) and owl habitat trends are ongoing monitoring needs that are essential to understanding Northern Spotted Owl status. Currently, there is also an emerging need to monitor the effects of West Nile Virus. All these monitoring needs are likely to continue into the foreseeable future.

A second major conclusion from Table 12.1 is that a very large number of critical research needs have been previously identified but still remain unstudied. The panel has singled out, in their questionnaire responses and elsewhere, that Barred Owls and prey are long overdue for study. The panel is well aware that Spotted Owl researchers have attempted to obtain funding for such work, without success. Similarly, there has long been a call for a systematic effort to understand the causes of demographic change. This remains a critical and frustrating gap in our knowledge, which seriously hampers conservation, management, and a clear assessment of status.

In a few cases (inventory and, to an extent, dispersal, Barred Owl hybridization, and predation), research has been sufficient to definitively answer questions, so that new work is not necessary to understand status. In another area (taxonomic status of the Northern Spotted Owl subspecies) no group identified this as critical research, but it was carried out anyway, by researchers who provided definitive answers on status. Some research needs identified in the ISC, were not investigated, but no longer appear critical (e.g. social facilitation, imprinting).

Several emerging issues and threats such as West Nile Virus and Sudden Oak Death have unknown but potentially major consequences for Northern Spotted Owls. Other 'new' information needs concern information that has only recently achieved recognition as important. We single out for particular mention the recognition that synergistic interactions between multiple factors may have important consequences for Northern Spotted Owls. Only a large, comprehensive research effort will be able to adequately understand such effects, and these are best conducted in the context of existing demographic studies because of the long history of information. Other areas of particular concern to the panel include the effects of introgression between California and Northern Spotted Owls, and the extent of the contact or 'hybrid' zone, as well as a need to understand the contributions to conservation from, as well as trends in habitat on, non-federal (including private) lands.

It is important to recognize that many previous efforts, including the ISC, Recovery Team, and NWFP reports, all emphasized the opportunities provided by active experimentation, through a program of adaptive management. Forest management has much promise for the promotion of conservation objectives through acquisition and application of new knowledge. The integration of research, monitoring and management design was raised to a programmatic level under the NWFP, with dedicated Adaptive Management Areas. Despite all these efforts, adaptive management remains a largely unfulfilled objective.

We agree with the authors of the NWFP that:

> "Monitoring is a key component of adaptive management and a needed activity for ecosystem management, implementation of conservation strategies, and compliance with forest management laws and policy. Monitoring is significant because of the uncertainty of our predictions. Though currently required, this activity, up to the present, has not been well-designed effectively implemented, or adequately funded.

> "Adaptive management will be successful only to the degree that it is based upon accurate and credible monitoring. Because adaptive management is based on the ability to monitor and to make modifications, the lack of monitoring sufficiently sensitive to detect changes of ecological importance will result in the failure of adaptive management. Monitoring should occur at the relevant resource scales – the region, the basin, the watershed, and the site (project) – and thus be sensitive to responses of ecological systems to individual and cumulative management actions. The system should provide an acceptable basis for natural resource policy decisions. Monitoring can be costly, so the system should be designed to serve particular policy and management needs. Additionally, monitoring should strive for collective efficiency so that data from individual projects can be integrated into a common regional data base for use beyond the original site"

5 CONCLUSIONS

We have identified a large number of areas for which more information is needed for an accurate understanding of status. Many of these same information needs were previously identified by those concerned with conservation and recovery of the Northern Spotted Owl, and with management of its habitat (including the provision of economic benefits through timber production). Some of these information needs are ongoing (monitoring), or new (emerging threats or recent discoveries/theories). However, many other data gaps have been previously recognized but remain unfilled. Only a systematic effort to address and answer these questions will allow the authors of the next Status Review to have more complete information for their assessments than we do. We do not regard any of the data gaps we have identified as 'optional' or of low priority –all have the potential to significantly affect the understanding of the owl's status.

Finally, it should be acknowledged that, while the community of Spotted Owl researchers and managers have achieved much (notably the unprecedented coordination of the demographic studies), there is currently no central coordinating effort, and no systematic priority of research and monitoring needs, with a concomitant effort to acquire funding; for other listed species, a Recovery Team sometimes fills this coordinating role. Some important and potentially critical information (e.g. on genetics, taxonomy, habitat effects on demography, prey relations, and Barred Owls) has been collected as a consequence of the initiative of individual researchers. Again, this is commendable, but hardly a prescription for moving forward, or more importantly improving the conditions for the owl through knowledge-based management such that the owl can be delisted. Recognition of the need for a coordinating position or body might significantly advance Spotted Owl conservation and management.

6 TABLES

Table 12.1. Information needs for the Northern Spotted Owl suggested by various management plans, including this status review.

	ISC	FDRP	FEMAT	This review	NSOWP (Canada)
Owl population trends and demographic studies	X	X	X	X	X
Additional inventory and survey of sites	X				X
Habitat trends	X	X	X	X	X
West Nile Virus effects				X	X
Dispersal behavior and habitat	X	X	X		X
Effects of demographic isolation of populations				X	
Habitat associations	X	X	X	X	X
Effects of forest conditions on demographic performance	X	X		X	X
Effects of past habitat loss on populations (lag effects)				X	
Prey biology and dynamics	X	X	X	X	X
Effects of predator community on prey					
Integrated study of factors affecting demographic success				X	X
Synergistic interactions between factors				X	
Social facilitation	X				X
Imprinting of juveniles on habitat	X				
Energetic costs of foraging in different habitats	X				
Factors affecting elevational and latitudinal limits	X				
Predation (incl. effects of fragmentation on levels)	X	X			
Interactions with Barred Owls	X	X		X	X
Genetic diversity in populations	X			X	X
Introgression/hybridization with CSO				X	
Effects of timber harvest on demographic performance	X	X		X	
Effects of silviculture on demographic performance	X		X	X	X
Effects of displacement by timber harvest	X				
Effects and distribution of Sudden Oak Death				X	
Effects of fire				X	X
Habitat on private lands				X	
Integrative models of habitat and owl dynamics	X	X	X	X	X
Forest growth models (including ingrowth)	X		X	X	X
Spatially explicit landscape simulation models of threats	X		X	X	X

Scientific evaluation of the status of the Northern Spotted Owl
Appendices

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APPENDICES

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4	Summary of Prey Biology	L. Sztukowski and S. Courtney
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8	Sudden Oak Death	J. F. Franklin
9	Analyzing data on Barred Owl effects	A. B. Franklin
10	Developing Recovery Strategies for Northern Spotted Owl Populations	B. R. Noon
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Appendices include supplementary material, as well as commissioned papers by Monahan, Carey and Noon. These commissioned papers represent the work and opinions of the individual authors, not the SEI status review panel as a whole.

APPENDIX 1

MORPHOLOGICAL ANALYSIS METHODS

By W. Monahan
Commissioned by SEI for Northern Spotted Owl Status Review

Specimens were scored using eight characters; several others were examined but excluded from the final dataset due to lack of repeatability.

Character	Criteria
LTC & RTC	upper surface of middle claw, from tip to point of insertion with skin (left and right)
LWING & RWING	longest flattened primary, from tip to wrist joint (left and right)
LWBAR & RWBAR	dorsal surface of wing, mean number of bars on outter margins of exposed primaries 6,7,8,and 9 (left and right)
TAIL	longest flattened tail feather, from tip to point of insertion of middle two rectrices with skin
TBAR	dorsal surface of tail, mean number of bars on inner and outter margins of middle two rectrices

Characters considered but excluded because the criteria were either obscured (due to different methods of preparing specimens) or impossible to ascertain: 1) length of rictal bristles, 2) greatest diameter of facial disc, 3) total length with feathers, 4) length of exposed culmen, 5) length of bill from nostril, 6) height of bill at base, 7) height of bill at nostrils, 8) width of bill at base, 9) length of mandible to feathering on chin, 10) width of mandible at base, 11) length of gonys, 12) length of tarsus.

In testing for subspecific differences, characters were first analyzed using ANOVAs that also considered the effects of sex and season (molting vs. non-molting). Season criteria are detailed in Gutiérrez et al. (1995); we arbitrarily assigned “1” to April – September (molting) and “2” to October - March (non-molting). ANOVAs were conducted using all data for *occidentalis* and *caurina* and again after limiting the *caurina* records to “pure” northern individuals collected north of central Oregon (Haig et al. accepted).

Sexual differences were apparent in all characters except RWBAR (Table 3.2A). In the case of TBAR where the differences were especially pronounced, females possessed on average approximately two more bars than males. However, TBAR was not diagnostic for assigning sex in either subspecies. Seasonal or molt effects were only significant for RTC. While molt-status would certainly have an important effect on the plumage characters considered (e.g. LWING, TAIL, RWBAR), all specimens examined possessed the full complement of wing or tail feathers used to establish character criteria.

Principal components analysis (PCA) was subsequently conducted separately for each sex using unstandardized LWING, RWING, TAIL, TBAR, RTC, and RWBAR measurements. We selected these characters in order to maximize the limited number of *occidentalis* specimens included in the multivariate data matrix. PCAs were repeated using mensural characters only (LWING, RWING, and RTC) and again using the plumage pattern characters (TBAR and RWBAR). Results were qualitatively similar to the combined analysis and are hence not discussed further. Missing characters for many *caurina* specimens collected in Washington prevented us from performing PCAs with “pure” northern individuals. Hence, multivariate analyses included specimens that were potentially from mixed populations.

APPENDIX 2 ECOLOGICAL NICHE MODELING

By W. Monahan
Commissioned by SEI for Northern Spotted Owl Status Review

Here we consider the large-scale bioclimatic evidence on whether *occidentalis*, *lucida*, and *caurina* represent valid geographical subspecies. Analyses also consider subspecies status in light of new genetic data suggesting recent gene flow or introgression from *occidentalis* (Haig et al. accepted). In establishing the validity of a subspecies, we adopt the 75% rule as proposed by Amadon (1949). Using this definition, geographical and genetic subspecies are considered valid from a bioclimatic perspective if less than 25% of the modeled ecological niche of the focal subspecies intersects the modeled niche of the sister taxon.

Ecological niche models were developed using 1,075 spatially unique *S. occidentalis* point localities (obtained from Breeding Bird Surveys, USGS Bird Banding Lab data, and museum specimens) in conjunction with 19 climate variables summarizing global temperature, precipitation, and seasonality (methods in Appendix 3). We first tested for sampling biases in the occurrence dataset by comparing observed multivariate climate space against the breadth of climate conditions encompassed by each subspecies' geographic range. PCA results suggest that the current sample sizes are generally representative of each subspecies' potential niche (Fig. 3). Sampling is weakest for MSO, suggesting that model predictions for *lucida* will be conservative and likely tend to underestimate niche breadth. However, an alternative interpretation is that the *S. occidentalis* range map (accessed from NatureServe) is not representative of the true distribution of the species (Fig. 4). Congruence between the actual point occurrence data and range map is poor, particularly in the case of *lucida*. Future analyses will consider possible sampling biases relative to other and perhaps more accurate estimates of the *S. occidentalis* range.

Figure 3.4 shows a large point locality gap running through central Shasta County, California. This gap overlaps the purported geographical break separating CSO from NSO (Grinnell and Miller 1944) and coincides with transitions/breaks between populations of plants (Soltis et al. 1997) and other vertebrates, including *Ensatina eschscholtzii*, *Bufo boreas*, *Elgaria coerulea*, *Contina tenuis*, *Lampropeltis zonata*, and *Thamnophis atratus* (Stebbins 2003); *Sorex* (Shohfi and Patton unpub.), *Thomomys monticola*, *Clethrionomys californicus*, and *Zapus princeps* (Department of Fish and Game 1990a). The region also marks the northern/southern distributional limits for *Taricha granulosa*, *Batrachoceps attenuatus*, *Ascaphus truei*, *Rana cascadae*, *R. muscosa*, *R. pretiosa*, and *Masticophis lateralis* (Stebbins 2003); *Picoides nuttallii*, *Empidonax traillii* (summer), *Sayornis saya* (winter), *Pica nuttalli*, *Phainopepla nitens*, *Guiraca caerulea* (summer), *Spizella atrogularis* (summer), and *Carduelis lawrencei* (summer) (Department of Fish and Game 1990b). Such consistent distributional breaks, transitions, and limits across taxa legitimize the separation of point occurrence data as presented in Figure 3.4.

All models developed with the geographically assigned point locality data (Fig. 4) performed well relative to random expectations (Table 3.2). Additionally, the models generally yielded low errors of omission and commission. We selected the 1 km^2 WorldClim data and 2.5-97.5% bounding envelope for subsequent analyses because this combination provided the strongest overall performance while allowing us to retain point localities in Canada and Mexico (i.e. the geographic extremes). Geographic projections of these models revealed that predicted niche overlap only occurred between *caurina* and *occidentalis*, covering approximately 78,500 km^2 (Fig. 5). Because *occidentalis* and *lucida* are collectively sister to *caurina* (Barrowclough et al. 1999, Haig et al. accepted), we compared the predicted NSO niche relative to the predicted niche for CSO and MSO combined. However, since the *lucida* niche did not overlap with either *caurina* or *occidentalis*, this was effectively the same as comparing *caurina* against *occidentalis*. Percentage overlap totaled 22% for *caurina*, an estimate just shy of the 25% cutoff established by Amadon (1949).

We repeated the *occidentalis* models after re-assigning individuals to subspecies based on mitochondrial haplotype frequencies furnished by Haig et al. (accepted) (Fig. 6). Geographic projections of these new models (1 km^2 WorldClim data, 2.5-97.5% envelope) revealed a predominantly northwestward expansion of the *occidentalis* niche (Fig. 7). Niche overlap totaled 42% for *caurina* (148,200 km^2) and, as revealed in the previous models, no overlap occurred between *lucida* and either of the other two subspecies. Hence, MSO and CSO consistently fall out as valid subspecies according to the bioclimatic data. However, depending on how the *caurina* boundaries are delineated (geography vs. genetics), different results emerge regarding the validity of the NSO subspecies.

The aforementioned analyses fail to compare *caurina* relative to its sister taxon, the most recent common ancestor (MRCA) of *occidentalis* and *lucida*. Ideally, patterns of niche overlap for NSO should be examined using niche models reflecting climate conditions around the time of CSO/MSO divergence. Future research will incorporate these analyses. However, as an approximate method permissible with our current resources, we estimated the ecological niche of the MRCA while assuming that climate conditions around the time of divergence were roughly similar to the present day (see Appendix 3). While this assumption is biologically tenable, it nevertheless provides for a second method of considering subspecies validity relative to the 75% rule. According to these methods, percentage overlap totaled 19% (geographical) and 22% (genetic) of the predicted *caurina* niche and 13% (geographical) and 14% (genetic) for the MRCA.

