Animal Conservation

Animal Conservation. Print ISSN 1367-9430

Preserving genetic diversity in threatened species reintroductions: how many individuals should be released?

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Keywords
allele frequency; genetic diversity; *Mohoua ochrocephala*; reintroduction; release number; translocation.

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Editor: Karen Mock
Associate Editor: Karen Mock

Received 27 May 2010; accepted 18 January 2011

doi:10.1111/j.1469-1795.2011.00448.x

Abstract

Reintroduction guidelines recommend that 'adequate' numbers of individuals be released to minimize loss of genetic diversity, but these numbers are rarely quantified. We present a framework for assessing the number of individuals required for an island reintroduction that takes account of allele loss both during the founding event and in the following establishment phase with a low population size. This is the first attempt to model release numbers for reintroductions in order to preserve alleles with a specified initial frequency, while taking post-release mortality rates, population growth rates and site carrying capacity into account. Probability of allele retention was sensitive to both release number and post-release demography. The rate of allele loss was strongly influenced by both environmental stochasticity and delayed population growth but was little affected by increasing the annual turnover rate of the breeding population. We illustrate the model's application using parameter estimates from a threatened New Zealand passerine, the mohua *Mohoua ochrocephala*, for which reintroduction is a common management tool. Our modelling indicates that when population growth is moderate ($\lambda = 1.3$), *c*. 60 individuals would need to be released to achieve at least 95% certainty that alleles at an initial frequency of 0.05 would be retained after 20 years (five overlapping generations), which is double the number typically released in translocations of mohua and other threatened forest passerines in New Zealand.

Introduction

The World Conservation Union (IUCN) recognizes the need to conserve genetic diversity as one of three global conservation priorities (McNeely *et al*., 1990). Populations with high levels of genetic diversity should be more likely to adapt to changes in habitat, climate or pathogens (Frankham, 2005). Perhaps nowhere is this more important than in translocated or reintroduced populations (Sarrazin & Barbault, 1996; Stockwell, Mulvey & Vinyard, 1996).

The goal of a reintroduction is to establish a viable, free-ranging population in the wild within the species' former natural habitat and range (IUCN, 1998). Reintroductions are becoming increasingly important in the management of threatened species (Seddon, Armstrong & Maloney, 2007), with the literature focusing mainly on factors affecting population establishment (i.e. population growth beyond the size at which transient factors associated with translocation may lead to extinction) which can take up to tens of years (Griffith *et al*., 1989; Fischer & Lindenmayer, 2000). Although population establishment is essential for successful reintroductions, recovery programs should also aim to maximize the chances of long-term persistence, which requires the maintenance of high levels of genetic diversity (Frankham, Ballou & Briscoe, 2002; Allendorf & Luikart, 2007; Armstrong & Seddon, 2008).

When small numbers of individuals are reintroduced to an isolated area such as an island, the new population is unlikely to be representative of the source population's gene pool and will generally have lower genetic diversity (e.g. Stockwell *et al*., 1996; Tarr, Conant & Fleischer, 1998; Mock, Latch & Rhodes, 2004). Typically, only a portion of the released individuals survives to breed and contribute genetically to the next generation (Jamieson, 2011). The smaller the founding population size, the greater the initial deviation will be from the source population (founder effect). Genetic diversity is further reduced through genetic drift in subsequent generations when alleles are lost due to chance, especially if the population remains small or grows slowly (Frankham *et al*., 2002; Allendorf & Luikart, 2007).

There are three main ways in which loss of genetic diversity can be managed: (1) source founders from genetically diverse populations; (2) choose reintroduction sites with large carrying capacities; (3) release large numbers of founders (Allendorf & Luikart, 2007). Unfortunately, managers may not have prior knowledge of the genetic status of the source population and their choice of release sites could be limited, but they do tend to have control over the number of individuals caught and released. Although 'more is

usually better', managers would prefer to translocate the minimum number necessary to maintain genetic variability because of financial and logistic constraints. IUCN (1998) guidelines recommend that the release should be modelled under various sets of conditions, in order to specify the number and composition of individuals to be released. Studies have modelled the demographic and genetic consequences of varying sex and age composition of release groups with respect to detrimental effects of inbreeding depression (e.g. Sarrazin & Legendre, 2000; Robert *et al.*, 2004; Robert, Couvet & Sarrazin, 2007), but there are surprisingly no general rules available for calculating release numbers for preserving genetic diversity.

