Pheromones and Animal Behaviour

Communication by Smell and Taste

Tristram D. Wyatt

University of Oxford

CAMBRIDGE
UNIVERSITY PRESS

PUBLISHED BY THE PRESS SYNDICATE OF THE UNIVERSITY OF CAMBRIDGE
The Pitt Building, Trumpington Street, Cambridge, United Kingdom

CAMBRIDGE UNIVERSITY PRESS
The Edinburgh Building, Cambridge CB2 2RU, UK
40 West 20th Street, New York, NY 10011-4211, USA
477 Williamstown Road, Port Melbourne, VIC 3207, Australia
Ruiz de Alarcón 13, 28014 Madrid, Spain
Dock House, The Waterfront, Cape Town 8001, South Africa

http://www.cambridge.org

First published 2003

Printed in the United Kingdom at the University Press, Cambridge

Typeface Swift 9/13pt *System* QuarkXPress® [TB]

A catalogue record for this book is available from the British Library

Library of Congress Cataloguing in Publication data

Wyatt, Tristram D., 1956–
Pheromones and animal behaviour: communication by smell and
taste / Tristram D. Wyatt.
p. cm.
Includes bibliographical references (p.).
ISBN 0 521 48068 X – ISBN 0 521 48526 6 (pb.)
1. Animal communication. 2. Pheromones. 3. Chemical senses. I. Title.
QL776 .W93 2002
591.59 – dc21 2002024628

ISBN 0 521 48068 X hardback
ISBN 0 521 48526 6 paperback

Contents

Chapter 1

Animals in a chemical world

1.1 Introduction

Elephants and moths are unlikely mates, so scientists and the general public were surprised when it was discovered recently that one of the world's largest living land animals, the Asian elephant (*Elephas maximus*), shares its female sex pheromone with some 140 species of moth (Rasmussen *et al.* 1996). The compound is a small, volatile molecule (*Z*)-7-dodecen-1-yl acetate (Fig. 1.1). But before explaining why elephants and moths are not likely to be confused, I should introduce pheromones in general.

1.2 What are pheromones?

Pheromones are the molecules used for communication between animals. A broader term for chemicals involved in animal communication is **semiochemical** (from the Greek *semeion* sign) (Law & Regnier 1971). Strictly speaking, **pheromones** are a subclass of semiochemicals, used for communication *within* the species (intraspecific chemical signals). Pheromones were originally defined as 'substances secreted to the outside by an individual and received by a second individual of the same species in which they release a specific reaction, for instance a definite behaviour [releaser pheromone] or developmental process [primer pheromone]' (Karlson & Lüscher 1959); the division into primer and releaser pheromones is discussed in Section 1.8. The word pheromone comes from the Greek *pherein*, to carry or transfer, and *hormōn*, to excite or stimulate. The action of pheromones *between* individuals is contrasted with the action of hormones as internal signals within an individual organism. Pheromones are often divided by function, for example into sex

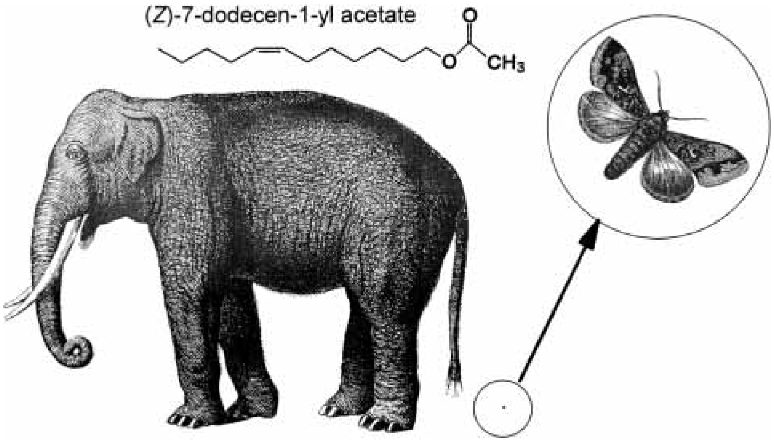

Fig. 1.1. The Asian elephant *Elephas maximus*, shares its female sex pheromone, (*Z*)-7-dodecen-1-yl acetate (top), with some 140 species of moth (Rasmussen *et al.* 1996). Animal figures from Harter (1979).

pheromones and aggregation pheromones. This functional division underlies the structure of the book, which has an emphasis on the ways evolved by different kinds of animals to solve the same communication needs. Communication itself is hard to define; various approaches are outlined in Box 1.1.

Individuals from other species can perceive signals broadcast to the wider world (Chapter 11). Semiochemicals acting between individuals from different species are called **allelochemicals** and are further divided depending on the costs and benefits to signaller and receiver (Nordlund 1981). Pheromone signals can be eavesdropped ('overheard') by unintended recipients: for example, in the way specialist predatory beetles use the pheromones of their bark beetle prey to locate them. The predators are using the bark beetle pheromones as **kairomones**. Animals of one species can emit signals that benefit themselves at the cost of the receiving species. Chemical signals used in such deceit or propaganda are termed **allomones**: for example, bolas spiders synthesise particular moth pheromones to lure male moths of those species into range for capture. Semiochemicals benefiting both signaller and receiver in mutualisms, such as those between sea anemones and anemone fish (clownfish), are termed **synomones**.

Classifications of semiochemicals rapidly become complicated, not least because the same chemical may be used as a pheromone within a species but may be exploited by specialist predators as a kairomone to locate their prey.

Just as communication is hard to define, the term **pheromone** leads to many questions. I have taken a broad and generous approach that includes many important examples of behaviours mediated or influenced by

Box 1.1 What is communication?