In summary, the bioclimatic models suggest that *occidentalis* and *lucida* are valid subspecies because the predicted niches of the two taxa consistently exhibit less than 10% joint overlap. The validity of *caurina* from a niche perspective currently remains uncertain but a priority of future research. In addition to *occidentalis* extending up into the *caurina* range from the south, both subspecies potentially face additional challenges from invasion by the Barred Owl, *Strix varia* (Peterson and Robins 2003). Peterson and Robins (2003) show that the areas of greatest displacement by *S. varia*, given its current westward spread, will overlap most extensively with the *caurina* distribution. When coupled with the apparent northward expansion of CSO, these results suggest that *caurina* faces a unique set of ecological pressures relative to *occidentalis* and *lucida*. Hence, it is critical to fully evaluate the bioclimatic evidence addressing the possible uniqueness of *caurina*. Results from such analyses will also be important in interpreting the intra- and inter-subspecific patterns of genetic and morphological variation described in the literature.

FIGURE A.2-1. Spotted Owl point localities obtained from USGS Bird Banding Lab records, Breeding Bird Surveys, and several major museum collections. Localities separated by geographic subspecies: *caurina* (blue, $n = 765$), *occidentalis* (red, $n = 178$), and *lucida* (green, $n = 132$). Current range map (gray regions) provided by NatureServe.

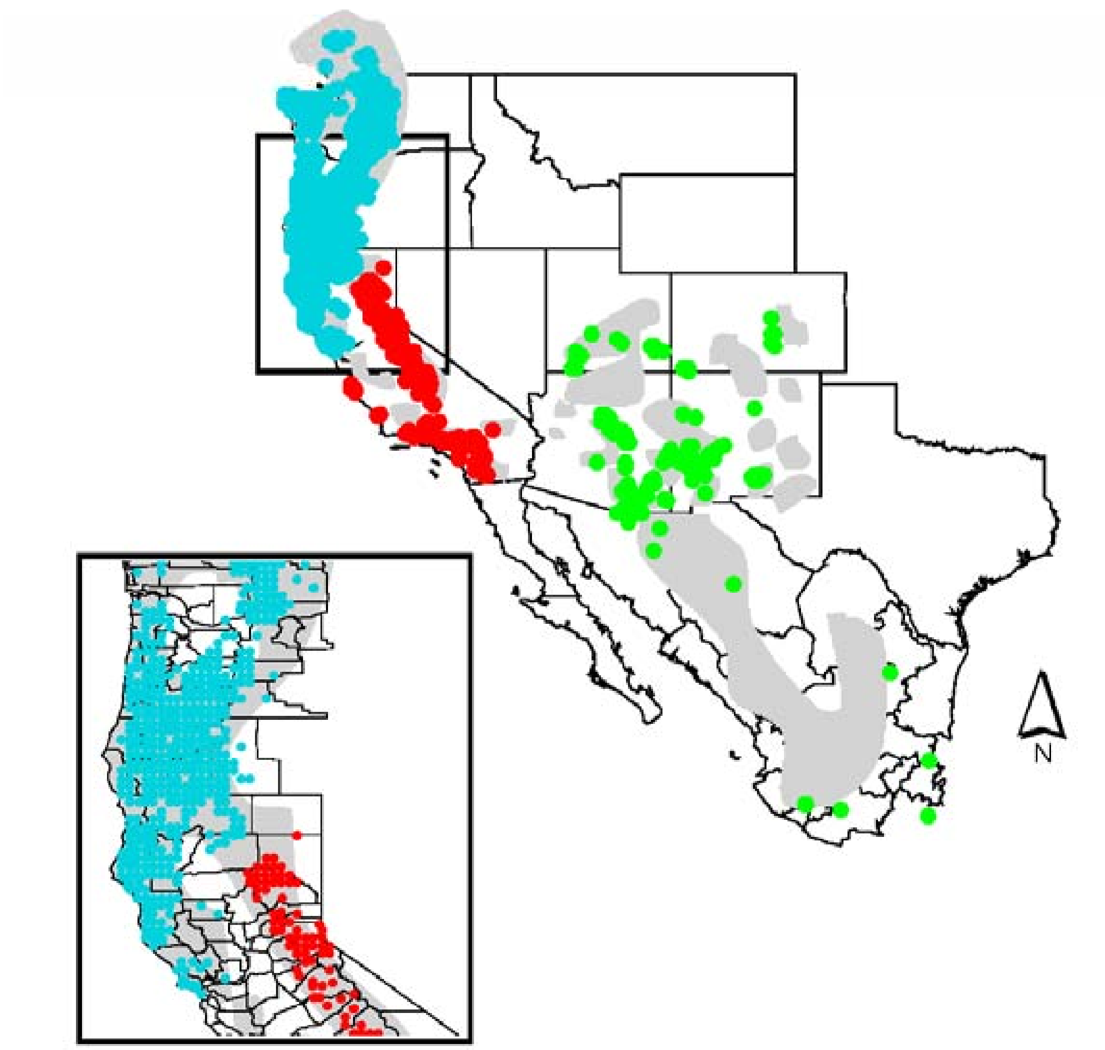


FIGURE A.2-2. Geographic projections of ecological niche models for *caurina* (blue), *occidentalis* (red), and *lucida* (green) obtained using point localities classified according to traditional subspecies criteria. Yellow areas identify regions of predicted niche overlap between *caurina* and *occidentalis* (78,500 km^2). Bold lines identifying subspecific "boundaries" were reconstructed from Grinnell and Miller (1944) and Gutiérrez et al. (1995).

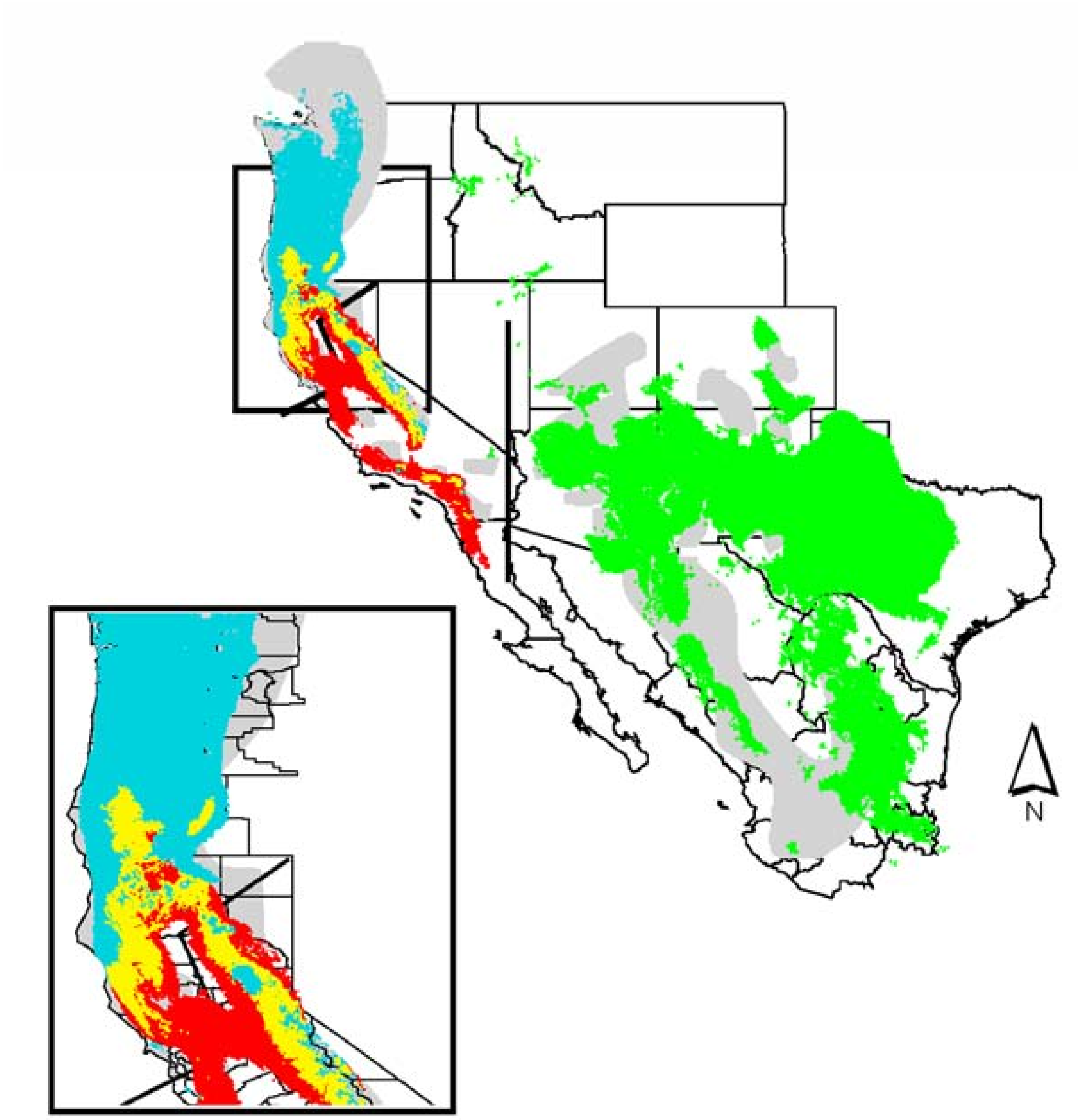


FIGURE A.2-3. Spotted Owl point localities separated according to mitochondrial haplotype frequencies: *caurina* (blue, *n* = 765), *occidentalis* (red, *n* = 178), and *lucida* (green, *n* = 132). Yellow points (*n* = 35) identify approximate locations of mixed NSO/CSO populations.

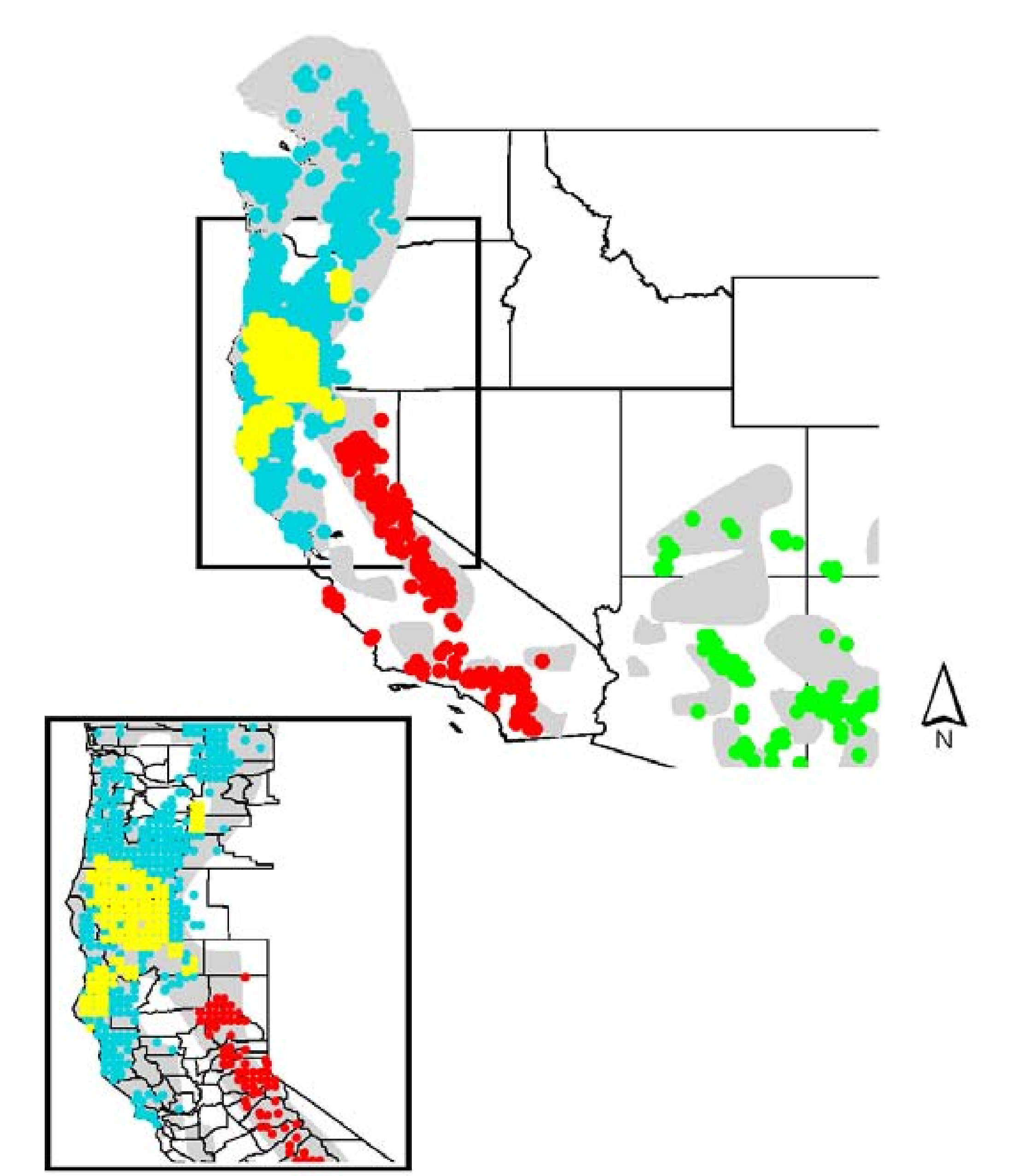
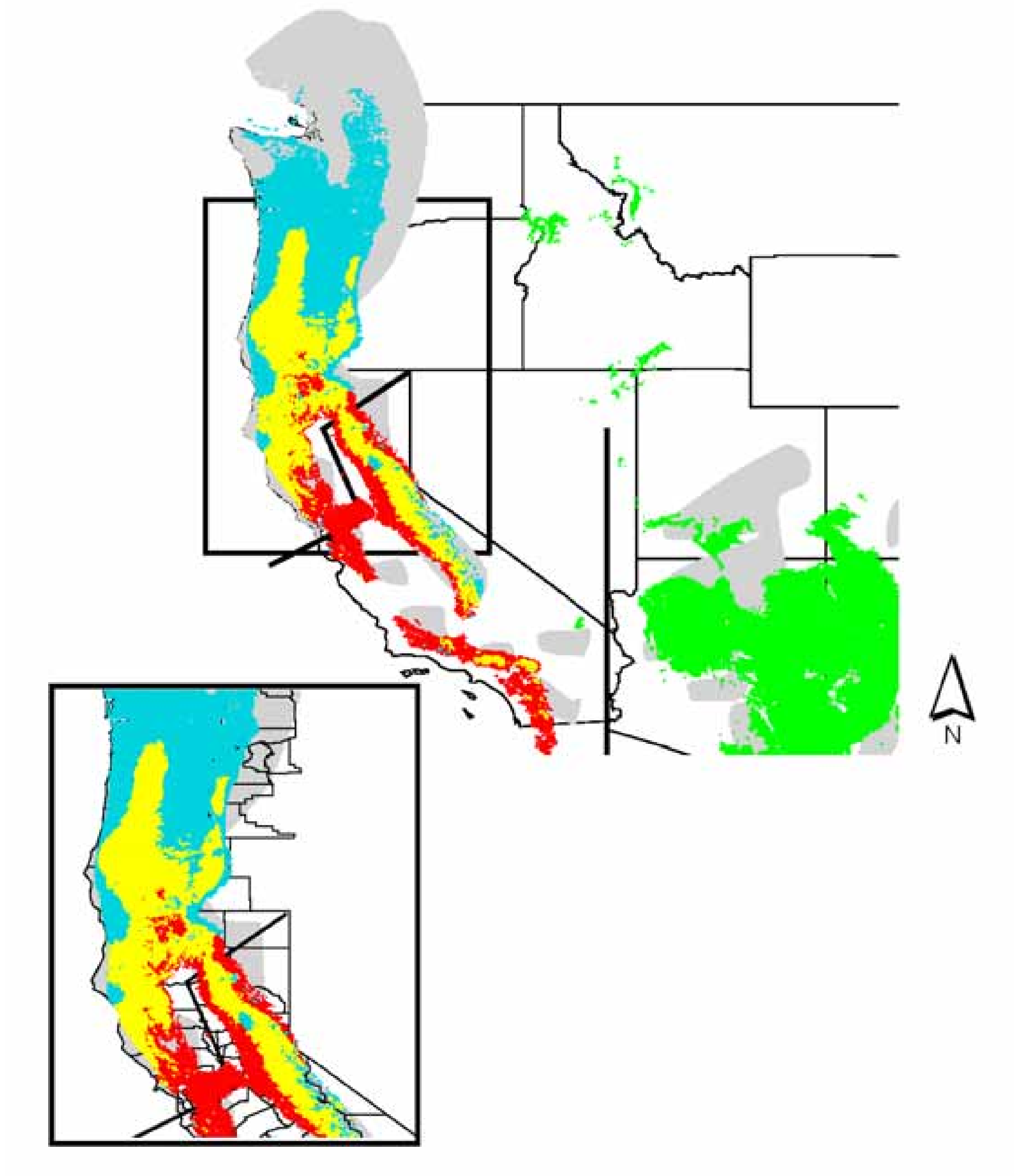


FIGURE A.2-4. Geographic projections of ecological niche models for *caurina* (blue), *occidentalis* (red), and *lucida* (green) obtained using point localities classified according to mitochondrial haplotype frequencies. Yellow areas identify regions of predicted niche overlap between *caurina* and *occidentalis* (148,200 km^2).