Zoo biologists recommend that 20 genetic founders (i.e. the subset of original founding stock that contribute genes in the form of independent offspring to the new population) are adequate for establishing a captive stock of endangered species, as these should contain 97.5% of the genetic variability as measured by heterozygosity or gene diversity present in a wild population (Foose *et al.*, 1986; Lacy, 1989; Willis & Wiese, 1993). However, guidelines for establishing captive breeding stocks are not directly transferable to reintroductions in the wild for three reasons. First, they focus on heterozygosity as a measure of genetic diversity, but little heterozygosity is expected to be lost even during severe bottlenecks if these are of short duration (Allendorf, 1986). Loss of alleles is a more appropriate measure of genetic diversity when considering long-term effects, because loss of allelic diversity will have significant effects on future adaptability and survival of species in the wild (Allendorf & Luikart, 2007). Second, reintroduced animals in the wild will often suffer higher mortality immediately after release (Armstrong *et al.*, 1999; Fischer & Lindenmayer, 2000), compared with those transferred to the more benign zoo or captive breeding environment. On the other hand, the ultimate size of reintroduced wild populations potentially exceeds the size of captive populations, assuming the agent of decline is absent or being managed. Finally, the common practice of managing pairings to equalize founder representation in captive populations, to minimize loss of genetic diversity (Lacy, 1989), would be difficult to implement in most wild populations.

The above arguments suggest the need for a new approach for deciding on the number of individuals to release in reintroductions to retain alleles of specified frequency through the colonization phase, beyond which increased effort in capturing and releasing more individuals provides only marginal gains in genetic diversity (i.e. a curve of diminishing returns). Here, we develop a relatively simple framework and apply it to mohua or yellowhead *Mohoua ochrocephala*, a threatened New Zealand forest passerine that is commonly translocated to offshore island refuges where exotic predators (rats and mustelids) are absent. Our approach is to model genetic drift in reintroduced populations by simulating the probabilities of retaining genetic diversity (allele retention) during and after reintroductions with varying numbers of released individuals. We consider scenarios in which the following parameters vary: allele frequency in the source population, initial survival rate after reintroduction, population growth rate and carrying capacity. We perform additional simulations to assess the effects of environmental stochasticity, delayed establishment and increased turnover in the breeding population on allele retention. Finally, we discuss the management implications of these models for mohua and other species facing potential translocations and reintroductions.

Methods

In order to model the number of released individuals needed to retain genetic diversity in reintroduced populations, we estimated the probability of preserving an allele of a given frequency over a period of 20 years after the reintroduction of different numbers of individuals. We developed a stochastic model in R (R Development Core Team, 2008) to simulate the loss of an allele during and after a bottleneck. The model and guidelines on how to run it are available as an online resource (see supporting information). Parameters are chosen to closely reflect the situation for mohua, although similar models could be developed for species with life-history characteristics that differ substantially from mohua (see 'Discussion'). We simulated the founding event or bottleneck by first selecting a given number of founders from a large source population. This source population segregated variation at a single bi-allelic locus, and was assumed to have an even sex ratio. The probability of retaining the allele in the initial founding event (P) was given by the equation:

$$P = 1 - (1 - q)^{2N_f} \quad (1)$$

where q is the allele frequency and N_f is number of genetic founders (Allendorf & Luikart, 2007). The program then simulated loss of the allele due to genetic drift as the population grew, assuming no mutation, migration or selection. We chose a 20-year timeframe because this is a plausible 'establishment' period for mohua to reach carrying capacity, given the model parameters. Twenty years represents approximately five generations based on an average adult life expectancy of 4 years at sites without introduced predators (G. Elliott, pers. comm.). The simulation was accomplished by randomly pairing adults, assuming monogamous mating and retaining of mates until widowed. New pairs were randomly chosen from the pool of available mates, which included new recruits (offspring from previous season) and widowed breeders, allowing overlap in generations. Adult survival rate from year to year was specified. Average growth rate was specified by the nominal finite rate of increase (λ). The average number of recruits per pair was varied to provide the required growth rate, given the adult survival rate. Recruitment was truncated when the population reached carrying capacity. Carrying capacity can be specified as the number of total individuals or the number of breeding pairs. We selected the latter because in mohua maturing individuals can become non-breeding helpers once territories have filled the available habitat (Elliott, 1990).

Stochasticity was allowed in sex ratio, number of recruits per pair and adult survival. We performed additional simulations to assess the effects on allele retention of environmental stochasticity, increased turnover in the breeding population (while keeping population growth rate constant) and delayed establishment (see 'Results'). The main parameters used for simulations are discussed in turn.

Initial allele frequency (q_0)

We simulated the probability of losing alleles with initial frequencies in the source population of 0.02, 0.05, 0.1 and 0.2. We henceforth refer to the first two allele frequencies as 'rare' and 'moderately rare', respectively.

Number of individuals released

We simulated allele retention over time with 15, 30, 45, 60, 75, 90, 105 and 120 individuals released. Previous reintroductions of mohua usually aimed to translocate 30 individuals, but a range of 6–75 has been recorded (C. O'Donnell, pers. comm.).