Wilson (1970) defined biological communication as 'action on the part of one organism (or cell) that alters the probability pattern of behaviour in another organism (or cell) in an adaptive fashion. By adaptive I mean that the signalling, or the response, or both have been genetically programmed to some extent by natural selection.' The mention of natural selection acting on signaller or receiver allows inclusion of deception and eavesdropping, the allomones and kairomones of earlier sections. This definition is more useful than ones which limit 'true communication' to situations where the signal is the function of the behaviour of the sender and the response is adaptive for the receiver (e.g. Dusenbery 1992, p. 37). Dusenbery's definition would confine 'true communication' to signals within a species, beneficial to the receiver. However, given the conflicts even between the sexes *within* a species, communication which is equally adaptive for both signaller and receiver is likely to be rare. Most biologists exclude incidental information, such as a twitch of a grasshopper's leg alerting a predator. In the context of behaviour mediated by chemicals, prey waste products such as CO_2 would not count as kairomones if they have no signal function for the prey.

Put more simply, 'communication occurs when one animal's behaviour can be shown to have an effect on the behaviour of another. 'Signals' are the means by which these effects are achieved' (Dawkins 1995, p. 73).

Communication is one of most contentious issues in animal behaviour and there is no commonly agreed definition (see discussion in Dawkins 1995 and Bradbury & Vehrencamp 1998). The complications come in refining the definition and attempting to include all communication in one definition.

Signals may often be ritualised, that is made conspicuous and exaggerated (Dawkins 1995). In the context of pheromones, ritualisation could be the evolution of pre-existing chemicals as a pheromone (for example in the way that goldfish sex pheromones have evolved from hormones leaking out across the gills, see Section 1.1). However, not all signals evolve to be conspicuous. Pheromone signals such as recognition cues in social insects and mammals may be subtle and complex.

Pheromones can be used as honest signals (Zahavi 1975) which provide reliable information because they accurately reflect the signaller's ability or resources (Guilford 1995). For example, female tiger moths (*Utetheisa ornatrix*) choose a male with the most pheromone. His pheromone is derived from the same plant poisons, used to protect the eggs, which he will pass to the female at mating. His pheromone load is correlated with the gift he will give (Chapter 3) (Eisner & Meinwald 1995). The males of another arctiid moth, *Creatonotus gangis*, display inflated coremata, releasing pheromone. The size of the coremata, which can be up to 1.5 times a male's body length, is directly related to the amount of plant poisons the male sequestered as a larva (Fig. 1.5) (Boppré & Schneider 1985). In garter snake females, the levels of skin pheromones reflect evidence of the previous season's fertility. Male garter snakes court larger snakes, which have more pheromone (Chapter 3). In mammals, production of pheromone is directly related to hormone levels (Chapter 3) and so scent marks will tend to be honest. Animals such as mammals and lizards that scent mark their territories (Chapter 5) leave signals that are inherently reliable – only if the owner does own the territory will his marks exclusively cover it. Where pheromones effectively have the role of badges of status as, for example, in cockroaches (Moore *et al.* 1997), queenless ants (Peeters 1997), or mice (Hurst & Rich 1999), the major cost may be that of maintaining the advertised status (see Chapters 3 and 6).

chemical cues that would currently fall outside a rigid definition of pheromone. First, I include the chemical cues used for social recognition in both mammals and social insects (see Chapter 6), which do not fit the original pheromone criterion of a ‘defined chemical mixture eliciting particular behaviour or other response’. The cues used for social recognition of kin, clans, colony members and the like are complex, greatly varied mixtures of many compounds (Box 6.1). The differences between the odour mixtures *are* the message. For example, as well as sex pheromones, each elephant will produce its own highly individual odour mixtures and this complex bouquet can be used by other elephants for recognition of kin, clan or social group, and perhaps individuals. Elephants spend much time sniffing each other (incidentally, people are also good at recognising their own family by smell, see Chapter 13).

Second, while we tend to think of pheromones as being detected by ‘sniffing’ air or water after travelling some distance from the signaller, many chemical cues are detected by contact chemoreception, as in the case of an ant tapping its antennae on a fellow ant to detect the complex mixtures of chemicals on its cuticle that differ between colonies and allow distinction of nestmates from strangers. Pheromones may be transferred directly from signaller to receiver. For example, male Queen butterflies (*Danaus gilippus*) deposit crystals of the pheromone danaidone from their hair pencils directly onto the antennae of the female (see Eisner & Meinwald 1995). The male of the terrestrial salamander (*Plethodon jordani*) directly transfers his high molecular weight glycopeptide pheromone from his chin gland to the nostrils of the female (Rollmann *et al.* 1999). The male of the related salamander, *Desmognathus ochrophaeus*, takes this a stage further by directly ‘injecting’ his pheromone into her capillary blood supply, using elongated teeth to pierce the female skin, thus bypassing her chemosensory system (Houck & Reagan 1990). In this same continuum I have included molecules passed, together with sperm, to the female during mating in many species: for example, the fruit fly *Drosophila melanogaster*, and garter snakes (Chapter 3).

ELEPHANTS AND MOTHS – CONVERGENT PHEROMONES

The discovery that elephants and some moths share the sex pheromone (*Z*)-7-dodecen-1-yl acetate is particularly interesting because it illustrates important points emerging about pheromones in mammals and insects, and animals in general.

First, it illustrates the ubiquity of pheromones. Across the animal kingdom, more interactions are mediated by pheromones than by any other kind of signal.

Second, the shared use of a compound as a signal illustrates a relatively common phenomenon of independent evolution of particular molecules as

Table 1.1. *Biochemical convergence of pheromones among ants, bees, moths and termites and other animals including mammals*

In some cases, the same compound is used for similar functions in different species. More commonly, the arbitrary nature of signals is revealed by different uses for same compound. See other chapters for more details of the functions of these pheromones.