APPENDIX 3 ECOLOGICAL NICHE MODELING METHODS

By W. Monahan
Commissioned by SEI for Northern Spotted Owl Status Review

Point Occurrence Data: Spotted Owl point localities were obtained from Breeding Bird Surveys (n = 38) (*Sauer et al. 2003*), USGS Bird Banding Laboratory records (n = 20,162), and museum specimens (n = 183). Contributing museums included the National Museum of Natural History, Museum of Vertebrate Zoology, California Academy of Sciences, Burke Museum, Los Angeles County Museum, and the Mexican Atlas (Navarro-Sigüenza et al. in prep.), which included contributions from Louisiana State Museum of Natural Science, Western Foundation of Vertebrate Zoology, U.S. National Museum of Natural History, Texas Cooperative Wildlife Collections, Museum of Comparative Zoology, and Moore Laboratory of Zoology. This complete dataset reduced to 1,075 spatially unique occurrences (Geographic subspecies: n_{NSO} = 765, n_{CSO} = 178, n_{MSO} = 132). Given the new evidence documenting CSO mitochondrial haplotypes in habitats encompassed by the NSO range (Haig et al. accepted), we simulated mixed populations for use in assigning point localities to subspecies based on genetic (rather than purely geographic) criteria. This was achieved by applying the haplotype frequencies reported in Haig et al. (accepted) for southern Oregon and northern California to our original complete *S. occidentalis* point locality database consisting of 20,383 records. After eliminating duplicate coordinates, an additional 35 records were included to simulate mixed populations (Genetic subspecies: n_{NSO} = 765, n_{CSO} = 213, n_{MSO} = 132).

Climate Data: Models were developed using two sources of climate data. Daymet data, accessed from http://daymet.org/ (January 2004), provided coverage of the conterminous United States at 1 km^2 spatial resolution (18-year summaries, 1980-97, for 17 total variables). WorldClim bioclimatic data (Hijmans et al. 2004) provided global coverage for 19 variables at five minute (approximately 10 km^2) and 30 second (approximately 1 km^2) spatial resolutions (10- to 50-year summaries, 1950-2000). Daymet variables included temperature (max, min, and mean air temperature; day-to-day variability in max, min, and mean air temperature; number of frost days, growing degree-days, heating degree-days, and cooling degree-days), precipitation (mean daily rate and total), radiation (total and day-to-day variability in total shortwave radiation), and humidity (daily mean and day-to-day variability in water vapor pressure). WorldClim variables only summarized temperature (mean annual; mean diurnal range; isothermality; seasonality; max and min of warmest and coldest months; annual range; mean of wettest, driest, warmest, and coldest quarters) and precipitation (mean annual; mean annual of wettest and driest months; seasonality; mean annual of wettest, driest, warmest, and coldest quarters). See original references for additional information.

Sampling Biases: For each geographically defined subspecies, we used principal components analysis to screen for possible sampling biases by contrasting observed multivariate climate space against the multivariate climate space extracted from a range map. This was achieved by first intersecting the observed point localities with the climate variables of interest (10 km^2 WorldClim variables to limit computation time and match the spatial resolution of the USGS data). We then extracted all points at 10 km^2 from each subspecies' range and intersected these with the climate layers. Standardized variable values from the observed and range point datasets were reduced to two axes explaining the majority of the variation (PC1 and PC2). In the absence of sampling biases, a high degree of overlap is expected between the observed and range datasets when plotted in the same component space. With the possible exception of MSO, sampling appeared to be representative of the current range for each subspecies. As explained in the niche modeling section of the report, discrepancies between the observed MSO point localities and the MSO range map could mostly reflect inaccuracies in the range data provided by NatureServe (http://www.natureserve.org/).

Ecological Niche Models: Modeling procedures were carried out using BIOCLIM, a profile-matching algorithm that first computes the portion of multivariate climate space occupied by the original point localities and then extrapolates a bioclimatic envelope across the entire geographic area considered (Busby 1991). We ran BIOCLIM separately for each geographically defined subspecies using both Daymet (1 km^2 resolution) and WorldClim (1 and 10 km^2 resolution) climate data as input variables. Models were further separated according to different bounding envelopes of increasing stringency (0-100%, 2.5-97.5%, and 5-95%). After selecting an optimal model (see below), new bioclimatic envelopes were generated using the genetically assigned point localities for *occidentalis*. We then averaged the CSO-MSO minimum and CSO-MSO maximum climate values on a per variable basis and used these new climatic ranges to extrapolate hypothetical niches of their most recent common ancestor (according to both geographic and genetic criteria). Unfortunately, this averaging method assumes that climatic conditions around the time of divergence were similar to present day. Future analyses will circumvent this problem by utilizing climatic reconstructions c. 8,000-10,000 ybp.

Quantifying Model Performance and Patterns of Niche Overlap: Our goal was to select a single model that provided significant improvement over chance while minimizing errors of omission and commission. These criteria were assessed using three confusion matrix measures reviewed in Fielding and Bell (1997): Kappa, false positive rate (FP), and false negative rate (FN). To obtain the measures, we first randomly subsampled 50% of the geographically assigned point localities for each subspecies and used these in conjunction with the climate data to develop BIOCLIM models. The remaining point localities were then intersected with the BIOCLIM distributions and summarized according to true and false positives. Secondly, we combined the point localities of the other subspecies (NSO-CSO, NSO-MSO, and CSO-MSO) to generate absence data. These were intersected with the BIOCLIM models to yield true and false negatives. After calculating the three performance measures (Kappa, FN, and FP), we computed a single weighted score for purposes of prioritizing the models (Kappa-FN+FP*2). The weighting penalized false positives by a factor of two since our conclusions are especially sensitive to overprediction errors that potentially arise when reducing an *n*-dimensional niche to a handful of variables. Using these criteria, two optimal models emerged (Daymet 0-100% and 1 km^2 WorldClim 2.5-97.5%). We selected the WorldClim model because it allowed us to retain all point localities from Canada and Mexico (i.e. the geographic extremes). Lastly, we re-combined all point locality data by subspecies and used BIOCLIM in conjunction with the 1 km^2 WorldClim data to extrapolate new 2.5-97.5% environmental envelopes for use in estimating niche overlaps. In quantifying the degree of niche overlap among sister taxa, we intersected all pertinent combinations of the BIOCLIM outputs and summarized areas of predicted sympatry relative to each subspecies' total potential niche projected in geographic space.

APPENDIX 4 SUMMARY OF PREY BIOLOGY

Prepared by Lisa Sztukowski and Steven Courtney

This appendix provides a brief introduction to prey biology, including recent literature. Useful recent summaries of prey ecology are also provided by Aubry et al. (2003), Hallett et al. (2003) and Smith et al. (2003).

1. Northern Flying Squirrel (*Glaucomys sabrinus*)

The 25 recognized subspecies of Northern flying squirrel are nocturnal arboreal rodents that are active year-round in both coniferous and deciduous forest with a variety of stand conditions (Wells-Gosling and Heaney 1984, Rosenberg et al. 1996). Considered a keystone species, they disseminate the spores of etcomycorrhizal fungi, which enhance nutrient and water absorption in trees and are predated by a variety of mid-sized predators and owls (Carey et al. 2002, Carey 2000). Mycorrhizal and epigeous fungi are prominent in the diet of Northern Flying Squirrels; however, seeds, fruit, nuts, vegetative matter, insects, and lichens may also represent a significant proportion of their diet (Carey 1995a, Carey 2000, Carey et al. 1999, Thysell et al. 1998, Waters and Zabel 1995, Rosenberg et al. 1996). The overall diet is similarly between old and young forest types, but diversity and abundance of fungi vary between forest type, stand type and structure (Waters and Zabel 1995, Carey et al. 2002, North et al. 1997, Colgan et al. 1999, *Lehmkuhl et al. draft 2004b*).

Flying squirrel "den sites include: (1) cavities in live and dead old-growth trees, (2) cavities, stick nests and moss-lichen nests in small (10-50 cm dbh) second-growth trees, (3) cavities in branches of fallen trees, (4) nests in decayed stumps of felled old-growth trees and suppressed young trees [Carey et al. 1997] and…(5) witches broom formed by mistletoe infections" (Carey 2000:54).

Life history characteristics vary "from north to south, including adult body mass, rate of juvenile weight gain, age of sexual maturation for females, proportion of females that are sexually active, survivorship, population age structure, and population density. Some life-history attributes and predation seem density-dependant" (Carey 2000:45). Adults may weigh up to 194 g, but varies by physiographic province, age class, season, and occasionally between sexes (Villa et al. 1998, *Lehmkulh et al. draft 2004*, Carey 2000, Rosenberg and Anthony 1992, Witt 1991). Body mass is highest in winter and lowest in spring and summer, which corresponds to the fruiting cycles of Basidiomycetes and Ascmycetes, respectively (Carey 2000, Witt 1991). Seasonal abundance and diversity of hypogeous fungi may also influence reproductive chronology and population density (Forsman et al. 1994, Witt 1991, Carey 2000, Waters and Zabel 1995 Rosenberg et al. 1996, *Lehmkuhl et al. draft 2004b*).

Densities of Flying Squirrels generally tend to decrease toward the northern edge of the Spotted Owl's range (southern Coast Ranges and Western Cascades vs. Olympic Peninsula and North Cascades of Washington), with a few exceptions (Carey 1995a, 2000). In British Columbia, old spruce-fir forests of east of the Cascades had similar flying squirrel densities to northwestern Washington and high densities were found in coastal areas of western hemlock forests (Carey 2000). Density estimates may be influenced by region, methods, and analysis used (Martin and Anthony 1999). Densities tend to increase with stand age but results vary and are not always significant (Zabel and Waters 1995, Carey et al. 1992, Rosenburg and Anthony 1992, Witt 1992, Carey 1995, Rosenberg et al. 1996). Densities are generally influenced by forest type, legacy retention, management strategy, stand age and structure (Carey 1995a, 2000, *Lehmkuhl et al. draft 2004*). The three main factors may limit population densities: den structures, food, and predation limiting population size (Carey et al. 1992, Carey 2000, Carey et al. 2002, Witt 1991 and others).

2. Woodrats

Two species of woodrat occur within the range of the northern spotted owl. They include the bushy-tail woodrat (*Neotoma cinerea*), which has a broad patchy distribution throughout the Pacific Northwest, and the dusky-footed woodrat (*Neotoma fuscipes*), which is distributed through northern California, southwestern Oregon, and the Willamette Valley (Hall 1981, Carey et al 1999). Both species are “more common in the mixed-conifer forests of the Umpqua Valley margins… than in the southern Douglas-fir-western hemlock forests of the Coast Ranges or Western Cascades” (Carey et al 1999:73).

Dusky-footed woodrats are nocturnal, arboreal herbivores that are a major prey species for owls below 1,250 m (Barrows 1980, *Solis 1983*, Forsman et al. 1984, *Ward 1990*, Carey et al. 1992, Sakai and Noon 1993; Gander 1929, Linsdale and Tevis 1951, Sakai and Noon 1997). Dusky-footed woodrats are not found in Washington, and Douglas-fir-western hemlock forests in Oregon provide poor habitat as do some mixed-conifer and transition forest stands (Carey et al. 1999).

Generally, dusky-footed woodrat densities appear to follow stages influenced by habitat quality; the progression follows as: unsuitable habitat (recently burned clearcuts), to optimal habitat (sapling/bushy poletimber 15-40 years old and young redwood forest 5-20 years old) then a gradual decline to marginal habitat (small and large sawtimber stands/intermediated-aged forests) with a possible second peak in abundance in old forest as openings form in the canopy structure creating patches of stable, bushy understory (*Hamm 1995*, *Hamm and Diller 2002 draft*, Raphael 1988, Sakai and Noon 1993, Carey 1994, Carey et al. 1999). The gradual decline in abundance may reflect a change in habitat quality, including changes in the understory influencing food and nest site availability or reduced protection from predators. There is also a significant difference in abundance between thinned and unthinned mature stands, which may be also attributed to change in the understory (*Hamm and Diller 2002 draft*). Increases in woodrat abundance in redwood forests have been associated with increased vegetation density and increased amounts of redwood cover and decreased amounts of Pacific rhododendron and salal cover (*Hamm 1995*, *Hamm and Diller 2002 draft*).

Four subspecies of bushy-tailed woodrats exist in the Pacific Northwest and are active throughout the year (Carey 1991, Moses and Millar 1992). Bushy-tailed Woodrats use a variety of den/nest sites which appear to be climate dependant (Carey et al. 1999). Their reliance on patchy resources (such as rock outcrops, talus) increases the likelihood of intraspecific competition and may increase the home range size necessary to meet their needs (Moses and Millar 1992, Topper and Miller 1996).

Bushy-tailed woodrat abundance was low in upland Douglas-fir-western hemlock forests, and Douglas-fir transition forests. Bushy-tailed woodrats are generally absent from oak woodland, Douglas-fir forest-prairie habitats and some upland sites (Ryan and Carey 1995 in 655 Carey et al. 1999). Bushy-tailed woodrat densities increase in stream-side sites associated with bounders as well as old forests, valley-margins, and mixed conifer sites (Carey et al. 1999). Throughout Washington and Oregon, Bushy-tailed woodrat abundance varied in late-seral and stream-side stands but woodrats consistently occupied old, natural stands and were absent from 35-80 year old managed stands (Carey et al. 1999). "Overall, relative frequencies (percent of sites with woodrat captures…) suggest that optimum habitat for bushy-tailed woodrats was old, natural forests (>two-fold margin) with streams (almost a four-fold margin)" (Carey et al. 1999:73).