Number of individuals released versus genetically contributing founders

In most cases only the number of individuals released is known and recorded even though a significant portion of these may die before producing offspring and contributing to the founding gene pool. Our model assumed that 80% of the released mohua survive, estimated from a previous mohua reintroduction (Oppel & Beaven, 2004), although lower survival rates during reintroductions are known (Taylor, Jamieson & Armstrong, 2005).

Annual survival rate

A previous study of mohua on the mainland estimated adult survival at 73–80% in years with low predator numbers (Elliott, 1996). For island reintroductions where introduced predators are absent, we have chosen an individual year-to-year survival rate of 80%.

Finite rate of increase (λ)

To take into account the initially positive growth rates typical of reintroduced avian populations (Taylor *et al.*, 2005), we considered high ($\lambda = 1.8$), medium ($\lambda = 1.3$) and low ($\lambda = 1.1$) growth rates in our models. These values also fell between the population growth rates for two reintroduced mohua populations for which we have data (Tracy, 2009). Stochasticity in the model caused the long-term growth rate to fall slightly below the specified λ (Lande, Engen & Saether, 2003). Environmental stochasticity was modelled separately by varying λ between years according to a lognormal distribution with mean (λ) = 1.3 and two levels of variability in population growth rate [expressed as the coefficient of variation (CV) of λ] of 0.2 and 0.4. Variation was applied equally to the components of λ (annual survival and recruitment), except that when survival reached 1.0 recruitment was increased relatively more to achieve the required value for λ.

Carrying capacity (K)

We simulated the probability of allele retention in island populations with two different carrying capacities (100 and 150 breeding pairs) based on estimates for mohua provided by the Department of Conservation (H. Edmonds, pers. comm.).

Recruitment age

Mohua typically do not breed until their second year, although first-year breeding may occur more frequently when populations are at low density (Elliott, 1990). We simulated breeding at age one or two and found an allele retention probability difference between the two scenarios of <0.013 with overlapping confidence limits. Therefore in further simulations we considered only the scenario that allowed breeding from age one.

Extinction

Due to stochasticity in the model, it may happen that all individuals are of the same sex, leading to population extinction. All runs in which extinction occurred were counted as 'allele not retained'.

For each scenario we conducted 1000 replicate simulations. We report the proportion of simulations in which the allele was retained, with 95% binomial confidence limits.

Results

We modelled loss of alleles over 20 years after a bottleneck with varying number of individuals released. As expected, the probability of retaining alleles increased with the number of individuals released, both in the first generation of reintroduction and after 20 years, and the effect of release number was especially marked for rare alleles (Fig. 1). For example, when the growth rate was slow ($\lambda = 1.1$) and 30 individuals were released the probability of retaining a rare allele was only 0.29 when $q_0 = 0.02$ and 0.51 when $q_0 = 0.05$ (95% confidence intervals around this and the other probability estimates were $< \pm 3\%$; see Fig. 1). Releasing 60 individuals increased the probability of retaining a rare allele to 0.48 when $q_0 = 0.02$ and 0.82 when $q_0 = 0.05$, and releasing 120 individuals increased the probability to 0.74 and 0.97, respectively. Therefore, with a slow growth rate ($\lambda = 1.1$), *c.* 105 individuals would need to be released to achieve 95% certainty that alleles at initial frequency of 0.05 would be retained after 20 years (Fig. 1a).

The model above is sensitive not only to the number of individuals released, but also to the growth rate of the population. With a moderate growth rate of $\lambda = 1.3$, the release of 60 individuals gives a 95% certainty that an allele at an initial frequency 0.05 would be retained after 20 years (Fig. 1b). When growth rate is as high as $\lambda = 1.8$ (Fig. 1c), then the probability of retention after 20 years is similar to