		Occurrence	
Compound	Function	Family	Genus
Benzaldehyde	Trail pheromone	Bee, Apidae	*Trigona*
	Defence	Ant, Formicidae	*Veromessor*
	Male sex pheromone	Moth, Amphipyrinae	*Pseudaletia*
2-Tridecanone	Alarm pheromone	Ant, Formicidae	*Acanthomyops*
	Defence	Termite, Rhinotermitidae	*Schedorhinotermes*
Dehydro-*exo*-brevicomin	Male sex pheromone	Mammal	Mouse, *Mus*
Exo-brevicomin	Aggregation pheromone	Insect	Bark beetle, *Dendroctonus*
(*Z*)-7-Dodecen-1-yl acetate	Female sex pheromone	Mammal	Asian elephant *Elephas maximus*
		Insect	~140 species of moth (as one component of a multi-component pheromone)

After Blum (1982), with additional information from Kelly (1996).

signals by species that are not closely related (Table 1.1) (Kelly 1996). Such coincidences are a consequence of the common origin of life: basic enzyme pathways are common to all multicellular organisms, and most classes of molecule are found throughout the animal kingdom.

However, despite sharing an attraction to (*Z*)-7-dodecen-1-yl acetate, male moths and elephants are unlikely to be confused. Apart from the mating difficulties should they try, male moths are unlikely to be attracted by the pheromones in female elephant urine because moth pheromones are multicomponent (Section 1.6). The (*Z*)-7-dodecen-1-yl acetate would be only one of perhaps five or six other similar compounds making up a precise blend for each moth species. Male elephants are unlikely to be attracted to a female moth because she releases such small quantities (picograms per hour) that they would not be noticed by a male elephant (but can be tracked by the specialised sensory system of a male moth).

Third, it is an important illustration that, like insects, mammals can use small molecules, singly or in simple mixtures, as pheromones for sexual signalling. It is harder to identify mammalian pheromones than those of insects (Chapter 2) but this does not necessarily mean that their pheromones are more complicated. One difference may be that unlike insects, mammals may increase the activity of their pheromones by interaction with carrier proteins in the urine, as is the case in the elephant and also in mice.

1.3 Evolution of chemical cues into signals

Chemical senses are the oldest, shared by all organisms including bacteria, so animals are pre-adapted to detect chemical signals in the environment (Wilson 1970). Chemical information is used to locate potential food sources and to detect predators as well as to receive the chemical signals in the social interactions that form the focus of this book.

Signals are derived from movements, body parts or molecules already in use and are subsequently changed in the course of evolution to enhance their signal function. Thus pheromones evolve from compounds originally having other uses or significance, for example from hormones, host plant odours, chemicals released on injury, or waste products. There is selection for functional signal features such as longevity and specificity (Section 1.5). There is also evolution in the senses and response of the receiver. The original functions of the chemicals may or may not be eventually lost.

The ubiquity and extraordinary diversity of pheromones are the evolutionary consequence of the powerful and flexible way the olfactory system is organised (Chapter 9); taste does not have this flexibility. Most animal olfactory systems have a large range of relatively *non*-specific olfactory receptors which means that almost any chemical in the rich chemical world of animals will stimulate some olfactory sensory neurons and can potentially evolve into a pheromone. If detection of a particular chemical cue leads to greater reproductive success or survival, there can be selection for receptors more sensitive to it or expressed in greater numbers. In some cases animals may evolve a finely tuned system, including specialised sensory organs and brain circuits, such as those of male moths used to detect and respond to female pheromones (Chapter 9).

Any pheromone signal that overlaps the receiver's pre-existing sensory sensitivities, for example for food odours, is likely to be selected over others. This is the phenomenon of sensory drive (Fig. 1.2) (see reviews in Endler & Basolo 1998, Ryan 1998). For example, female moths use plant odours to find host plants when egg laying, so their olfactory system is already tuned to these odours – and male pheromones have evolved to exploit the sensory bias of females (Fig. 1.2) (Chapter 3) (Birch *et al.* 1990; Phelan 1997).