3. Red Tree Voles (*Arborimus or Phenacomys longicaudus*)

Red Tree Voles are highly specialized, colonial, arboreal species weighing approximately 27g found mostly in Douglas fir forests in the humid temperate region of Western Oregon, and northwestern California (Gillesberg and Carey 1991- Baily 1936 Hall 1981 Johnson 1973, Johnson and Maser 1982, Meiselman and Doyle 1996, Carey 1991, Johnson and George 1991, Maser 1998, Carey 1992). Due to difficultly in capturing and studying these specialized small mammals, their entire range may still be unknown as their known range has expanded as recently as 1995 (Corn and Bury 1986, 1988, Gillesberg and Carey 1991, Manning and Maguire 1995, Meiselman and Doyle, 1996).

Highest abundances occurred most frequently in old-growth with consistent patterns of variation in the Oregon Coast Range and Cascade Range provinces (supported by Carey 1989, Corn and Bury 1986, 1991, Aubry et al. 1991, Meiselman and Doyle 1996, Zentner 1977, Gillesberg and Carey 1991). However, many studies use nest abundance as the index of abundance, which may vary in nest detectability, and the accuracy of determining activity levels and type (*Swingle presentation*, Meiselman and Doyle 1996). Other studies use pitfall traps that may be biased as they are based on terrestrial activity which has not been accurately assessed and may be higher in older forest than in younger stands (*Forsman pers. comm.*). Nests are found in a patchy distribution with individual voles using multiple nests (*J. K. Swingle Conference 2003*).

Our knowledge of this species has increased primarily due to its importance as prey to the spotted owl and its use as an indicator species for old growth forests. However, much of its behavior, habitat, and microhabitat use remain elusive due to the expense and time-consuming nature of studying them. Radio tracking holds promise, expanding our knowledge of their behavior. Large expanses of habitat have yet to be surveyed and may result in future extension of their range. Felled tree surveys, in conjunction with current timber harvest practices, could be used as a cost-effective method of surveying large areas (Gillesberg and Carey1991). Unfortunately, this method destroys habitats and colonies. The red tree vole is listed as "closely associated" with old growth and therefore "the most vulnerable of the arboreal rodents to local extirpations resulting from the loss or fragmentation of old-growth Douglas-fir forests"

(Ruggiero et al. 1991, Huff et al 1992). Factors limiting red tree vole populations seem to "be the size of the old-growth stand, the length of time it has been colonized by red tree voles, and the noncatastrophic influences of fire, windstorms, and predation by owls" (Carey 1991). Dependence on large continuous tracks of old growth may limit population growth as the forest becomes more fragmented over time, increasing isolated populations and local extinction events.

4. Red-backed Voles

Two species of red-backed voles are prominent prey items of the northern spotted owl. These include the southern red-backed vole (*Clethrionomys gapperi*) and the western red-backed vole or California red-backed vole (*Clethrionomys californicus*).

Southern red-backed voles inhabit the Cascades, eastern Washington, northeastern Oregon (*Web-general description*). In the southern Washington Cascades, southern red-backed voles account for about 23% of the total captures (Aubry et al. 1991). Few studies in the Pacific Northwest have focused on this species, and most of those studies occurred prior to 1990.

Western red-backed voles occur in western Oregon and northwestern California (Alexander and Verts 1992, Rosenberg et al. 1994). Patterns of abundance associated with stand age have been inconsistent. Some studies indicate voles "occur more frequently in managed closed-canopy forests with little understory development, and select for habitat that has significant amounts of coarse woody debris (Tevis 1956, Gashwiler 1959, Maser 1981, Doyle 1987, Gomez 1992) or greater food resources (hypogeous fungi, Ure and Maser 1982)" (Rosenberg et al. 1994:266). Others have found no significant difference in the abundance of voles between young and older forests, but the stands selected in these studies were mostly naturally regenerated from wildlife (Corn and Bury 1991, Aubry et al. 1991, Gilbert and Allwine 1991, also listed in Rosenberg et al. 1994). Red-backed vole are "exceptionally rare in clearcuts" and their abundances were "strongly and negatively affected by clearcutting forests" which may have an effect for 10 to 60 years following clearcutting (Hooven and Black 1976, Taylor et al 1988, Raphael 1988, Rosenberg et al. 1994 in Mills 1995).

The presence of coarse woody debris, forest floor structure (i.e. organic soil depth) and food availability may influence vole abundance in old-growth forests and young fire-regenerated stands. In the Oregon Cascades, vole abundance was positively correlated with organic soil depth (Gomez 1992, Rosenberg et al. 1994). Inconsistent results indicate large amounts of coarse woody-debris may be critical habitat for voles. Numerous studies have found a relationship between coarse woody debris and vole abundance (Doyle 1987, Hayes and Cross 1987, Tallmon and Mills 1994). However Mills (1995) did not find that vole abundance corresponded with coarse woody debris. In this study there was a build up of woody-debris at the edge of remnant patches by fallen trees, blow downs and death that was not of advanced-decay class, which voles select (Tallmon and Mills 1994, Mills 1995).

Temporal fluctuations in trends of abundance were not consistent between areas; abundance would increase in one area, while decreasing in another (Rosenberg et al. 1994). Space-use trends by voles are consistent with the distribution of hypogeous sporocarps of mycorrhizal fungi, the primary component of their diet (Maser et al 1978, Ure and Maser 1982, Mills 1995).

5. Deer Mice

Two species of *Peromyscus* that are potential or actual Spotted Owl prey, *Peromyscus maniculatus* and *P. oreas*, have been studied in Washington and Oregon. The common deer mouse (*Peromyscus maniculatus*) occurred in relatively low numbers throughout Washington and Oregon with a strong association with clear-cuts and fragments; the forest deer mouse (*P. oreas*) was more abundant in old-growth, especially in forests of the Olympic Peninsula (Carey and Johnson 1995, Songer et al. 1997). *Peromyscus oreas* and *P. maniculatus* show an inverse correlation in relative densities at all sites and showed significant niche segregation across macroclimates (Songer et al. 1997). Competition between these species may limit *P. oreas* densities, as *P. oreas* reach "much higher" densities in fragment sites when *P. maniculatus* is absent (Songer et al. 1997). "As an arboreal species, *P. oreas* also is likely to be a more accessible prey for the spotted owl than *P. maniculatus*, which typically restricts its movements to the lowest stratum of the forest " (Songer et al. 1997:1037).

In the West Cascades, the average density of deer mice was 7.3±0.9 mice/ha deer mice and represented a biomass of 161 g/ha, similar to the biomass of northern flying squirrels (173 g/ha) (*Rosenberg et al. 2001*). However temporal variability accounted for 67.6% of process variation among years with over a 20-fold fluctuation in abundance (*Rosenberg et al. 2001*). This may account for the high annual variability of each prey species in the diet.

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APPENDIX 5 RELATIONSHIP OF PREY AND FOREST MANAGEMENT

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Paper commissioned by SEI for Northern Spotted Owl Status Review

Spotted owls use diverse prey, ranging from insects to arboreal mammals (Forsman et al. 1984). While spotted owls may forage opportunistically, in any one region and in any one home range within a landscape, spotted owls (and other predators) tend to search for and prey upon a limited number of focal species in any given landscape or period (Forsman et al. 1984, Carey et al. 1992, Zabel et al. 1995). Other species may be taken opportunistically on a regular basis. For example, in western Washington, northern flying squirrels (Glaucomys sabrinus) constitute the predominant biomass in the diet. But spotted owls will regularly take the semi-arboreal Keen's mouse (Peromyscus keeni) and occasionally Douglas' squirrels (Tamiasciurus douglasii), despite the mouse's relatively small size and the squirrel's primarily daytime activity. Juvenile lagomorphs (hares and rabbits) will be taken in the summer when they are abundant, even though they seem to be at the upper size limit that a spotted owl can handle. And if rock outcrops are nearby and inhabited by bushy-tailed woodrats (Neotoma cinerea), the woodrats will be avidly hunted until reduced in abundance or extirpated. In the Pacific Northwest, the northern flying squirrel is the most universally sought after and consumed prey. However, in southwestern Oregon and northern California, dusky-footed woodrats (Neotoma fuscipes), bushy-tailed woodrats, or red tree voles (Arborimus longicaudus) may predominate in the owl's diet, even when and where flying squirrels are a mainstay. Regularly taken prey not only includes mice in the genus Peromyscus, but terrestrial rodents as well. Where the prey base consists of diverse and abundant arboreal and semi-arboreal small mammals >20 g and <400 g in body mass, spotted owl home ranges are smaller and more concentrated than when one or two prey species are in abundance or where prey biomass is low (Carey et al. 1992). Such conditions exist, for example, in valley margin old-growth forests in southwestern Oregon, where bushy-tailed woodrats, dusky-footed woodrats, flying squirrels, and red tree voles all may be abundant in the same 40-ha patch (Carey 1995, Carey et al. 1999a, c). In mosaics of forests of different seral stages and species composition, not all highly-valued prey may occur in each landscape unit (patch), but spotted owls will seek out and repeatedly use diverse patches, each containing an abundance of one or more prey (Carey and Peeler 1995, Zabel et al. 1995). Not all patches, by any means, will contain exploitable prey populations, and numerous patches of low foraging quality can have negative impacts on owl demography and behavior (Carey et al. 1992). Where prey populations are high, owls will forage in uncharacteristic environments—clearcuts near old growth with dusky-footed woodrats, deciduous riparian zones or rock outcrops with bushy-tailed woodrats, and dense stands of small-diameter trees containing dusky-footed woodrat colonies. But, even in the appropriate zoogeographic area, not all clearcuts, thickets, rock outcrops, or riparian areas will contain woodrats.

The owl's prey base not only differ in diversity spatially but the prey species themselves differ in their relative abundances among seral stages and forest types as animal and fungal diversity differs also and in their habitat relationships among biogeographic provinces (Gunther et al. 1983; Carey et al. 1992, 1999a, c; Rosenberg and Anthony 1992; Sakai and Noon 1993; Carey

1995, 2000a,b; Carey and Johnson 1995; Waters and Zabel 1995; Wilson and Carey 2000; Carey and Harrington 2001; Ransome and Sullivan, 2003; Ransome 2004; and many others). This phenomenon, once well understood (ecotypes, Odum 1971; populations in heterogeneous environments, Fretwell 1972), has often been overlooked in studies of the spotted owl prey base. Not all old growth is alike, not all second growth is alike, and flying squirrels in western British Columbia (Ransome 2004) may exhibit significantly different habitat relationships from flying squirrels in southwestern Oregon (Carey et al. 1999a) or northeastern California (Waters and Zabel 1995). In between, across the Western Hemlock Zone, flying squirrels (and other major prey species) exhibit large variation in population responses to seral stages and various habitat elements and habitat elements can differ markedly in their abundance within seral stage across a region (Carey 1995, 2002; Carey et al. 1997, 1999a, 2002; Carey and Harrington 2001). Rarely are animal abundances accurately predicted by the abundance of a single habitat element or a simple linear combination of >1 habitat element except for in geographically, seasonally, and developmentally limited samples. Liebig's law of the minimum seemed to work well for plants in homogeneous environmental conditions as individual soil elements were manipulated. But Shelford formulated his law of tolerance to emphasize the tremendous effects of interactions among biologically important variables as they jointly approached minima. And today, we recognize that floristic diversity as it influences dietary diversity and vegetation structural diversity as it influences availability of essential habitat elements mediate important effects of competition, competitive release, disease, and predation on small mammal abundances. Environmental conditions, floristics, and zoogeography condition the abundance and diversities of small mammals and their interspecific- and habitat relationships (Carey et al. 1999a, b; Carey and Harrington 2001, Johnson and O'Neil 2001). Competition among prey species for limited food or den resources and predation by various predators seem important. Even where prey may be abundant, however, vegetation structure may not be conducive to owl foraging—a prey species may be abundant, but unavailable. Such a condition may exist in second-growth forests with dense, low understory and large gaps between the understory and the nearest perches in the canopy. Spotted owls and other predators such as long-tailed weasels (Mustela frenata) may decimate prey populations in some patches and may not return to forage heavily in those patches for 1-2 years (Carey et al. 1992, Rosenberg and Anthony 1992, Carey and Peeler 1995, Wilson and Carey 1996). If owls are attracted to dense concentrations of prey that they are able to exploit, and if this exploitation can significantly reduce the density of the prey, then the history of foraging by owls (or weasels) must be accounted for before the value of any one or any one set of habitat elements to the prey species can be understood. Given all this complexity, the question is what do we know about the effects of forest management (positive and negative) on the diversity and biomass of prey available to the spotted owl?

Timber Harvest

Timber harvest (clearcutting, partial cutting, and variable retention harvest systems) is a catastrophic disturbance with both short- and long-term effects on prey. Surprisingly many forest-floor small mammals respond positively to clearcutting in the short-term (Gunther et al. 1983). This is simply because any disturbance entails release of certain resources that then become available to various life forms, including small mammals. Cone- and seed-laden branches come to the forest floor to be exploited by diverse small mammals. With site preparation, these are often destroyed but colonization by grasses, forbs, and shrubs benefits diverse prey species (dusky-footed woodrats, deer mice, Oregon creeping voles [Microtus oregoni]) but the site might well be uninhabitable for a considerable period by the most arboreal rodents—red tree voles, flying squirrels, and Douglas's squirrels. The degree to which legacies are retained during timber harvests is an important determinant of recolonization of the site by all life forms (Perry et al. 1989, Franklin et al. 2000), including the fungi that are the mainstay of the flying squirrel and California red-backed vole diets (Clethrionomys californicus) (Amaranthus et al. 1989). These legacies are diverse but include fungal mycelia (indeed intact forest floor microbial communities in patches of intact forest floor), coarse woody debris, intact vascular plants, and fungal and plant propagules. Intentional retention of legacies can accelerate the pace of ecosystem recovery (Franklin et al. 1997)—the rate of change in the new, self-organizing community will be rapid and prey species will be affected differentially. Dusky-footed woodrats are benefited by delayed recruitment of a dominant cohort of conifers and rapid recruitment by evergreen hardwoods; flying squirrels respond oppositely.

Perhaps the biggest consequence of conventional clearcutting comes not during the disturbance itself or the period of rapid reorganization, but later when the conifer canopy closes (the stem-exclusion or competitive exclusion stage, Oliver and Larson 1996, Carey et al. 1999c). Dense, closed-canopy second-growth without legacies can not only be devoid of exploitable prey populations (Carey 1995, Carey and Johnson 1995, Carey and Harrington 2001) but also poorly suited for owl roosting, foraging, or nesting (Carey et al. 1992). This period of low structural diversity can last >100 years (Carey et al. 1999c, Franklin et al. 2002) and can have profound effects on the capacity of the forest to develop biocomplexity in the future (Halpern et al. 1999, Carey 2003a). However, with legacy retention, patchy regeneration of multiple species including hardwoods, and natural disturbances during the periods following either a natural catastrophic disturbance by wind or fire or following partial cuts, the prey base can reach or exceed levels of diversity and abundance found in many old-growth stands and will be used for foraging and roosting by spotted owls (Carey et al. 1992, Rosenberg and Anthony 1992, Carey 1995, Glenn et al. 2004).