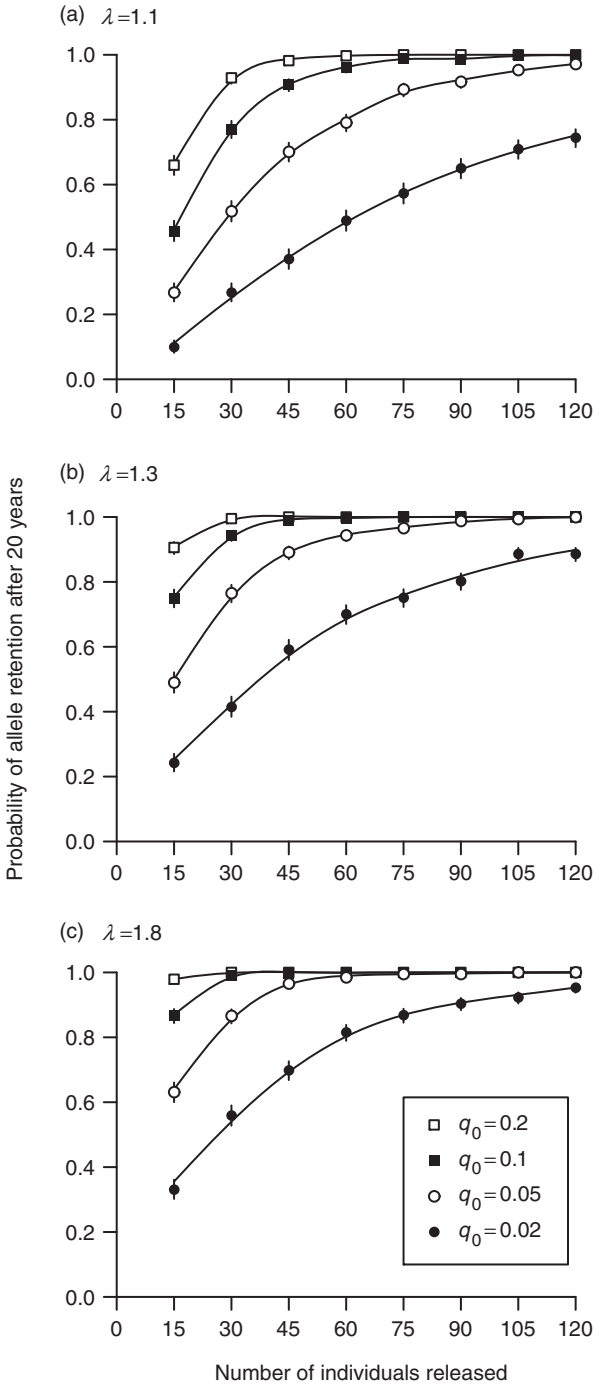

Figure 1 Probability of an allele being retained after 20 years based on 1000 replicates with initial allele frequencies (q_0) of 0.20, 0.10, 0.05 and 0.02 for (a) λ=1.1, (b) λ=1.3 and (c) λ=1.8. Bars indicate 95% confidence limits.

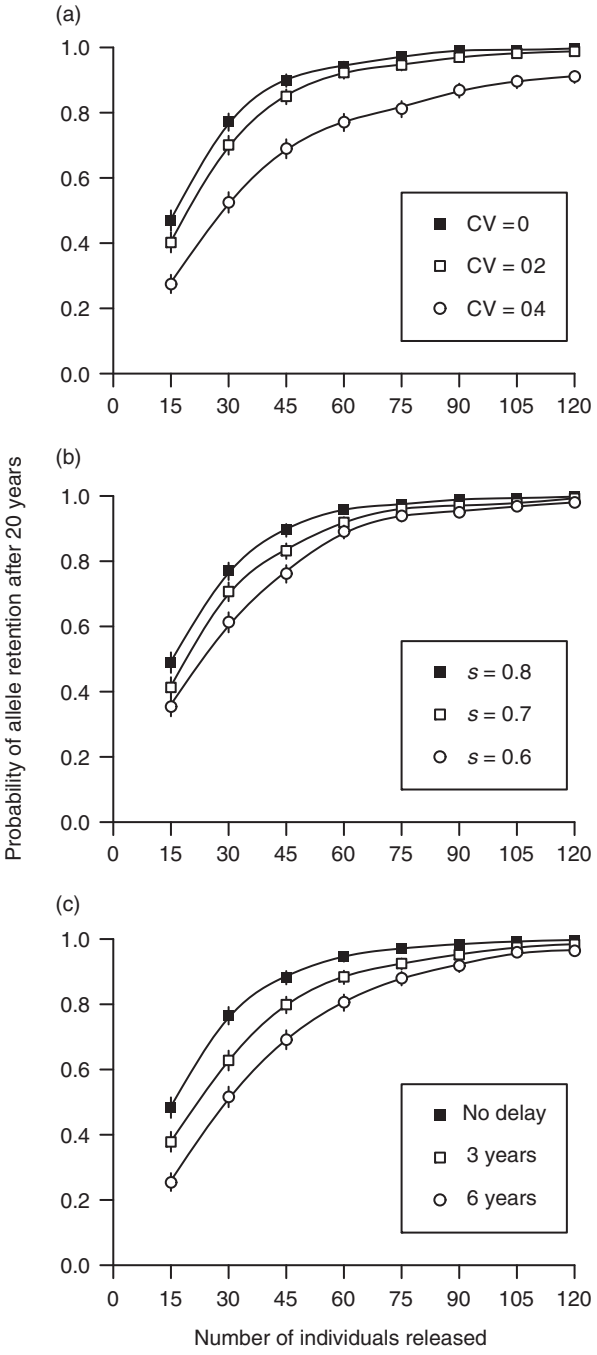

Figure 2 Predicted effect of additional variation on allele retention. (a) Variability in population growth rate, expressed as the coefficient of variation (CV) of λ, (b) increased turnover of adult breeders, expressed as reduced annual survival (s), and (c) delayed population growth after introduction. Initial allele frequency q_0=0.05 and mean λ=1.3 for all simulations. Bars indicate 95% confidence limits.

that predicted for the first generation of a bottleneck [equation (1)]. Changing K from 150 to 100 breeding pairs had minimal effect on the final outcome of allele retention after 20 years, as most of the loss occurred in the first few generations (L. Tracy unpubl. data).