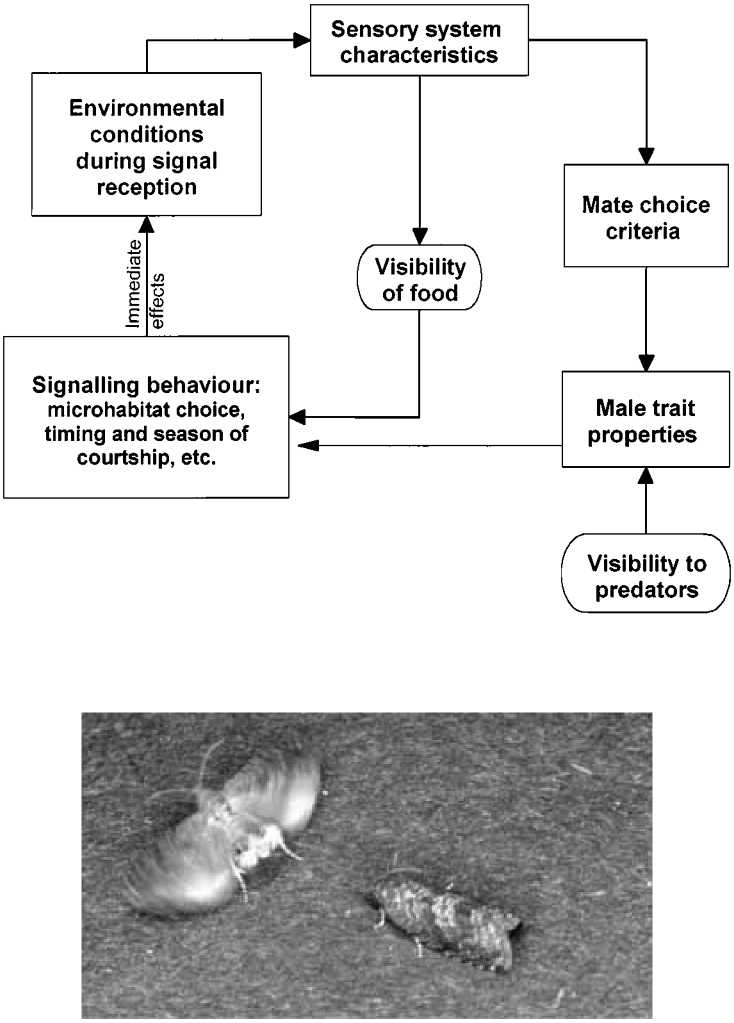

Fig. 1.2. Sensory drive. (Left) Signals that exploit the existing senses of the receiver will be selected for: this is the phenomenon of sensory drive. In the diagram, arrows indicate evolutionary influences (except for the one labelled 'immediate effects'). Predators can have a counter-selection pressure on conspicuous signals. Different authors have emphasised different, partially overlapping, aspects of the phenomenon, terming them 'sensory traps', 'preexisting bias', 'sensory drive', 'sensory exploitation', 'receiver psychology', 'hidden preference', and 'perceptual drive' (Endler & Basolo 1998). Figure after Endler (1992).

(Right) A male oriental fruit moth, *Grapholitha molesta*, displays its hair pencils in courtship to a female. The male's hair pencils are loaded with plant-derived pheromones including ethyl-*trans*-cinnamate, a signal which may have evolved through sensory drive exploiting female sensitivity for odours present in their fruit food (Löfstedt *et al.* 1989). The females prefer males with the most cinnamate. Photograph by Tom Baker.

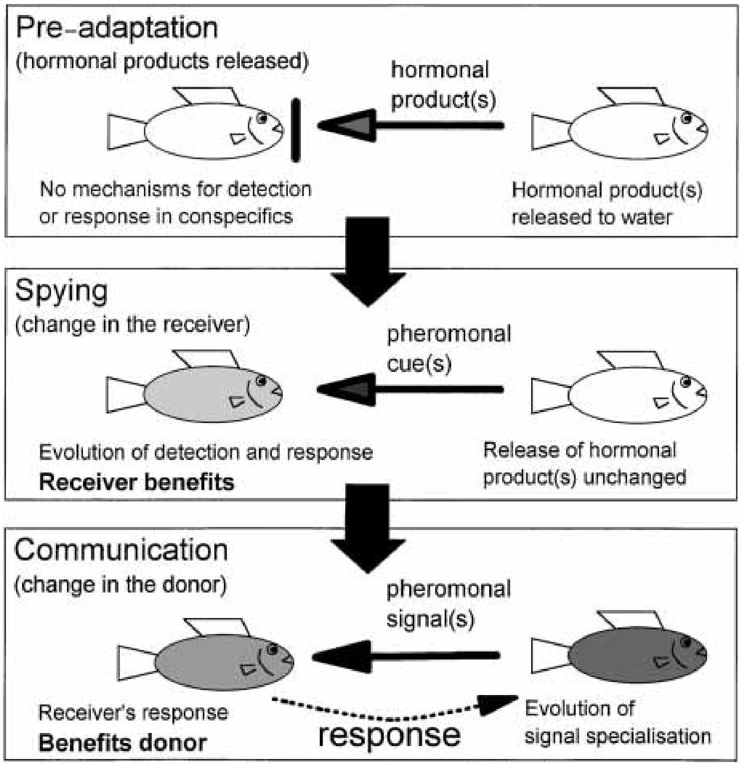

Fig. 1.3. Proposed stages in the evolution of a communication function for hormonal pheromones from pre-existing hormones by intraspecific eavesdropping or spying. In the 'spying phase' only the receiver benefits. The transition to bilateral benefit to both sender and receiver could occur later if there is a selective advantage to the sender. In the 'spying phase' there need not be changes in the signal released by the sender (see Fig. 1.11). Figure redrawn from Sorensen & Stacey (1999).

Pheromones evolved from leaking hormones or from compounds used in defence provide illustrations of the way that evolution can act on available chemical cues.

1.3.1 Pheromones evolved from leaking hormones or other metabolites

Coordinating reproduction is very important, particularly for externally fertilising animals, which must release gametes (sperm and eggs), at the same time as their partner(s). Molecules in body cavity fluids normally released with the sperm or by sexually mature adults may become pheromones. For example, marine polychaete worms release sex pheromones with their gametes, which immediately prompt the other sex to release its gametes (Chapter 3).

Hormones or other molecules associated with reproductive cycles have evolved into pheromones by eavesdropping ('spying') in many animals (Fig. 1.3) (Sorensen & Stacey 1999). In terrestrial animals such as elephants and mice, some pheromones are excreted in the urine. In aquatic animals such as fish and lobsters, pheromones may have evolved from molecules excreted in urine or leaking into the water across permeable membranes such as gills.