Thinning

Thinning can be done in many ways and for many purposes and has differing and diverse consequences on the ecosystem including effects on the prey themselves, the plants that provide them with food and cover, the fungi that provide them with food, and the health and resilience of the forest (Waters et al. 1994; Carey et al. 1996, Colgan et al. 1999; Graham et al. 1999; Carey 2000b, 2001; Thysell and Carey 2000, 2001; Wilson and Carey 2000a, b, 2002b; Carey and Wilson 2001; Sullivan et al. 2001; Muir et al. 2002). All thinning has short-term negative effects on understory plants (mechanical destruction) and below-ground fungi (death of host trees and mechanical destruction). Heavy thinning in the Mixed Conifer/Mixed Evergreen Zone may benefit woodrats and deer mice in the mid-term, but to the detriment of flying squirrels. Conventional thinning in the Western Hemlock Zone may result in very low flying squirrel populations through negative effects on truffle production and arboreal travelways (Colgan et al. 1999, Carey 2000b) and reduced foraging by spotted owls (Meiman et al. 2003) for a long time while increasing numbers of forest-floor rodents (Wilson and Carey 2000). Conventional thinning, however, may result in uniform dense understories unfavorable to both flying squirrels and owl foraging in the midterm. Variable-density thinning, however, hold promise for acceleration of the development of spotted owl habitat and dense prey populations (Carey 1995, 2001, 2003a. Carey et al. 1999a,b; Carey and Wilson 2001; Muir et al. 2002) especially when appropriate attention is paid to decadence (snags, cavity trees, and coarse woody debris) (Bunnell et al. 1999; Carey et al. 1999a, b; Carey 2002). There maybe a short-term impact on truffle production, flying squirrel abundance, and owl foraging, the ecosystem recovers more quickly and begins to develop more quickly and completely than following conventional thinning. Variable-density thinning has all the positive effects of conventional thinning, such and increased growth of trees, crown differentiation, development of understory, and increased flowering and fruiting of understory plants (Harrington et al. 2002, Wender et al. 2004) that provide important ancillary foods to spotted owl prey (Carey 2000a) without the same extent of negative mechanical impacts, loss of canopy connectivity, loss of spatial heterogeneity, loss of woody plant diversity (variable-density thinning stresses multipspecies management).

Fire Suppression

Fires play different roles in different ecosystems (Franklin et al. 2002). Some forests and their fauna are well-adapted to fire—understory may be highly flammable, but quick to recover, and overstory trees may be quite fire resistant. This is true of the mixed-conifer forest of southwestern Oregon and northern California, where the old-growth is even more patchy and coarse-grained than the forests to the north, with the forest incorporating various evergreen hardwoods and hard-leaved shrubs especially supportive of dense woodrat populations. Forest to the north in western Oregon and Washington have increasing fire return intervals up through British Columbia where millennia might pass without catastrophic fire on some sites. Wind can be an important catastrophic disturbance in coastal forest, but intermediate disturbances due to wind, ice, snow, and disease may prove to be more important in forest developmental processes. East of the Cascades, forest historically appeared to have shorter, but spatially highly variable fire return intervals, often with frequent fires of low to moderate intensity. There, fire suppression has altered the ecology of the forests with fire-adapted understories of grasses, forbs, and low shrubs being replaced by flammable ladder fuels that may threaten catastrophic destruction of the forest when fire does occur. But eastside forests are diverse and conditions in dry site ponderosa pine (*Pinus ponderosa*) are too often generalized to other types. Furthermore, grazing and silviculture has compounded the changes in eastside forests (Graham et al. 1999). Franklin et al. (2002) point out the patterns in eastside forest are often misunderstood, with patches within late-seral forests interpreted as independent stands instead of part of the forest mosaic. The traditional forestry view of stands as homogeneous units of vegetation and the human tendency to reduce variability to one or two dimensions portend many management mistake eastside. Researchers in interior forests have found that approaches to managing forest for diversity and support of top avian predators, like the goshawk (*Accipiter gentilis*) (Reynolds et al. 1992) entail much the same approach adopted by researchers seeking to solve the spotted owl/spotted owl prey base dilemma in Westside forests (Carey et al. 1992, 1999a, b, 2003a,b). The same will likely prove true in management of spotted owls and spotted owl prey eastside—spatial heterogeneity (patchiness) may prove to be the key to restoration of forest health and low intensity fire regimes while retaining patches of complex forests that benefit owls and their prey.

Forest Management & Owl Prey

The complexity associated with management of forests, spotted owls, and owl prey requires those who are interested in conservation of spotted owls to step back and take a decentered view. The focus of conservation might best be centered on the dynamics of ecosystems and landscapes, not individual species (Franklin 1993). Single-focus management, especially with a short-term view, has repeatedly had unintended consequences and produced big surprises. Any single forest management activity has the potential to have negative or positive consequences for one or more or all spotted owl prey depending on how it is implemented and what other measures are taken concomitantly. Thus, well thought out integrated management systems are necessary (Bunnell et al. 1999; Carey et al. 1999b; Lindenmayer and Franklin 2002; Loehle et al. 2002; Muir et al. 2002; Carey 2003 a,b,c). Not only must the life history of keystone species be considered (Holmes and Austad 1994, Stapp 1994, Carey 2000a) but also must various aspects of biodiversity, including that of soil organisms (Amaranthus et al. 1989, Perry 1989, Tilman 1999), complex ecological processes such a decadence resulting from tree death (Franklin et al. 1987, Bunnell et al. 1999), multiple processes involved in forest succession and development (Canham et al. 1990, Carey et al. 1999a, Franklin et al. 2002), and spatial scale both within ecosystems and among ecosystems within landscapes (Carey et al. 1999a, Carey 2003a,b). Key variables in management that will determine the effects of forest management include degree of (1) legacy retention and conservation, (2) multispecies management (conifers, hardwoods, and shrubs), (3) precommercial thinning (as it relates to precluding competitive exclusion and fostering species diversity and crown differentiation), (4) inducing heterogeneity at the proper scale with variable-density thinning while maintaining canopy connectivity in some places and interrupting it in other places, (5) conserving and augmenting natural decadence processes, (6) restoration of biodiversity lost to single-purpose management, (7) extended rotations; (8) consideration given to geotechnical analysis in providing a template for legacy patch retention; (9) conservation of biodiversity as it relates to ecosystem resilience and capacity to adapt to changing fire conditions; and (10) ability to grasp the complexity of highly altered ecosystems and determine which of multiple alternative relatively stable states might be achievable in the long terms and what mix of these to pursue and maintain on the landscape. There is no one-size-fits-all or any canned prescriptions; diagnosis must be done watershed by watershed and prescription should follow diagnosis. It must be recognized that past management has had diverse effects on spotted owls and their prey; some second growth has abundant prey, some second growth is depauperate in prey and other species. No one has yet demonstrated successful intentional acceleration of development of diverse and abundant spotted owl prey or spotted owl habitat—too little time has passed since attempts to do so were begun.

APPENDIX 6: TABLES FOR REFERENCE TO CHAPTER SIX (HABITAT TRENDS)

Prepared by Richard Bigley

Table 6.1. Estimates of Old Conifer (>150 Years of Age) Forest by World Wildlife Fund Ecozone.

Ecozone	Ecoregion Area (ac)	Historic Old Conifer Area (ac)	Percent Historic Old Conifer Area	Current Old Conifer Area (ac)	Percent Current Old Conifer Area
Northern Cascades Forests	3,158,076	1,894,846	60	1,263,650	40
Cascade Mountains Leeward Forests	3,954,697	2,372,818	60	1,038,794	26
Puget Lowland Forests	4,249,443	3,399,554	80	262,294	6
Central Pacific Coastal Forests	10,546,198	7,909,648	75	1,651,322	16
Willamette Valley Forests	3,676,277	735,255	20	86,468	2
Central and Southern Cascades Forests	11,073,240	8,304,930	75	3,283,455	30
Eastern Cascade Forests	13,338,801	5,335,520	40	1,699.643	13
Klamath-Siskiyou Forests	12,436,990	6,218,495	50	2,338,540	19
Totals	62,433,724	36,171,066	58	11,624,177	19

Source : *Jim Strittholt (Personal communication)* World Wildlife Fund Ecozones are approximately equal to the NSO habitat provinces see Jiang at al. (2004) for a description of the WWF Ecozones.

Table 6.2. Published Estimates of Annual Percent Change in Stand Replacement Disturbance (both human-caused and natural).

Location	Periods	Public Land	Private Land	Total Land	Reference
Klamath-Siskiyou	1972-1992	- 0.25	- 0.42	- 0.53	Staus et al. 2002
Rogue Basin	1972-1992	- 0.36	- 0.46		Staus et al. 2002
Klamath Basin	1972-1992	- 0.48	- 0.96		Staus et al. 2002
Central Cascades, OR	1972-1988	- 1.20	- 3.90		Spies et al. 1994
Tillamook Basin, OR	1972-1992			- 1.00	Strittholt and Frost 1995
Hoh River Basin, WA	1975-1991	- 1.47	- 3.45		Turner et al. 1996
Western Oregon	1972-1995			-0.9	Cohen et al. 2002

Table 6.3. Change in habitat from 1994 to 2003 resulting from Federal management actions and natural events by physiographic province. Habitat additions to the Federal land base through land transfers and exchanges are not included as they represent a change in ownership rather than a physical change to habitat across the landscape. Source *USDI 2004*

Physiographic Province	Forest Plan baseline	CAUSES OF HABITAT LOSS				TOTAL
		Mgmt[1]	Fire[2]	Wind	Insect/ Disease	
Olympic Peninsula	560,217	-87	-299	0	0	-386
WA East Cascades	706,849	-5,024	-5,754	0	0	-10,778
WA West Cascades	1,112,480	-11,139	0	0	-250	-11,389
Western Lowlands	0	0	0	0	0	0
OR Coast	516,577	-3,278	-66	0	0	-3,344
OR Klamath Mountains	786,298	-53,468	-117,622	0	0	-171,090
OR Cascades East	443,659	-13,867	-4,008	0	-55,000	-72,875
OR Cascades West	2,045,763	-51,122	-24,583	0	0	-75,705
Willamette Valley	5,658	0	0	0	0	0
CA coast	51,494	-250	-100	0	0	-350
CA Cascades	88,237	-5,091	0	0	0	-5,091
CA Klamath	1,079,866	-12,673	-15,869	-100	-390	-29,032
TOTAL	7,397,098	-155,999	-168,301	-100	-55,640	-380,040

[1] Includes all updates submitted by the Federal action agencies.
[2] Fires occurring in 2003 were not included here as the data were not yet available.

Table 6.4. The percentage of Federal Forest Plan baseline affected by habitat loss within each province and across the range of the Northern Spotted Owl. Source *USDI 2004*

Physiographic Province	Forest Plan baseline	Total	Within Province loss		% of Range-wide Loss[1]
			Total % change	Annual rate of change (%)	
Olympic Peninsula	560,217	-386	-0.07	-0.01	0.10
WA East Cascades	706,849	-10,778	-1.52	-0.17	2.84
WA West Cascades	1,112,480	-11,389	-1.02	-0.11	3.00
Western Lowlands	0	0	0	0	0
OR Coast	516,577	-3,344	-0.65	-2.42	0.88
OR Klamath Mountains	786,298	-171,090	-21.76	-1.83	45.02
OR Cascades East	443,659	-72,875	-16.43	-0.41	19.18
OR Cascades West	2,045,763	-75,705	-3.70	-0.41	19.92
Willamette Valley	5,658	0	0	0	0
CA Coast	51,494	-350	-0.68	-0.08	0.09
CA Cascades	88,237	-5,091	-5.77	-0.64	1.34
CA Klamath	1,079,866	-29,032	-2.69	-0.30	7.64
TOTAL	7,397,098	-380,040	-5.41	-0.57	100

[1] The contribution of habitat loss within each physiographic province to the range-wide total loss of habitat.

Table 6.5. Distribution of habitat effects on Federal lands by state from 1994 - 2003. Source USDI 2004

State	Forest Plan baseline[1]	CAUSES OF HABITAT LOSS			**% state baseline**	% total loss
		Mgmt loss	**Natural events**	Total		
WA	2,379,546 (32%)	-16,250	-6,303	-22,553	-0.95	5.95
OR	3,797,955 (51%)	-121,735	-201,279	-323,014	-8.50	84.99
CA	1,219,597 (17%)	-18,014	-16,459	-34,473	-2.83	9.07
All	7,397,098	-155,999	-224,041	-380,040		

[1] Percentages in parentheses is the percent of the Forest Plan baseline habitat.

Table 6.6. Comparison of Federal habitat trends presented in the listing document to recent trends of habitat change due to Federal management activities. Source *USDI 2004*

	Listing Document[1]		This report
Management agency and state	Pre-listing period (about 1981 to 1990)[2]	Anticipated rates (about 1991 to 2000)[3]	Calculated rates[4] (1994 to 2003)
FS in WA and OR	64,000 (1.33)	39,400 (0.82)	10,341 (0.21)
FS in CA	Not reported[5]	4,700 (0.41)	1,653 (0.14)
BLM in OR	22,000 (2.35)	23,400 (2.50)	4,911 (0.52)
Total		67,500 (0.98)	16,905 (0.24)

[1] Habitat change values were presented in the listing document in units of acres per year, rather than as a percentage of total available habitat per year. We converted these values to annual percentage rates by dividing by the habitat amount in the Forest Plan baseline for each management agency and geographic group and multiplying by 100 (annual percentage rates in parentheses, indicating negative changes).
[2] Reported in the listing document as observed trends from 1981-1990.
[3] Estimated in the listing document as trends expected in the next decade (1991-2001).
[4] Annual acreage totals calculated as the sum of effects from 1994 to 2003 divided by 9 years of record. Annual percentage rates calculated as described above.
[5] The listing document references a rate of 12,000 acres of habitat loss per year in California, but it was unclear what time period this rate represented. Consequently, we did not include it here.

The USFWS compared Forest Plan baseline acreages of suitable Northern Spotted Owl habitat for each administrative unit to their local habitat baselines . The purpose of this comparison was to assess the potential for bias in evaluation of project effects. Local habitat baselines were not available for all administrative units within the Forest Plan area.