Environmental stochasticity was modelled by varying λ between years according to a lognormal distribution with

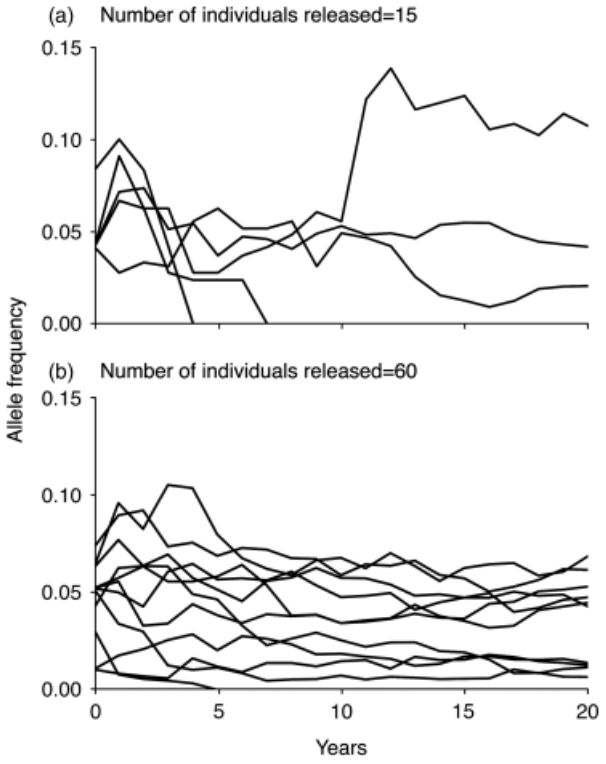

Figure 3 Examples of allele frequencies during 10 simulations over 20 years when the initial allele frequency was 0.05 and the number of individuals released equalled (a) 15 and (b) 60. Note that in (a), the allele was not present in founding individuals in five out of 10 replicates (refer to equation (1) of 'Methods').

mean = 1.3 and two levels of CV (λ) (0.2, 0.4). Population turnover was increased by reducing annual survival while increasing recruitment to maintain constant $\lambda = 1.3$. The possibility that the introduced population began to increase only after a time lag, and therefore experienced a protracted bottleneck, was simulated by imposing an initial period of stasis ($\lambda = 1.0$) for 3 or 6 years. The results of these separate variations on the base scenario are shown in Fig. 2. Environmental stochasticity exacerbates allele loss at small release numbers, and at moderate to high levels [CV (λ) = 0.4] could reduce allele retention even with large release numbers (Fig. 2a). Increased annual turnover of the breeding population had a smaller effect on allele loss (Fig. 2b), and even the lowest survival rate considered (0.6 year^{-1}) is probably extreme, especially for an increasing population. Delayed population growth exposes founding populations to greater allele loss during the extended bottleneck (Fig. 2c).

Because genetic drift is simply sampling error, there will be variation among runs with the same set of parameters. To illustrate this, we graphed the allele frequency during 10 simulations with two parameter sets: $q_0 = 0.05$, $\lambda = 1.3$, $K = 150$ breeding pairs and number of individuals released = 15 (Fig. 3a) and 60 (Fig. 3b). The figures also illustrate how overall variation in allele frequency decreases as release number increases.

Discussion

Guidelines for reintroductions recommend that 'adequate' numbers should be released to minimize loss of diversity (e.g. Frankham *et al.*, 2002; Allendorf & Luikart, 2007), but this number is unquantified. We have presented a framework for assessing the number of individuals required for a reintroduction. The probability of retaining a rare allele through the founding phase increases with increasing founder number, and is also strongly affected by demography during the establishment phase. The relationship between allele retention and release number is curvilinear (i.e. it shows a 'diminishing return' for effort, which we assume to increase linearly with founder number).

We apply the model to a threatened forest passerine, the mohua, which has been translocated to several offshore island refuges where introduced predators are absent. We considered loss of alleles over 20 years, a plausible timeframe for population establishment by mohua. Our results indicate that retention of moderately rare alleles ($q_0 = 0.05$) will require release of more than double the number of individuals currently used.