Hormone-based sex pheromones in the goldfish *Carassius auratus* provide a good model system (Sorensen & Stacey 1999). A chance observation revealed that male goldfish are extraordinarily sensitive (with picomolar thresholds) to steroid and prostaglandin hormones and their metabolites released into the water by females (see Chapter 2). The released molecules reflect the blood concentrations of the hormones in the female and are a reliable indicator of her biological state. In the evening while the female matures her eggs before release, rising levels of the steroid 4-pregnen-17α-, 20β-diol-3-one (17,20β-P) in her blood leak into the water. The pheromone stimulates physiological responses in the male (Section 1.8). When the female spawns the next morning, males respond to other hormone pheromones released by the female: blood prostaglandin F2α (PGF2α) and 15-keto-PGF2α.

1.3.2 Alarm pheromones and compounds released by fighting or injured animals

Many alarm pheromones, which provoke fight or flight in receivers, appear to have evolved from compounds released by fighting or injured conspecifics (Chapter 8). There will be a selective advantage to potential receivers sensitive to these compounds and responding appropriately. Over evolutionary time, defensive compounds may gain a signal function: for example, most ant species use the same chemicals for defence and alarm, to repel enemies and to alert and recruit nestmates (Hölldobler & Wilson 1990, p. 260). This pattern is shown across the arthropods (Blum 1985).

In other animals, alarm pheromones may derive from compounds evolved to make the flesh unpalatable or toxic to predators (Chapter 8). These compounds would be released by an injured animal, for example anthopleurine in the sea anemone and the bufotoxins and larval skin extracts which elicit an alarm response in toad tadpoles. The alarm pheromone of fish is not an antifeedant but may have evolved with a primary function such as control of skin pathogens.

1.4 Secretory organs for pheromones

The independent and multiple evolution of pheromones is illustrated not only by the diversity of compounds produced but also by the enormous variety of specialised secretory glands among male mammals and male Lepidoptera (moths and butterflies). The variety is probably largely the

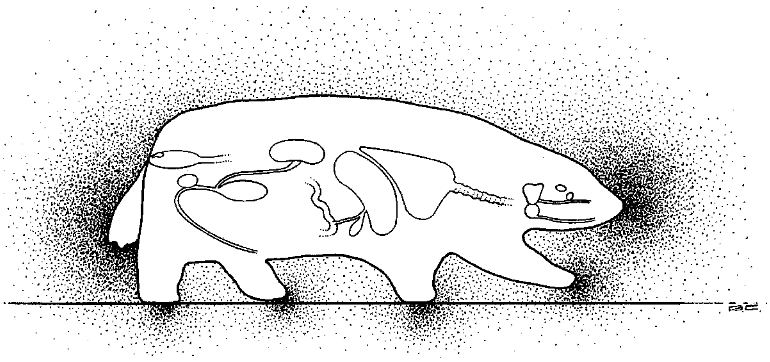

Fig. 1.4. A summary diagram of an imaginary mammal illustrating a variety of possible odour sources. The stippling indicates a potential distribution of odorants in the immediate environment. The following are shown: salivary glands and glands associated with the eye (e.g. preorbital glands); the lungs and trachea; the liver, gall bladder, bile duct, and portion of the small intestine; the kidney, ureter, bladder, urethra, and male accessory gland; the rectum; and an anal sac. The female genital system could be readily substituted for the male (plus specific glands on the feet and legs and on skin in many parts). Figure from Flood (1985).

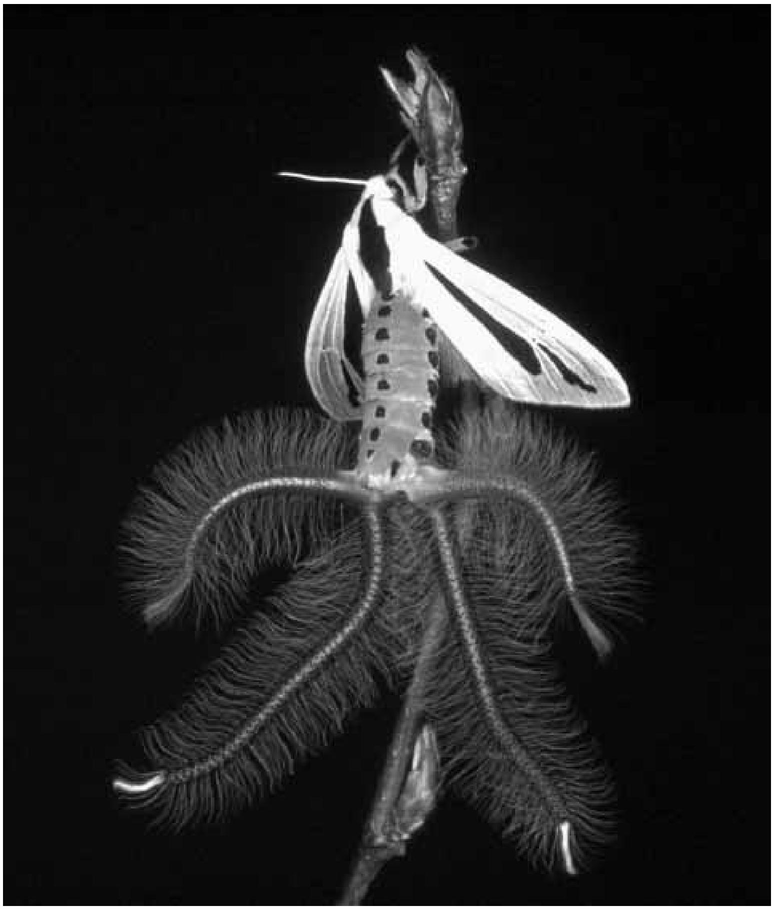

Fig. 1.5. The expanded coremata of a displaying male of an arctiid lekking moth, *Creatonotus gangis*. Photograph by M. Boppré.