Table 6.7 Comparison of habitat estimated by the local habitat baseline and the Forest Plan baseline. Source USDI 2004

Administrative Unit	Subset of Forest Plan Baseline	Local Baseline	Difference from Forest Plan in acres	Percent Difference from Forest Plan
Mount Baker-Snoqualmie NF	581,447	408,750	-172,697	-29.7
Olympic NF	250,714	246,175	-4,539	-1.8
Wenatchee NF	540,626	927,402	386,776	71.5
Gifford Pinchot NF	497,491	510,000	12,509	2.5
Mt. Hood NF	568,488	419,791	-148,697	-26.2
Deschutes NF	144,932	123,135	-21,797	-15.0
Siuslaw NF	234,257	270,343	36,086	15.4
Willamette NF	767,001	740,053	-26,948	-3.5
Umpqua NF	501,390	432,880	-68,510	13.7
Rogue Basin Riv. Sis/Rog NF and Med. BLM))	913,497	1,060,728	147,231	16.1
Klamath NF[1]	407,803	479,763	71,960	17.7
Shasta Trinity NF[1]	266,409	372,621	106,212	39.9
Six Rivers NF[1]	341,716	379,522	37,806	11.1
Mendocino NF[1]	101,168	133,432	32,264	31.9
Salem BLM	150,605	149,544	-1,061	-0.70
Eugene BLM	106,425	81,440	-24,985	-23.5
Coos Bay BLM	115,207	118,580	3,373	2.9
Roseburg BLM	196,039	205,330	9,291	4.7
Totals	6,685,215	7,059,489	374,274	5.60

Sources USDI 2004
[1] Local habitat baselines include only nesting/roosting habitat from the California Baseline.

USDI 2004 Appendix 10: Comparison of Northern Spotted Owl Location Data with Suitable Habitat Maps for Washington, Oregon, and California

A comparison of available (1994 vintage) spotted owl location and suitable habitat maps were made to help respond to questions over how representative the 1994 NW Forest Plan suitable habitat baseline map is of actual spotted owl habitat on Federal lands. An additional analysis was done for Northern California using a more current (and updated 1998) habitat map, which should provide habitat estimates more comparable to Oregon and Washington. Spotted owl sites, located using survey protocols, were mapped as points in the GIS database. Because of questions about the accuracy of recorded site locations[1], the points were buffered in this analysis to allow for recording discrepancies up to ¼ mile (400m) around each plotted location. Given the inherent biases in both the site location and habitat datasets (see earlier discussion about habitat map accuracy), these results provide only a relative sense of the utility of the suitable habitat map.

Table 1: Percent of Known Northern Spotted Owl Locations Found within Mapped Suitable Spotted Owl Habitat (data from 1994 NWFP/FEMAT databases)

	Washington		Oregon		California[a]		Rangewide Totals	
Size/Buffer	Owl Sites	Percent	Owl Sites	Percent	Owl Sites	Percent	Owl Sites	Percent
Point	558	67%	1873	69%	388	40%	2819	63%
100M	658	79%	2228	82%	521	54%	3407	76%
200M	702	84%	2360	87%	584	61%	3646	81%
400M	751	90%	2462	91%	683	71%	3896	86%
Total Sites	833		2716		961		4510	

[a] – habitat maps used for FEMAT in 1994 were considered to under-represent suitable spotted owl habitat on National Forest lands within the four Northern California Forests (Thomas et al. 1990, USDI 1992).

[1] Metadata shows that known spotted owl location points (1988-1995) were derived by Federal and State agencies from several agency databases with varying levels of accuracy. For example, most sites were located by field survey crews on 1:24,000 Quad maps (accuracy estimated at +/-250 feet) and then transferred by database staff to GIS databases. Few, if any, sites were located using GPS technology, but were based on the locator's estimation of the site center using maps, photos, and other materials. Depending on the complexity of the topography and distance from known locations and the accuracy of the underlying maps relative to known points such as roads, these could vary widely in point accuracy.

Table 2: Percent of Northern Spotted Owl Locations Found within Updated Suitable Spotted Owl Habitat Map for Northern California (habitat data from 1998 interagency database)

Size/Buffer	California[b]		Adjusted Rangewide Totals	
	Owl Sites	Percent	Owl Sites	Percent
Point	554	58%	2985	66%
100M	723	75%	3609	80%
200M	773	80%	3835	85%
400M	790	82%	4003	89%

[b] – in 1995 the USDA Forest Service (Region 5) and the USFWS initiated a mapping effort to update suitable habitat maps for the four Northern California Forests (completed in 1998; Zabel et al. 2003).

APPENDIX 7 ALTERNATIVE BASELINES CONSIDERED

7.1.1 LOCAL HABITAT BASELINES

Many National Forests, BLM Districts, and National Parks within the Forest Plan area have local vegetation databases and habitat maps that have finer resolution and local accuracy than the Forest Plan baseline. Most local baselines were developed by individual administrative units and have not benefited from review outside of the land management agencies that developed the evaluation methods. These "local habitat baselines" are used to assess evaluating project-scale effects and to assist in analyses for Land and/or Resource Management Plan revisions (e.g., National Forests and BLM Districts).

7.1.2 THE CALIFORNIA BASELINE

Significant revisions to the California baseline have been proposed. The current baseline represents habitat largely defined using data collected in Oregon and thus excludes some vegetation types (e.g., smaller tree size classes) and does not consider some physical attributes (e.g., aspect) important for defining suitable Northern Spotted Owl habitat in northern California (Zabel et al. 2003). Northern Spotted Owls in the Klamath Province often utilize younger stands then in other provinces. Zabel et al. (2003) suggests that Northern Spotted Owl habitat selection differs from that observed in the northern portion of the range. Consequently, the Fish and Wildlife Service and the Pacific Southwest Region of the Forest Service recognized the need for a habitat baseline that more accurately reflected Northern Spotted Owl distribution in the Klamath Province for both management and regulatory purposes.

Zabel et al. (2002) refined the habitat baseline for the Northern Spotted Owl on Federal lands in California. Products of this effort included among other accomplishments, a new map of owl habitat for five National Forests in northern California. The California baseline effort applied a standardized approach across multiple administrative units in California, incorporated a high level of interagency participation, and underwent external peer review. The revised baseline has not been accepted as the Forest Plan baseline for that area by the Federal Agencies.

7.1.3 INTERAGENCY VEGETATION MAPPING PROJECT

The Interagency Vegetation Mapping Project is an effort by the Forest Service to develop maps of existing vegetation for the entire range of the Northern Spotted Owl using satellite imagery from Landsat Thematic Mapper. Field data from inventory plots and photo interpretation of plots, among other sources of ancillary data, are being used to develop regression models to predict vegetation characteristics from the Landsat data.

The expectation is that the resulting maps will provide a new baseline evaluation of Northern Spotted Owl habitat that was developed using a consistent approach across the entire range of the species. The Interagency Vegetation Mapping Project holds promise for providing improved information about Northern Spotted Owl habitat in the near future. It is anticipated that the project will be published within a year.

7.2 EVALUATION OF LOCAL BASELINES

The USFWS collected information on the relationship between the Forest Plan and local habitat baselines (USDI 2001; 2004). Local baselines are developed by individual administrative units and act as the basis for the evaluation of individual projects that are evaluated under section 7 consultations.

Across the range of the Northern Spotted Owl, these local habitat baselines contain approximately 374,000 acres more of Northern Spotted Owl habitat than estimated for the Forest Plan (7,059,489 acres versus 6,685,215 acres). Significant disparities exist between some local baselines and estimates of suitable habitat from the Forest Plan. The overall comparison of total habitat estimated by the local habitat baseline and the Forest Plan baseline obscures the wide variance in the deviation of each local habitat baseline from the Forest Plan baseline (Appendix 2 Table7). Concerning these difference the USFWS (USDI 2004:page number) stated:

> "Some administrative units have disproportionate influence on the outcome of the range-wide summary. For example, the local habitat baselines for eight administrative units show less habitat than estimated for the Forest Plan baseline. Taken together, lower baseline habitat estimates reported by these eight administrative units were lower than the Forest Plan baseline estimates by approximately 470,000 acres, with the Mount Baker Snoqualmie National Forest contributing about 172,000 acres (37 percent) to the overall difference. Twelve administrative units reported local baseline estimates that were greater that the Forest Plan baseline by a total of 844,000 acres, with the Wenatchee National Forest contributing 387,000 acres (46 percent) to the overall difference."

Since the USFWS depends on USFS for primary data, they cannot document the disparities

The USFWS offered a rationale for not using local baselines as a basis for regional comparisons. They make a logical argument that these local habitat baselines are unsuitable for broad-scale analyses due to several factors that limit the potential for aggregation in a range-wide summary. The procedures used to develop local habitat baselines varied with local information availability and needs, which in turn reflect administrative boundaries unrelated to biological differences. The same argument can be made for the Forest Plan baseline, however the Forest Plan baseline was designed to provide a regional perspective and with influence from the local baselines of the time. The specificity that is possible at the local scale may have little significance once effects are at the scale at which an understanding of a species' overall condition or status needs to be assessed because of averaging.

It is to be expected that local habitat definitions used by different administrative units also vary across the range of the owl (USDI 2004 Appendix 3). These differences may reflect biological differences in habitat use, however, methodological and subjective factors may also mask or exaggerate biological differences. Although some local baselines may have been subjected to rigorous validation, the procedures for validation have not been standardized. Thus, there is a large amount of variability among local baselines, which lowers our confidence in the information.

The Forest Plan baseline has remained constant while some local habitat baselines continue to evolve. As new technology has become available, local administrative units have continued to refine their estimates of suitable habitat. Unfortunately, changes in methods over time make it difficult to evaluate what habitat trends are due to differences in methods versus actual changes to habitat that have occurred. The USFWS notes (USDI 2004)

> "many of the local habitat baselines now in use across the range of the Northern Spotted Owl were developed after the Forest Plan baseline, shortening the time period that rates of change calculated using these baselines would represent. As seen with the revised California baseline, local habitat baselines generally have not been formally accepted at regional management levels of the land management agencies."

It is more effective to delineate suitable habitat at the local scale, because most local habitat baselines are developed using aerial photo interpretation. However, such photo interpretation may or may not have field verification. In theory, local baselines have the potential to increase site specificity and relation to the habitat that is actually being used by the owl (e.g., Klamath province habitat revision). However, in order for this to occur, a coordinated effort to understand the interface between local and provincial baselines must be undertaken. IVMP products have the potential to be validated on the local and provincial levels and will serve the need.

7.2.1 EVALUATION OF CALIFORNIA BASELINE

The USFWS recognized revisions to the California baseline, but cited several shortcomings on using the California Baseline as a reference condition. They determined that although the California baseline may be very useful for predicting owl presence or absence across the landscape (Zabel et al. 2003), it is not useful as a reference baseline condition against which to evaluate temporal and spatial changes in habitat range-wide.

The California baseline does not include suitable habitat on BLM lands in California and therefore does not provide a seamless habitat layer across all Forest Plan lands in California. Further, the California Baseline covers only a portion of the California range, which introduces discontinuity between similar habitat types in California and Southern Oregon. The California baseline was developed using different methods than those broadly applied across Oregon and Washington by not allowing a consistent reference point against which to evaluate changes in habitat conditions range-wide.

The California baseline was completed in 1999, and, therefore, only allows for examination of habitat trends over four years (1999-2003). Projects completed before 1999 may have been accounted for in the new baseline, but we were unable to discern if this were true. The difference in time frames between the California baseline and the Forest Plan baseline used in Oregon and Washington could make the California Baseline inconsistent given the nine years of forest change activities in Oregon and Washington. Lastly, the California baseline has yet to be adopted formally by the Forest Service as the revised habitat baseline for the Northern Spotted Owl in California.

APPENDIX 8 SUDDEN OAK DEATH

Prepared by J. F. Franklin

Sudden Oak Death (SOD) is a forest disease caused by the fungus-like pathogen, *Phytopthora ramorum* that was recently introduced from Europe. At the present time SOD is found in natural stands from Monterey to Humboldt Counties, California, and has reached epidemic proportions in oak and tanoak forests along approximately 300 km of the central and northern California coast (Rizzo et al. 2002a). It has also been found near Brookings, Oregon, killing tanoak and causing dieback of closely associated wild rhododendron and evergreen huckleberry (Goheen et al. 2002). It has been found in several different forest types and at elevations from sea level to over 800 m.

SOD is continuing to spread. Substantial transport of the pathogen within the Pacific Northwest and the North American continent has occurred as a result of the movement of infected nursery stock, the means by which it was originally introduced from Europe where it originated. Much of the following description of the organism and its effects comes from the web site of the California Oak Mortality Task Force (www.suddenoakdeath.org).

8.2 CHARACTERISTICS AND HOSTS OF SUDDEN OAK DEATH

SOD is currently known to infect a wide variety of herb, shrub, and tree species native to the Pacific Northwest in the form of trunk, twig and foliar infections (Rizzo et al. 2002b). Many species have exhibited only relatively benign foliar infections up to this point but tanoak (*Lithocarpus densiflorus*) and California black oak (*Quercus kelloggii*), among others, sustain lethal stem infections (Rizzo et al. 2002a). Species that are infected include: bigleaf maple (*Acer macrophylllum*), Pacific madrone (*Arbutus menziesii*), tanoak, Douglas-fir (Davidson 2002), Canyon live oak (*Quercus chrysolepis*), California black oak, Pacific rhododendron (*Rhododendron macrophyllum*) plus many other rhododendron and azalea species, wood rose (*Rosa gymnocarpa*), coast redwood (*Sequoia sempervirens*), western starflower (*Trientalis latifolia*), California bay laurel (*Umbellularia californica*), evergreen huckleberry (*Vaccinium ovatum*), grand fir (*Abies grandis*), California hazelnut (*Corylus cornuta*), salmonberry (*Rubus spectabilis*), cascara (*Rhamnus purshiana*), and poisonoak (*Rhus diversiloba*). Additional species are being added to the list nearly daily and may ultimately include many other plants native to forests occupied by Northern Spotted Owls since members of the Ericaceae, Rosaceae, Taxaceae, Taxodiaceae, and Pinaceae have all shown vulnerability.

SOD has caused widespread dieback of tanoak and several oak species in the central and northern coastal counties of California as a result of aggressive lethal bark infections (cankers) (Rizzo et al. 2002a). Tree death appears to occur when cankers expand in the trunk effectively girdling the tree and disrupting physiological function. Diseased trees are often attacked by other pest organisms, such as fungi that decay sapwood (*Hypoxylon thourasianum*) and bark beetles. In shrub species, symptoms can range from leaf spot to twig girdling, which do not necessarily result in the death of the plant.

Sudden Oak Death is so named because the whole crown of many affected trees appears to die rapidly with the foliage turning from a healthy green to brown over several weeks. The time from initiation infection to tree death may actually range from several months to several years. ***Tanoak appears to be the most susceptible species.*** All size classes from seedlings to large trees may be infected and killed (Rizzo et al. 2002a). A large number of opportunistic organisms are commonly observed on oak and tanoak trees and may hasten tree death. SOD infections also kill large trees of Canyon live oak and California black oak. SOD causes branch cankers and death of new shoots and small branches on Douglas-fir and coast redwood and death of sprouts of redwood; the long-term impacts of SOD on saplings and trees of Douglas-fir and coast redwood are unknown at this time. Death of Pacific madrone saplings has been observed and it is suspected that SOD can kill mature madrone trees.

Many of the species with foliar infections play a key role in spread of SOD by providing a reservoir of inoculum, which spreads aerially via wind-blown rain. Sporangia and chlamydospores are the most likely dispersal propagules and are generated on foliage. Two taxa known to provide massive foliar sources of inoculum are California bay laurel and rhododendron spp. (Davidson, Rizzo, and Garbelotto 2002).