Although our results were sensitive to both the number of individuals released and the growth rate of the population, managers may have little control over the latter so we focused on the effects of changing release number. With our approach, the number of individuals recommended in a release is dependent on the initial frequencies of the alleles that one is attempting to preserve. Managers involved in threatened species reintroductions should evaluate the costs and benefits of allele retention and protection of evolutionary potential. A goal of retaining rare alleles of $q_0 \leq 0.02$ will be ambitious in terms of the number of released individuals required, while choosing the release number to retain only common alleles ($q_0 \geq 0.1$) could result in the loss of many rarer alleles that may have an important role in future adaptability. In the case of the mohua, we suggest an intermediate goal of retaining moderately rare alleles – those at an initial frequency of 0.05.

The assumptions associated with our parameter estimates for mohua were in some cases optimistic. Subjecting simulated populations to increased annual turnover, environmental stochasticity, and a lag in initial population growth, resulted in lower retention probabilities, although retention rates appear to be more sensitive to the latter two factors (see Fig. 2). We did not model variance in reproductive success due to individual 'quality', which would also lead to greater allele loss. The obvious implication is that immediate, stable population growth of the reintroduced population is highly desirable, and without it the model's recommended release numbers may be inadequate.

Reintroduced populations can also be 'topped up' by releasing additional individuals in subsequent years. The effect of adding new individuals within the first few generations is roughly equivalent to increasing the initial release number. If, however, additional individuals are released after the island population has reached carrying capacity, the probability of breeding greatly diminishes and

proportionally more individuals would need to be added to increase the probability of retaining alleles (Mills & Allendorf, 1996; Grueber & Jamieson, 2008).

As far as we know, this is the first attempt to model release numbers for reintroductions by taking into account post-release mortality, population growth rate and carrying capacity of the release site. Others have attempted to calculate the number of genetic founders required to maintain observed levels of heterozygosity in source populations. For example, Taylor & Jamieson (2008) calculated that 30 genetic founders (15 breeding pairs) would be enough to maintain current levels of allelic diversity (estimated from six microsatellite loci) for island reintroductions of the South Island saddleback *Philesturnus c. carunculatus*. Miller *et al*. (2009) used a similar approach to investigate the effect of founder group sizes on loss of heterozygosity in reintroduced populations of a long-lived reptile, the tuatara (*Sphenodon spp*.).

In an attempt to test our model's predictions, Tracy (2009) found that small release numbers of 33 and 27 in two island reintroductions of mohua resulted in the loss of some rare alleles based on 11 microsatellite loci. However, the data were limited due to the small sample size of alleles within each frequency class and possible sampling error at the source population in particular (only 19 samples), but they illustrate how these models could be tested. The collection of DNA samples from translocated individuals before release could provide baseline data for tracking changes in genetic diversity relative to the source population and the extent of genetic drift during the period of population establishment (Cardoso *et al*., 2009). There is increasing emphasis on post-release monitoring of reintroductions (Armstrong & Seddon, 2008; Sutherland *et al*., 2010), and identifying low initial survival rates or slow population growth could signal the need for follow-up translocations to preserve genetic diversity.

As with all models, the one presented here has its limits. Our model does not allow for mutation or migration, which can replenish genetic diversity. Introduction of new alleles by mutation during the initial stages of reintroduction is negligible compared with the high rate of allele loss (Frankham, 2005), and most island reintroductions are too far from mainland populations for natural migration to occur (Frankham *et al*., 2002). Also, we have modelled the retention of neutral alleles only. The three major types of selection (directional, balancing and disruptive) could affect the observed genetic diversity following reintroduction in various ways. In particular, balancing selection might favor the retention of rare alleles, yet its effect would have to be strong to overcome the dispersive force of drift in small populations (Allendorf & Luikart, 2007).

Finally, our single gene model is of limited value in relation to loss of genetic variation in quantitative traits, which retain the ability to respond to selection for longer, since they only require variation at some portion (even just one) of their underlying genetic loci. Additionally, these traits derive variance from epistatic effects and with environment interactions, to the extent that variance can even increase subsequent to bottlenecking (Bryant, McCommas & Combs, 1986). In summary, our models apply only to neutral alleles or to alleles that are effectively neutral because of small effective population size, and also those alleles that are currently neutral but have the potential to contribute to fitness differences among individuals under new environmental challenges (e.g. MHC alleles when exposed to new pathogens).