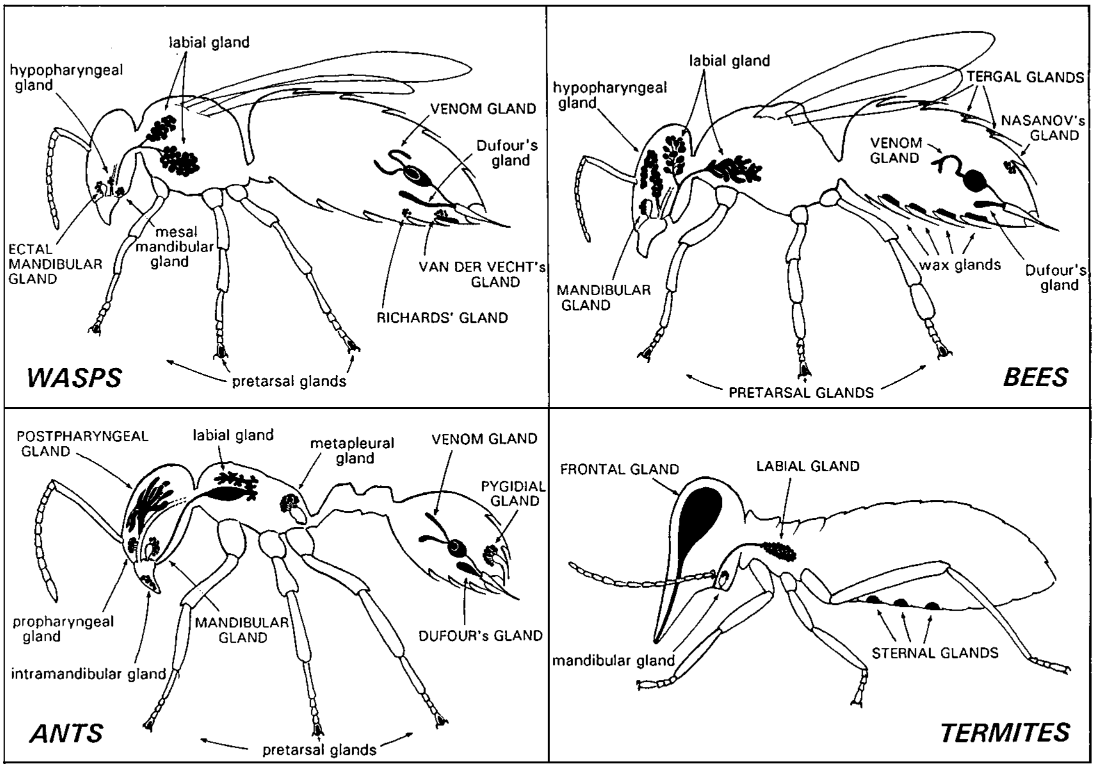

Fig. 1.6. Schematic profile drawings of the commonly found exocrine glands in wasps, bees, ants, and termites. Glands with a pheromonal function are given capital lettering. Pheromones may be identified in future from other glands. Figure from Billen & Morgan (1998).

result of sexual selection (Andersson 1994) (Chapter 3). In mammals there are secretory glands in species-specific positions such as the flanks, around the eye, around the genitals and anus (Fig. 1.4). The equivalents in male Lepidoptera are a profusion of specialised brushes, fans, inflatable balloons (coremata) and other structures on the wings, legs, and abdomen for exposing the pheromones produced in associated glands (Fig. 1.5) (Chapter 3). There is convergence in the special lattice-like hairs to soak up and emit pheromone in some moths and mammals. Among ants, the range of alarm pheromones is matched by the extreme diversity of glands involved (Fig. 1.6) (Hölldobler & Wilson 1990).

While the signaller itself synthesises and secretes most pheromones, some components of pheromones may be collected or gained in other ways. For example, the complete aggregation pheromone for some bark beetle species includes components produced by the host tree as well as components produced by symbiotic bacteria in the beetle gut (Chapter 4). Similarly, many mammal pheromones are produced by the action of bacterial fermentation, for example of fatty acid secretions in the anal glands of foxes (Albone & Perry 1976).

Plants containing pyrrolizidine alkaloids (PA), which are poisonous to most vertebrates and other insects, are sought out and fed on by specialist moth and butterfly species (Lepidoptera), a behaviour known as pharmacophagy (Boppré 1990). In some species only the larvae sequester the alkaloids, in others, such as the milkweed danaine butterflies (Nymphalidae), adults also feed on these PAs. Courtship in PA-sequestering species usually involves display of hair pencils or coremata loaded with derivatives of these alkaloids (Box 1.1). Males without chemical riches are rejected (see Chapter 3). Likewise, to be successful in attracting mates, male euglossine bees in the American tropics must collect perfume oils such as mono- and sesqui-terpenes from orchid flowers (Schemske & Lande 1984).

1.5 Functional signal design: contrasting different signal modalities

The chemical senses of olfaction and taste are very different from vision, hearing and touch, which detect energy in the form of light, sound or pressure: chemical senses rely on the physical movement of odour molecules from the signaller to the receiver (Table 1.2).

Table 1.2. *Characteristics of different sensory channels of communication*

	Type of signal			
Feature of channel	Chemical	Acoustical	Visual	Tactile
Range	Long	Long	Medium	Very short
Transmission rate	Slow	Fast	Fast	Fast
Flow round barrier?	Yes	Yes	No	No
Locatability of sender	Difficult	Medium	High	High
Energetic cost to sender	Low	High	Low to moderate	Low
Longevity (fade-out)	Variable, potentially high	Instantaneous	Instantaneous	Short
Use in darkness	Yes	Yes	No (unless make own light)	Yes
Specificity	Potentially very high	High	More limited	Limited

After Alcock (1989).