APPENDIX 9 ANALYZING DATA ON BARRED OWL EFFECTS

Prepared by A. B. Franklin

Examples of Alternative Analyses evaluating the Effects of Barred Owl Presence on Trends in Territory Occupancy by Northern Spotted Owls in Redwood National Park (data from Appendix B in Schmidt 2003).

The purpose of this Appendix is to provide examples of 1) analyses that illustrate the problem in inferring that Barred Owls are replacing Spotted Owls (i.e., having a negative impact) when the inference is based solely on cumulative occupancy of sites, rather than annual occupancy, and 2) how different covariates can yield different results, and hence, provide different inferences.

We feel that more estimates (or inferences) should be based on *annual occupancy* (Figure 7A.1) because there may actually be a higher occupancy of the Spotted Owl territories than Barred Owl territories if Barred Owl territories are based almost solely on detections at night and not on roost and nest locations. We analyzed the data available to us from Schmidt (2003) where we had to assume that detectability was constant over time. This is a difficult assumption to meet so we present the analysis of these data as an example, rather than as a definitive analysis. Moreover, we do not know if these data are complete or if there are any other properties associated with the sampling design or field procedures that might also affect the results. A more appropriate analysis would use the occupancy estimators developed by MacKenzie et al (2003). ***A key point is that we are not trying to make inference from the data in Schmidt (2003) but are merely using it as an example***. Further, we consider the data in Appendix B of Schmidt (2003) to be proprietary to the biologists gathering this data, and thus feel it is their purview to fully explore the data they gathered post *Tanner (1999)* for future publication.

In our examples, there have been 36 Spotted Owl territories identified in Redwood National Park since 1993. Over the ten years from 1993-2002, 18 (50%) of these territories have had Barred Owl detected in them. The correlation of Barred Owl detections in Spotted Owl territories coupled with the apparent decline in the occupancy of these historic Spotted Owl territories could be improperly inferred as cause-and-effect. However, examination of the data on an annual basis (Table 7A.1), shows that only 6-20% of the territories have had Barred Owl detections in any given year, and some of these detections have been simultaneous with Spotted Owl detections in the same territory in the same year. In order to evaluate whether the decline in occupancy was related to Barred Owls we modeled the data from Appendix B of Schmidt (2003) using an information-theoretic approach.

Example 1. In the first example, we used annual number of Spotted Owl territories with Barred Owl detections as a covariate of Barred Owl presence (Table 9A.1). We then examined the trend in the proportion of Spotted Owl territories occupied each year using generalized linear models. We examined three time trends in the annual proportion of Spotted Owl territories occupied, a linear time trend (year), a log-linear time trend (lnyear), and a quadratic time trend (year*year). We also examined time trends using the Barred Owl covariate (BO) and no time trend (intercept). Thus, there were three hypotheses examined: 1) There was a time trend (either year, lnyear, or year*year models) in the annual proportion of territories occupied by Spotted Owls with no effects of Barred Owls, 2) the trend in annual proportion of territories occupied by Spotted Owls was due to Barred Owl presence in Spotted Owl territories (BO model), or 3) there was no discernible change in the annual proportion of territories occupied by Spotted Owls over time (intercept). Of the five models, the most parsimonious model was a log linear decline (Table 9A.2) which had the lowest AIC_c and more than 60 percent of the Akaike weight was attributable to that model. This model indicated that the annual number of occupied Spotted Owl territories was declining ($\hat{\beta}$ = -0.302, 95% CI = -0.381, -0.222) and explained 84.8% of the variation in Spotted Owl occupancy (Table 9A.2). The Barred Owl effect model had essentially no Akaike weight (i.e., provided no explanatory power for the decline), which indicated that Barred Owl detections in Spotted Owl territories did not explain the negative trend in Spotted Owl occupancy. Although negative, the Barred Owl effect was not different from zero, based on 95% confidence intervals ($\hat{\beta}$ = -0.0134. 95% CI = -0.0374, 0.0105). This model explained only 5.1% of the variation in the Spotted Owl occupancy data. These results do not mean that another Barred Owl covariate, such as number of Barred Owls in the park (regardless of whether they were in Spotted Owl territories) would have had better explanatory power. However, evaluating cumulative numbers of Barred Owls occupying Spotted Owl territories suggests an impact on Spotted Owls, whereas this analysis shows that Barred Owls were not a plausible explanation for the decline in occupancy of territories by Northern Spotted Owls.

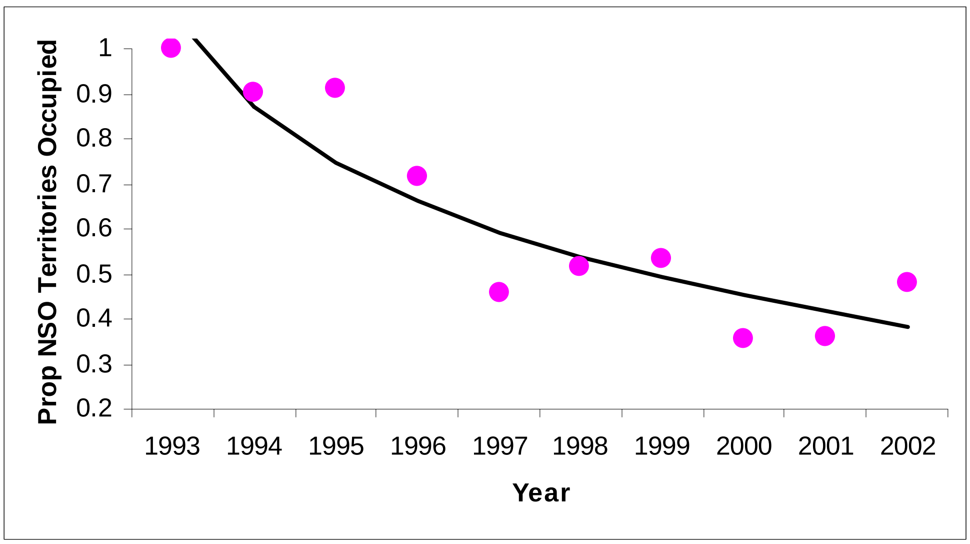

Figure 9A.1. Proportion of Northern Spotted Owl territories occupied annually. Solid line represents log-linear trend model {lnyear} selected based on minimum AICc.

Table 9A.1. Annual occupancy data from Redwood National Park used to analyze time trends and effects of Barred Owl detections on Spotted Owl occupancy (from Schmidt 2003 Appendix B).

Year	Prop. Territories occupied by Spotted Owls (OCC)	Prop. Spotted Owls with Barred Owl detections (BO)
1	1.000	0.222

2	0.903	0.065
3	0.909	0.121
4	0.714	0.057
5	0.457	0.086
6	0.514	0.114
7	0.533	0.133
8	0.355	0.194
9	0.361	0.194
10	0.481	0.222

Table 9A.2. Model selection results from analysis of proportion of territories occupied by Spotted Owls in Redwood National Park. The selected model {lnyear} based on minimum AICc is bolded

Model	-2log*L*	*K*	AIC	AICc	ΔAICc	Akaike Weight	R2
Year	-17.416	3	-11.416	-7.416	2.611	0.170	0.802
Lnyear	**-20.028**	**3**	**-14.028**	**-10.028**	**0.000**	**0.626**	**0.848**
$Year^2$	-23.780	4	-15.780	-7.780	2.248	0.204	0.895
BO	-1.738	3	4.262	8.262	18.290	0.000	0.051
Intercept	-1.211	2	2.790	4.503	14.531	0.000	0

Example 2. In evaluating Example 1, *S. Gremel* (*personal communication 2004*) suggested that a more appropriate covariate would be to categorize Spotted Owl sites as to whether they had ever had at least one Barred Owl detection during the period of data collection (BO+) and then to examine those sites separately from Spotted Owl territories that never had Barred Owl detections during the period of data collection (BO-). This response variable was the mean number of Spotted Owls surveyed per site for each year in the two different categories. Although Gremel also presented a re-analysis of these data through 2003, we present here a modified analysis that includes only 2002 to make it comparable with our Example 1. We also modified the analysis proposed by Gremel by using an analysis of covariance approach under the information-theoretic framework used in the first example. Although the covariate used cumulative information on Barred Owls in Spotted Owl sites, the analysis still examined annual rates rather than the cumulative number of sites affected over a given time period. The data used in this analysis are presented in Table 9A.3.

Table 9A.3. Mean number of Spotted Owls/surveyed site with (BO+) and without (BO-) Barred Owls on Redwood National Park from 1993-2002.

	Mean number of Spotted Owls/surveyed site	
Year	BO+	BO-
1993	2.00	1.57

1994	1.44	1.87
1995	1.40	1.85
1996	1.00	1.60
1997	0.60	1.00
1998	0.70	1.20
1999	0.75	0.86
2000	0.44	0.85
2001	0.43	0.80
2002	0.56	1.18

We examined five simple models, which were: 1) no time or Barred Owl effects (Intercept), 2) Barred Owl effects but no time trends (BO), 3) linear time effects but no Barred Owl effects (year), 4) a Barred Owl effect with a linear time effect that was the same for BO- and BO+ categories (BO+year; e.g., an additive effect of Barred Owls on time), and 5) a Barred Owl effect with a linear time effect that was different for BO- and BO+ categories (BO*year; e.g., and interaction between the Barred Owl effect and time). From this set of models, model {BO+year) was selected as the best model based on minimum AICc (Table 9A.4). This model had 76.3% of the Akaike weight, which was more than 3 times more likely than the next ranked model {year) with an Akaike weight of 21.9%. The selected model also explained 75.4% of the variation in the data (Table 7A.4).

Table 9A.4. Model selection results from analysis of Spotted Owl territories classified as having Barred Owl presences versus those where Barred Owls were absent in Redwood National Park. The selected model {year+BO} based on minimum AICc is bolded

Model	-2log*L*	*K*	AICc	ΔAICc	Akaike Weight	R2
Year	7.799	3	17.799	2.496	0.2189	0.624
BO+year	-0.697	4	15.303	0	0.763	0.754
BO*year	-2.247	5	22.753	7.45	0.018	0.772
BO	24.558	3	34.558	19.256	0	0.13
Intercept	27.349	2	33.063	17.76	0	0

Model {BO+year} had a negative time trend for both BO+ and BO- sites ($\hat{\beta}$ = -0.1318, 95% CI = -0.168, -0.096) and the detection of a Barred Owl in a Spotted Owl territory at least once during the study period appeared to have a negative effect on the mean number of Spotted Owls per site ($\hat{\beta}$ = -0.346, 95% CI = -0.554, -0.138) (Figure 7A.2).

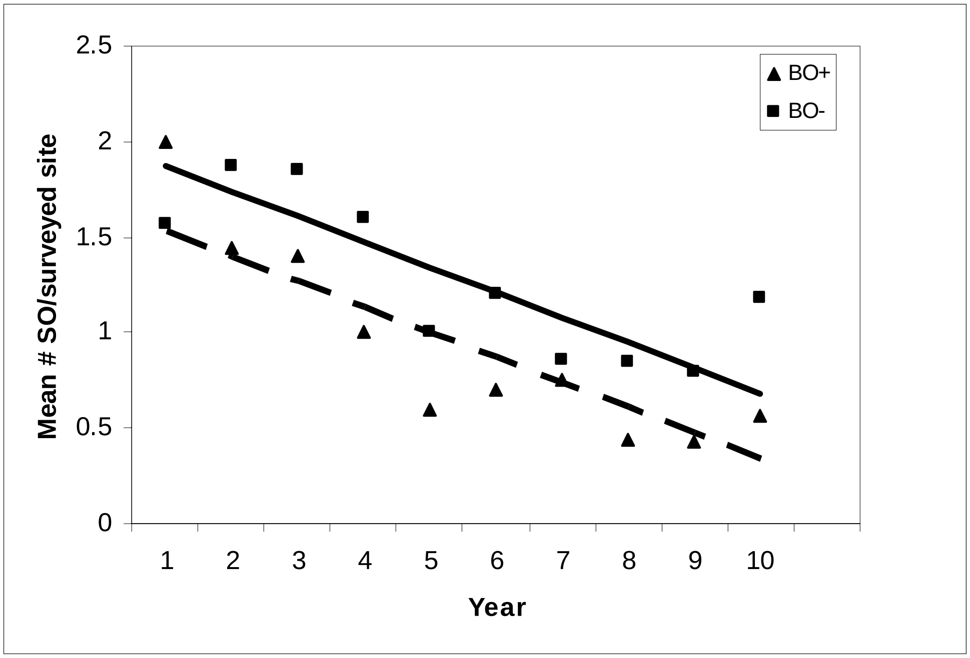

Figure 9A.2. Mean number of Northern Spotted Owls per site in sites where Barred Owls were detected at least once during the study period (BO+) and where Barred Owls were never detected (BO-). Solid and dashed lines represent trends from model {BO+year) for BO+ and BO- sites, respectively.

However, the presence of a Barred Owl effect in this analysis does not differentiate between the hypotheses that 1) Barred Owls are the effect or 2) BO+ sites were of lower habitat quality for Spotted Owls, which experienced inherently lower occupancy than BO- sites and that Barred Owls merely replaced Spotted Owls on the BO+ sites. A designed experiment would be needed to further differentiate between these two hypotheses (see Information Needs section). Thus, this example illustrates how a retrospective observational study could be used to set up a designed experiment, such as removing Barred Owls from the BO+ sites and seeing if the BO effect disappears.

Conclusions – In the two analyses presented here, we attempted to appropriately analyze the available data on an annual basis to illustrate why we think analyses of annual trends are more meaningful than cumulative trends. However, the major problem with these example analyses is that the data available to us were incomplete. At some future date, these data might be analyzed more completely by the owners of this data. Specific issues related to the basic problem include:

1 *Lack of information to quantify detectability* – Both analyses assume either complete detectability or constant detectability over time for both Barred and Spotted Owls. These assumptions are rarely met in wildlife population studies. The use of occupancy estimators that also account for detectability (e.g., MacKenzie et al. 2003) would be more appropriate for these data but require the within-year survey information, which was unavailable to us. Recent occupancy estimators allow for inclusion of two species (D. Mackenzie (personal communication), which would be ideal for examining the effects of Barred Owls on Spotted Owl territory occupancy.

2 *Lack of sampling variance* – Inclusion of annual sampling variances in the analyses would affect the estimates of effects and their standard errors. In the two examples, we ignored the presence of sampling variance, the inclusion of which will probably affect the ranking of the models and their estimates.

Although no inferences can be made from our two examples, two important lessons can be learned from this exercise:

1. We feel it is very important to be cautious about inferences derived from analysis using cumulative to assess population size and trends in Barred Owls and, more importantly, their effect on Spotted Owls. In retrospective analyses of the effects of Barred Owls on Spotted Owls, we believe more emphasis should be placed on annual trends rather than the cumulative numbers of sites where Barred Owls are detected.

2. Covariates used to estimate the effect of Barred Owls on Spotted Owls should be chosen with care and, ideally, should be developed with a consensus among scientists (e.g., see Anderson et al. 1999). In our two examples, different results may have been largely due to differences in the covariate used. A forum similar to the recent Spotted Owl meta-analysis would be an appropriate venue for determining the appropriate direction to take across a number of Spotted Owl studies that have relevant data on Barred Owls.