Management implications

In the management of mohua and many other threatened New Zealand birds, it has become standard practice to aim to catch and release ~30 individuals, as this seems to lead to population establishment (i.e. consistent population growth) (Armstrong & McLean, 1995). However, when we additionally aim to maximize long-term viability and evolutionary potential via preservation of genetic diversity, we see that in the case of mohua, increasing the number of individuals released from 30 to 60 individuals would increase the probability of retaining alleles at $q_0 = 0.05$, by 18% if the growth rate is moderate ($\lambda = 1.3$) and by 31% if growth rate is low ($\lambda = 1.1$). Doubling the catching effort beyond 60 individuals leads to a disproportionately small benefit in terms of allele retention, unless population growth is extremely slow or initially delayed for some reason. Sourcing more than 60 individuals would, however, buffer against increased initial mortality or slower than expected population growth. Although releasing more than 60 individuals might seem excessive for establishing a population, the extra effort and cost can be justified if it increases the chances of preserving genetic diversity that has taken thousands of generations to generate, especially considering that these reintroduced populations may be the only safe refuges for a species for a long time to come.

Finally, modifications to the model will be required for species with different life-history characteristics. For example, species with unequal sex ratio among breeders due to non-monogamous mating systems will lose genetic diversity more quickly because the effective population size is reduced (Nunney, 1993). More individuals, therefore, would need to be released to maintain equal levels of genetic diversity.

Conclusions

The immediate aim of a reintroduction is to relocate sufficient individuals to establish a new population successfully (Fischer & Lindenmayer, 2000; Armstrong & Seddon, 2008). We further suggest that reintroduction programs set quantitative goals for preserving the genetic diversity of the source population. Our model translates a particular genetic goal (e.g. at least 95% chance of retaining an allele with an initial frequency = 0.05) into a required release number. Retaining genetic diversity will generally require more founders than would be needed merely to establish the population. Adoption of this quantitative framework by conservation managers can not only assist in the planning stages of reintroductions, but could also support their case

that reintroductions and subsequent monitoring needs to be resourced adequately (Sarrazin & Barbault, 1996; Sutherland *et al*., 2010).

Acknowledgments

H. Edmonds, R. Cole, G. Elliott, B. Lawrence and G. Loh of the Department of Conservation provided logistical support and helped collect samples. B. Masuda, M. Somerville, B. Rhodes and G. Pickerell assisted in the field; T. King and S. Boessenkool provided support in the laboratory. B. Lawrence, F. Allendorf, C. Grueber, S. Nakagawa and B. Robertson provided helpful discussion of ideas. Funding for this research was provided by the Department of Conservation and Landcare Research (contract no. C09X0503), the University of Otago, J.S. Watson Trust and N. Babbage of Mohua Inc.

References

Allendorf, F.W. (1986). Genetic drift and the loss of alleles versus heterozygosity. *Zoo Biol*. **5**, 181–190.

Allendorf, F.W. & Luikart, G. (2007). *Conservation and the genetics of populations*. Oxford: Blackwell Publishing.

Armstrong, D.P., Castro, I., Alley, J.C., Feenstra, B. & Perrott, J.K. (1999). Mortality and behaviour of hihi, an endangered New Zealand honeyeater, in the establishment phase following translocation. *Biol. Conserv*. **89**, 329–339.

Armstrong, D.P. & McLean, I.G. (1995). New Zealand translocations: theory and practice. *Pac. Conserv. Biol*. **2**, 39–54.

Armstrong, D.P. & Seddon, P.J. (2008). Directions in reintroduction biology. *Trends Ecol. Evol*. **23**, 20–25.

Bryant, E.H., McCommas, S.A. & Combs, L.M. (1986). The effect of an experimental bottleneck upon quantitative genetic variation in the housefly. *Genetics* **114**, 1191–1211.

Cardoso, M.J., Eldridge, M.D.B., Oakwood, M., Rankmore, B., Sherwin, W.B. & Firestone, K.B. (2009). Effects of founder events on the genetic variation of translocated island populations: implications for conservation management of the northern quoll. *Conserv. Genet*. **10**, 1719–1733.

Elliott, G.P. (1990). *The breeding biology and habitat relationships of the Yellowhead*. PhD thesis, Victoria University of Wellington, Wellington.

Elliott, G.P. (1996). Mohua and stoats: a population viability analysis. *N. Z. J. Zool*. **23**, 239–247.

Fischer, J. & Lindenmayer, D.B. (2000). An assessment of the published results of animal relocations. *Biol. Conserv*. **96**, 1–11.

Foose, T.J., Lande, R., Flesness, N.R., Rabb, G. & Read, B. (1986). Propagation plans. *Zoo Biol*. **5**, 139–146.

Frankham, R. (2005). Genetics and extinction. *Biol. Conserv*. **126**, 131–140.

Frankham, R., Ballou, J.D. & Briscoe, D.A. (2002). *Introduction to conservation genetics*. Cambridge: Cambridge University Press.

Griffith, B., Scott, J.M., Carpenter, J.W. & Reed, C. (1989). Translocation as a species conservation tool: status and strategy. *Science* **245**, 477–480.