Pheromones are not effectively instantaneous like sound or light, because the molecules of odour have to reach the nose or other sense organ of the receiving animal. For longer range attraction of mates, for example, pheromones offer many advantages over other sensory channels because chemical signals go round barriers, can be carried for long distances in the wind or water currents, and have low production costs (see below) (Thornhill & Alcock 1983). However, locating the pheromone source can be challenging (Chapter 10).

The use of pheromones as the dominant communication channel may be related to habitat and daily activity rhythm. For example, the grysbok (*Raphicerus melanotis*), a small antelope, occupies dense scrub and relies more heavily on olfactory communication than antelope species in more open habitats (Albone 1984). As might be expected, nocturnal animals such as bushbabies (*Galago* spp.) use odour or sound rather than visual signals.

For chemical signals used for marking, the whole function of the signal is the association of a message with a place. Pheromone deposited on a territory marker by an antelope or a lizard remains after the animal has moved on (Chapter 5). Whereas sound and visual signals only act at the time they are made, chemical messages can 'shout' long after the signaller has gone. This highlights one of the unique elements of chemical signals – that in evolutionary time, different lengths of signal life can be selected for: selection can work on the chemical characteristics of pheromones such as volatility and stability, giving signal durations from seconds to years.

1.5.1 Pheromones in terrestrial habitats

The characteristics of pheromones can be related to their signalling function and the signalling environment. Wilson & Bossert (1963) suggested that pheromones used in air should have 5–20 carbon atoms and a molecular weight (MW) of between 80 and 300. Below the lower limit, only a few permutations of molecule can be created; above it, molecular diversity increases very rapidly (Wilson 1970). For example, alarm pheromones have low molecular weights to allow fast diffusion from the source but a quick decline once the danger has past. In ants, most, but not all, alarm pheromones have molecular weights of between 100 and 200 (Fig. 1.7) (Hölldobler & Wilson 1990). Sex pheromones would be expected to be larger molecules to allow more specificity – in insects they typically have molecular weights of 200–300 (Fig. 1.7).

Alberts (1992) tested these ideas on mammalian chemical signals and found that in each of five orders, sex pheromones had lower molecular weights than territorial marking pheromones and would thus be more volatile and shorter lived. The signal life of mammalian pheromones used as territory markers was increased by carrier components in secretions such as sebum, a lipid-rich, oily

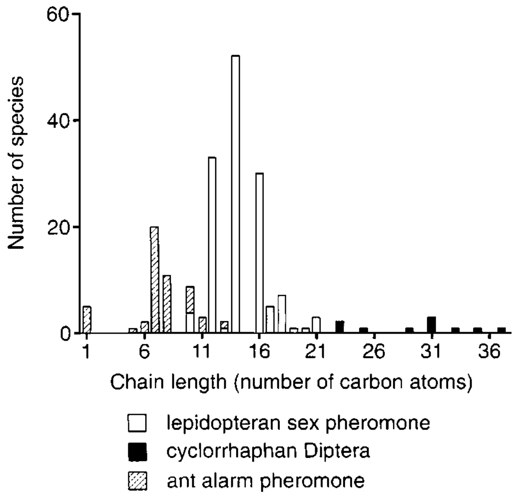

Fig. 1.7. Chain lengths of aliphatic hydrocarbons used as alarm pheromones by ants (short chain, low molecular weight), long range sex attractants by moths, and contact pheromones by cyclorrhaphan Diptera such as *Drosophila* (see Chapter 10 for discussion of molecular weight and diffusion). Figure from Chapman (1998).

substance produced by sebaceous glands (Alberts 1992). Higher temperatures and humidities increase evaporation rates, reducing the persistence of chemical signals. This may explain why the molecular weights of marking pheromones used by tropical forest species were higher than those from temperate forests, with temperate grassland species lowest of all (Fig. 1.8).

Another way, used by mice and other mammals, to increase the longevity of small volatile pheromones is to associate them with urinary protein molecules which release them slowly (Chapter 9).

Signal design must sometimes meet conflicting selection pressures. For example, the hot habitat of the desert iguana *Dipsosaurus dorsalis* presents a challenge to long-lasting but effective marks: volatile pheromones would fade quickly, but longer lasting, less volatile chemical signals would not be detected by intruders. This lizard has evolved high molecular weight scent marks which strongly absorb long-wave ultraviolet light, which lizards can see (Alberts 1990). Lizards orient towards these conspicuous visual ‘flags’ and, once at the mark, they tongue-flick to pick up the non-volatile pheromone molecules. The advantage of this composite signal is that the high information content from the non-volatile molecules is combined with long-distance visual attraction. In an analogous way, male butterflies use visual cues to find females at long range, and then at short range, in many species, they communicate with pheromones (Chapter 3) (Vane-Wright & Boppré 1993). Some animals, such as dogs, add their marks to conspicuous sites or landmarks.

The effect of habitat on signals is shown by comparison with another iguana species, the green lizard *Iguana iguana*, which lives in humid tropical

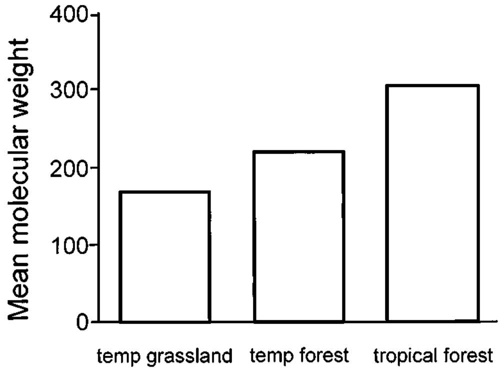

Fig. 1.8. Comparison of mean molecular weight of territorial scent marks from mammals living in temperate grassland, temperate forest, and tropical forest habitats. Data are pooled across seven orders of mammals. Figure redrawn from Alberts (1992).

forest. The green lizard has a higher percentage and more varied volatile lipids in its scent marks than the desert iguana, but does not include UV-absorbing molecules in its marks (Alberts 1993).