APPENDIX 10 DEVELOPING RECOVERY STRATEGIES FOR NORTHERN SPOTTED OWL POPULATIONS

By B. R. Noon

Commissioned by SEI for Northern Spotted Owl Status Review

Assessment of status and trends in population size, survival rates, and reproduction are succinctly summarized by time-specific estimates of λ_t, the finite rate of population change. Such assessments are typically retrospective—that is, they estimate how these parameters have changed from the initiation of a demographic study to the time of assessment. A description of what has occurred in the population is summarized by the time series of parameter estimates. Projections to the future status of the population are either not made or done very cautiously when evidence for temporal trends have been found.

Equally valuable are prospective analyses that project how various demographic rates are likely to change in the future under plausible land-use and environmental conditions. These analyses are inescapably less certain than retrospective analyses because the future is never known until it arrives. However, the endangered species evaluation and recovery process is inherently a type of risk assessment and thus requires prospective analyses (NRC 1995, Goodman 2002, Ralls et al. 2002). To develop a recovery plan strategy requires one to project the future consequences on the listed species of alternative management practices and conservation actions. Such evaluations logically fall until the broad category of population viability analysis (PVA) in that they project changes in population status given specific changes in one or more environmental variables. PVAs have traditionally focused on estimates of persistence likelihoods or times to extinction (e.g., Foley 1994). However, it is important to view PVA in a much broader context—that is, as an analytical tool to evaluate how resource management can change parameters influencing the probability of spotted owl persistence (Boyce 1992, Noon et al. 1999, Shaffer et al. 2002).

The critical parameter estimates required for informative PVAs have been thoroughly discussed by Boyce (1992), Noon et al. (1999), and White (2000). As discussed in the current assessment, reliable parameter estimates are available for most northern spotted owl populations and PVAs are justified given important caveats. Most important is that any population projections incorporate those factors that drive variation in birth and survival rates and include factors amenable to management intervention. Since causal relationships are still poorly known, future conservation actions should be conducted as large-scale manipulative experiments (Noon and Franklin 2002).

The history of demographic studies of northern spotted owl populations has been a combination of retrospective and prospective analyses. The emphasis in previous assessments has been on population dynamics with a particular focus on the estimation of λ. In all previous assessments, the owl researchers have taken great care to point out that estimates of λ are specific to the time and place in which they are estimated. Therefore, projections of λ (or its components) require an assumption of similar future conditions or a mechanistic understanding, or set of hypotheses, about future environmental conditions.

A Brief Historical Review

Initial assessments of the status of northern spotted owl populations used a hypothesis testing framework (Thomas et al. 1990, Murphy and Noon 1992). Three hypotheses were tested: 1) the finite rate of change (λ) is ≥ 1.0, 2) owls do not differentiate among habitats on the basis of forest age, structure, or composition, and 3) no decline has occurred in the areal extent of habitat types selected by owls.

Following an eigenanlysis of the stage projection matrix, the first null hypothesis was originally rejected based on the observation that λ was < 1.0 from two demographic study areas (Thomas et al. 1990). A 1995 reanalysis of demographic data from 11 study areas resulted in a more convincing rejection of this hypothesis (Burnham et al. 1996). At the time of this reanalysis, however, concerns were being expressed that estimates of λ may be biased low because of an underestimate of juvenile survival rate (Bart 1995).

The second null hypothesis addressed the question of whether the owl uses the forested landscape in the Pacific Northwest in a non-random fashion. At the time of listing, all of the northern spotted owl habitat studies concluded that owls select old forests, or younger forest that have retained characteristics of old forests, for nesting and roosting. Many studies published since the listing decision provide additional falsification of hypothesis 2. These studies were reviewed as part of the Northwest Forest Plan (NWFP) process (FEMAT 1993) and updated by Noon and McKelvey (1996).

The rejection of hypothesis 2 leads logically to a test of hypothesis 3. Based on data from National Forest lands in Oregon and Washington, Thomas et al. (1990) found significant declines since 1940 in the extent of owl habitat, a trend that was projected to continue into the future (Murphy and Noon 1992). Additional data since 1990 provided evidence of declines in California (McKelvey and Johnston 1992) and more regionally specific estimates of decline were reported in the draft Northern Spotted Owl Recovery Plan (USDI 1992).

Rejection of the three fundamental hypotheses listed above were fundamental to the listing of the northern spotted owl listing under the Endangered Species Act and of the initial development of the Northwest Forest Plan (FEMAT 1993). Landscape allocations adopted by the NWFP was based on an algorithm that focused on the location, size, shape, spacing, and context of current and regenerating late-successional forest patches planned for inclusion in a spotted owl reserve system. The goal of the design was to establish locally stable owl populations, widely distributed throughout their historic range. Even though suitable habitat was projected to decline outside of the reserves for several decades (FEMAT 1993), habitat loss within the reserves was projected to stop and the process of renewal to begin.

Role of Models. Models often serve as useful tools for prospective analyses because they are a means to project potential outcomes of alternative future states of the environment. In this context, models played a significant role in the development of the current conservation strategy for the northern spotted owl.

Model development and analyses progressed from simple to complex as more information became available. Initial analyses, focused on the Leslie projection matrix, explored life history sensitivities of spotted owls. Based on eigenanalysis methods, adult female survival was identified as the key demographic rate that most influences population growth (Lande 1988, Noon and Biles 1990). This insight contributed to the design of the current monitoring studies and led to an emphasis on obtaining precise and unbiased estimate of adult survival rates by using modern capture-recapture methods (Franklin et al. 1996).

An important area of uncertainty following rejection of the three hypotheses was the projected response of owl populations to continuing declines and fragmentation of suitable habitat. In this regard, a simple model developed by Lande (1987) for territorial species with obligate juvenile dispersal—the case for spotted owls—was deemed particularly relevant. This model predicted sharp, non-linear persistence thresholds as habitat was lost and fragmented. A variant of Lande's model, parameterized specifically for Northern Spotted Owls, suggested that an extinction threshold was being approached in the Pacific Northwest (Lamberson et al. 1992). The extinction threshold was attributable to two factors—the lost and fragmentation of habitat and the difficulty of a dispersing owl in finding suitable habitat and a mate.

Because the existing conservation literature and biogeographic principles were too broad for specific application, models were also used to refine the reserve design principles of the NWFP (Lamberson et al. 1994). These models suggested that persistence likelihood (as measured by the occupancy rate of territories) asymptotically increased as individual patch size increased to ~ 20 breeding pairs of owls. In addition, occupancy rates remained high if distances between patches were within 19 km of each other (intersecting the dispersal range of the majority of dispersing owls) and patch density was high. The models of Lamberson et al. (1992, 1994) could be considered a type of PVA since territory occupancy rates were a direct proxy variable for persistence likelihood. Collectively, these models suggested that long-term persistence required ~ 20% of the forested landscape to be maintained as suitable habitat with habitat arranged in patches of ≥ 20 pairs of owls connected by dispersal.

These initial models contributed significantly to the design of the NWFP. In retrospect, however, it was clear that these models were overly simplistic and based on several optimistic assumptions. These included no environmental stochasticity, optimal reserve shape (circular), no loss to sink habitats, and forest matrix conducive to dispersal, and 100% suitable habitat within reserves.

Even though the initial models of Lamberson et al. (1992, 1994) provided a plausible set of rules controlling the size and spacing of reserves, the actual landscape was highly constrained by geography, past land-use practices, and land ownership. Therefore, during the early stages of development of the NWFP work began on a new owl model designed to directly incorporate "real" habitat maps through a GIS interface. This model, a habitat-based population dynamics model, was spatially explicit, dynamic (it modeled landscape change and owl dispersal), and allowed investigation of the effects of individual heterogeneity (based on life stage and habitat quality) on owl population dynamics (McKelvey et al. 1993, Noon and McKelvey 1996).

The McKelvey model is initialized by intersecting the forested landscape with a hexagonal grid with cell size approximating the median size of an owl home range. Expected birth and survival rates at the scale of an individual cell are related to habitat attributes by a series of regression equations (e.g., Bart 1995). (Based on multiple studies, the amount of mature forest > 120 years old proved to be the strongest predictor variable). These functions provide initial estimates of the demographic rates for the current landscape. When the model is combined with timber harvest schedules, post-harvest recovery rates, and habitat quality functions it is possible to compare competing land management plans in terms of owl viability.

After the FEMAT team had defined the various land management options it was considering for adoption, the McKelvey model was used to evaluate several alternatives including one proposed by the FWS Recovery Plan. Given identical rules concerning initial habitat conditions and assuming no regrowth of owl habitat over the evaluation interval, the options diverged greatly in terms of both the expected number of owls and their distribution across the landscape (Noon and McKelvey 1996). In the end an option was selected that represented a compromise between maximizing owl viability, the viability of other species of concern, and competing economic interests.

Subsequent modeling efforts (Akcakaya and Raphael 1998, Hof and Raphael 1997) have not added greatly to our understanding of the factors putting spotted owls at risk or how to diminish those risks. In general, models of differing structure and invoking various assumptions have been consistent in recommending sizeable patches of habitat to support largely self-sustaining local populations connected by frequent dispersal events. In addition, there needs to be substantial redundancy (i.e., many large patches widely distributed throughout the range of the owl) because of strong spatial autocorrelation in the climatic events that affect northern spotted owl populations.

Perspectives on the Current Status and Trend

It is insightful to consider the current status and trend assessment in terms of the original three null hypotheses. Available data clearly indicate that hypotheses one and two would still be rejected. The current status review confirms that most owl populations are still in decline. In addition, habitat studies published since the review of Noon and McKelvey (1996) continue to demonstrate the association of owl nesting and roosting with late-successional forests (e.g., Franklin et al. 2000, Thome et al. 1999, Meyer et al. 1998, Ward et al. 1998). The decision on hypothesis three is less clear than in 1990. Since enactment of the NWFP, timber harvest rates on federal public lands have declined substantially with rates of harvest since 1994 averaging < 1% per year. Harvest rates on private and state lands within the range of the northern spotted owl are poorly known but it is probably safe to assume that they are greater than on federal public lands. In addition, suitable owl habitat has been loss since 1990 as a consequence of large, stand-replacing fire events (Chapter 6 of this review).

In summary, based on current population trends and habitat conditions it appears that the conditions that led the FWS to list the spotted owl as threatened in 1990 are still relevant today.

What are the expected population trends of spotted owls approximately a decade after enactment of the NWFP? Thomas et al. (1990) argued that population trend should stabilize at a lower equilibrium size sometime within the next 100 years. During the interim there was an expectation that the rate of decline would slowly decrease as habitat loss was arrested and new habitat regenerated in the habitat conservation areas. Two critical assumptions of Thomas et al. (1990) were that a case of no-net-loss of suitable habitat would be achieved prior to crossing an extinction threshold and that the conservation areas would eventually be fully occupied by owls (Murphy and Noon 1992). Current data on habitat trends suggest that the first assumption is approximately true on federal public lands. The second is probably false because of mixed ownership of many designated reserves and because of natural disturbance events.

It is possible that we are observing the transient dynamics of populations that are in the process of recovery but this is highly uncertain. Unfortunately, the most recent meta-analysis (Anthony et al. 2004) does not allow one to discriminate between the two key, opposing hypotheses—that is, 1) owl populations are slowly declining to a new, positive equilibrium, versus 2) owl populations have crossed a threshold and are slowly declining to extinction.

Future Strategy

As stated previously, recovery planning under the Endangered Species Act requires some sort of PVA to evaluate the likely outcomes associated with alternative conservation strategies (NRC 1995). To be beneficial, any viability modeling should be based on time horizons of a few decades (Goldwasser et al. 2000) and to the extent possible closely follow the guidelines proposed by White (2000): 1) be based on a realistic population model, or set of competing models, incorporating unbiased parameter estimates, 2) include spatial variation among local populations, 3) compute the distribution of persistence likelihoods based solely on estimates of the process variation (demographic and temporal) in demographic rates, and 4) incorporate individual heterogeneity in the demographic rates. In addition, a useful PVA for the purposes of recovery planning must include functions that relate the expected value of demographic rates (i.e., birth and survival) to key environmental drivers such as specific habitat elements, landscape patterns, and climatic variables (e.g., Franklin et al. 2000).

To initiate conservations action to accelerate the recovery of northern spotted owl populations requires a mechanistic understanding of the factors that affect λ. For the most part, these factors are poorly known (Noon and Franklin 2002). In addition, there is the strong possibility that the controlling factors vary among geographic locations. An appropriate framework for advancing understanding is to synthesize existing knowledge of plausible causal relationships in the form of predictive models. Inclusion of environmental drivers can be viewed as a multiple regression function in which the dependent variable is λ (or a given demographic rate) and the independent variables are various environmental factors. Independent variables can have positive or negative effects with effect size given by their regression coefficient. Disagreement over the factors to include in the model, or the size of the coefficients, can be viewed as competing models. In addition to the usual sources of uncertainty which accompany stochastic modeling, the inclusion of causal functions is accompanied by added uncertainty because: 1) the true relationship between environmental factors and the expected value of demographic rates may be poorly known (Noon and Franklin 2002), 2) the future value of the environmental factors is unknown, and 3) population outcomes associated with changes in multiple environmental factors are complex.

Because of numerous sources of uncertainty, the recovery planning process should be viewed in an active adaptive management context (sensu Walters 1986). The process is termed ‘active’ because the system is actively perturbed via experimentation (Walters and Holling 1990). Uncertainty or disagreement over what environmental variables are most relevant to future changes in spotted owl demographic rates would be addressed in the form of competing viability models. These models would make differing predictions over how owl populations would respond to changes in these variables. The degree of fit between prediction and observation would be used to discriminate among competing models and to update model structure and parameter estimates.

A test of competing recovery strategies could be implemented in the context of the current owl monitoring program. This would require the conduct of large-scale manipulative experiments across the different monitoring sites with a different set of variables changed at different sites in order to bracket the range of uncertainty or disagreement in different causal models. Also, it will be important to vary the types of conservation action taken because the factors limiting owl populations probably vary geographically. Continued monitoring of the local populations would be required in order to discriminate among competing models and to converge on what management actions are most likely to lead to owl recovery.

The scale of manipulation could focus on the individual territory or a subset of the study population. For reliable inference from the manipulations it is important that the essential elements of an experiment—randomization, replication, and control and treatment sites—be incorporated into the study design. Given the longevity of spotted owls and the possibility of lag effects, such experiments would need to be carried on over several years.

Examples of environmental factors under control of managers include manipulations of barred owl populations, use of small-diameter thinnings in late seral reserves to reduce fuel loads, closing and restoration of roads in areas of high owl density, supplemental feeding experiments, and total restriction on the harvest of large diameter trees. Based on existing understandings of plausible causal relationships, a priori predictions as to how these changes would affect the components of λ could be made and tested in the context of the existing monitoring program. To make progress in the recovery of owl populations, such large-scale manipulative experiments, conducted to reduce uncertainty over caused-effect relationships, need to be implemented.

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