Grueber, C.E. & Jamieson, I.G. (2008). Quantifying and managing the loss of genetic variation in a free-ranging population of takahe through the use of pedigrees. *Conserv. Genet*. **9**, 645–651.

IUCN. (1998). *Guidelines for re-introductions*. Cambridge: IUCN/SSC Re-Introduction Specialist Group.

Jamieson, I.G. (2011). Founder effects, inbreeding and loss of genetic diversity in four avian reintroduction programs. *Conserv. Biol*. **25**, 115–123.

Lacy, R.C. (1989). Analysis of founder representation in pedigrees: founder equivalents and founder genome equivalents. *Zoo Biol*. **8**, 111–113.

Lande, R., Engen, S. & Saether, B.E. (2003). *Stochastic population dynamics in ecology and conservation*. New York: Oxford University Press.

McNeely, J.A., Miller, K.R., Reid, W.V., Mittermeier, R.A. & Werner, T.B. (1990). *Conserving the world's biological diversity*. Washington, DC: IUCN, World Resource Institute, Conservation International, WWF-US and the World Bank.

Miller, K.A., Nelson, N.J., Smith, H.G. & Moore, J.A. (2009). How do reproductive skew and founder group size affect genetic diversity in reintroduced populations? *Mol. Ecol*. **18**, 3792–3802.

Mills, L.S. & Allendorf, F.W. (1996). The one-migrant-per-generation rule in conservation and management. *Conserv. Biol*. **10**, 1509–1518.

Mock, K.E., Latch, E.K. & Rhodes, O.E. (2004). Assessing losses of genetic diversity due to translocation: long-term case histories in Merriam's turkey (*Meleagris gallopavo merriami*). *Conserv. Genet*. **5**, 631–645.

Nunney, L. (1993). The influence of mating system and overlapping generations of effective population size. *Evolution* **47**, 1329–1341.

Oppel, S. & Beaven, B. (2004). Survival and dispersal of mohua (*Mohoua ochrocephala)* after transfer to Ulva Island, New Zealand. *Notornis* **51**, 116.

R Development Core Team. (2008). *R: a language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing.

Robert, A., Couvet, D. & Sarrazin, F. (2007). Integration of demography and genetics in population restorations. *Ecoscience* **14**, 463–471.

Robert, A., Sarrazin, F., Couvet, D. & Legendre, S. (2004). Releasing adults versus young in reintroductions: interactions between demography and genetics. *Conserv. Biol*. **18**, 1078–1087.

Sarrazin, F. & Barbault, R. (1996). Reintroduction: challenges and lessons for basic ecology. *Trends Ecol. Evol*. **11**, 474–478.

Sarrazin, F. & Legendre, S. (2000). Demographic approach to releasing adults versus young in reintroductions. *Conserv. Biol*. **14**, 1–14.

Seddon, P.J, Armstrong, D.P. & Maloney, R.F. (2007). Developing the science of reintroduction biology. *Conserv. Biol.* **21**, 303–312.

Stockwell, C.A., Mulvey, M. & Vinyard, G.L. (1996). Translocations and the preservation of allelic diversity. *Conserv. Biol.* **10**, 1133–1141.

Sutherland, W.J., Armstrong, D., Butchart, S.M., Earnhardt, J.M., Ewen, J., Jamieson, I.G., Jones, C.G., Lee, R., Newbery, P., Nichols, J.D., Parker, K.A., Sarrazin, F., Seddon, P., Shah, N. & Tatayah, V. (2010). Standards for documenting and monitoring bird reintroduction projects. *Conserv. Lett.* **3**, 229–235.

Tarr, C.L., Conant, S. & Fleischer, R.C. (1998). Founder events and variation at microsatellite loci in an insular passerine bird, the Laysan finch (*Telespiza cantans*). *Mol. Ecol.* **7**, 719–731.

Taylor, S.S. & Jamieson, I.G. (2008). No evidence for loss of genetic variation following sequential translocations in extant populations of a genetically depauperate species. *Mol. Ecol.* **17**, 545–556.

Taylor, S.S., Jamieson, I.G. & Armstrong, D.P. (2005). Successful island reintroductions of New Zealand robins and saddlebacks with small numbers of founders. *Anim. Conserv.* **8**, 415–420.

Tracy, L.N. (2009). *Historic and contemporary population genetics and their management implications for an endangered New Zealand passerine, the mohua (Mohoua ochrocephala)*. MSc thesis, University of Otago, Dunedin.

Willis, K. & Wiese, R.J. (1993). Effect of new founders on retention of gene diversity in captive populations: a formalization of the nucleus population concept. *Zoo Biol.* **12**, 535–548.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Simulating allele loss on reintroduction.

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