1.5.2 Aquatic pheromones

In water, the size rules for potential diversity of molecules still apply, but whereas volatility is a key signal design feature of pheromones in air, solubility of molecules is perhaps the functional equivalent in water. There appear to be two main types of molecules used as pheromones in aquatic species. First, there are soluble molecules similar in size to those used as pheromones on land, such as the steroid-based pheromones used as fish sex pheromones (Sections 1.3.1 and 1.8) and barnacle egg hatching pheromone (Section 4.2.2). Second, large, polar molecules can be used, which despite their size can be highly soluble. For example, anthopleurine, the alarm pheromone of a sea anemone (Chapter 8) is a large cation. Many other marine invertebrates use polypeptides as chemical signals (Chapter 4) (Zimmer & Butman 2000). These peptide pheromones are involved in gregarious settlement by oyster and barnacle larvae, precisely timed larval release by crabs to coincide with tides, and a sex pheromone of the sea-slug mollusc *Aplysia* (Painter *et al.* 1998). The barnacle cues are glycoproteins and water-borne peptides (Clare & Matsumura 2000). The crab 'pumping pheromone' is a short peptide, with activity at concentrations as low as 10^{-21}M (Pettis *et al.* 1993). The activity of synthetic peptides can be predicted by quantitative structure-activity relationships (Browne *et al.* 1998).

The first peptide pheromone to be identified in a vertebrate was the decapeptide, sodefrin, in the Asian red-bellied newt (*Cynops pyrrhogaster*) (Fig. 1.9) (Kikuyama *et al.* 1995).

Fig. 1.9. Two phases of the underwater courtship behaviour of the red-bellied newt, *Cynops pyrrhogaster*. (Top) The male wafts a decapeptide pheromone, sodefrin, from his cloacal glands towards the female's nostrils. (Bottom) The male (left) then moves in front of the female and she follows him with her snout in contact with his tail. Figure from Kikuyama & Toyoda (1999). Photograph by Sakae Kikuyama & Fumiyo Toyoda.

1.6 Specificity

In some biological signalling systems, selection pressures from sexual selection and speciation (Chapter 3) will lead to species-specific sex pheromones and responses. In other situations, such as alarm pheromones, there is little need for privacy in communication and alarm pheromones are often not species specific (Chapter 8). If a predator has alarmed individuals of another species, and it is of benefit to respond, then cross-species responses will evolve. Within a prey guild with shared predators, all species commonly respond to each others' alarm signals.

There are two main ways of gaining specificity in pheromone signals. One is by the evolution of a large unique molecule. Peptide pheromones, using the 20 coded amino acids available in eukaryotic systems, offer an extraordinary variety of unique sequences; with a five- amino-acid polypeptide there are $20^5 = 3.2$ million (Browne *et al.* 1998). For example, two related species of the newt *Cynops* have species-specific decapeptide pheromones which differ by just two amino acids (Yamamoto *et al.* 2000) (Section 1.5.2). Among insects, a very few species use a unique complex molecule as a single-component pheromone; for example, periplanone-B is the sex pheromone of the American cockroach (*Periplaneta americana*) (Roelofs 1995).

More commonly, specificity is gained largely by using a unique blend of relatively simple compounds as a *multi-component* pheromone. For example, female sex pheromones in moths usually consist of five to six fatty acids or their derivatives. Vertebrates may also have multi-component pheromones. For example the mouse pheromone, which elicits aggression in other males, consists of two compounds, each of which is inactive alone (Section 2.6). Similarly, in the goldfish, while each of two female prostaglandin pheromones, F2α (PGF2α) and 15-keto-PGF2α, have similar effects on male behaviour when presented singly, both are needed together to stimulate a gonadotropin surge in males (Sorensen & Stacey 1999). It is possible that other components add species specificity.

A particular specificity open to biological systems is to use stereoisomers (molecules that have the same atoms connected in the same order but differ in the arrangement of atoms in space, see Appendix A2). Pheromone synthesis is catalysed by enzymes and pheromones are detected by receptors. Enzymes and receptors are proteins and recognise their substrates and signal molecules (ligands), respectively, by shape, so that different stereoisomers will be treated differently. Stereoisomers are very important in pheromone signalling for both invertebrates and vertebrates (Silverstein 1979; Seybold 1993; Mori 1996). Some molecules are **enantiomers**, mirror images of each other (said to be chiral, from the Greek meaning hand). Some pairs of species gain specificity by using different enantiomers of the same compound; for example, among sympatric scarab beetles in Japan (Leal 1999), the Japanese beetle *Popilla japonica* uses (*S*)-japonilure as its female sex pheromone whereas the Osaka beetle (*Anomala osakana*) uses (*R*)-japonilure (see Appendix A2 for notation).

1.7 Composite signals: pheromones working in concert with other modalities

Pheromones are often just one of the sensory channels (modalities) involved in communicating a signal. The signals in parallel sensory channels can be important in three different ways. First, to ensure that the message gets through by having it repeated in each of the sensory channels; this is termed signal 'redundancy' (as for example when we write a cheque in both words and figures). Second, there may be modulation of the signal intensity by addition of other signals. Third, signals in each of the communication channels may be necessary for the message.

An example is given by the black-tailed deer, in which alarm signals are transmitted not only as an odour signal, but also as sounds and visual signals (Chapter 8). Any one of these may be effective in alerting other deer in

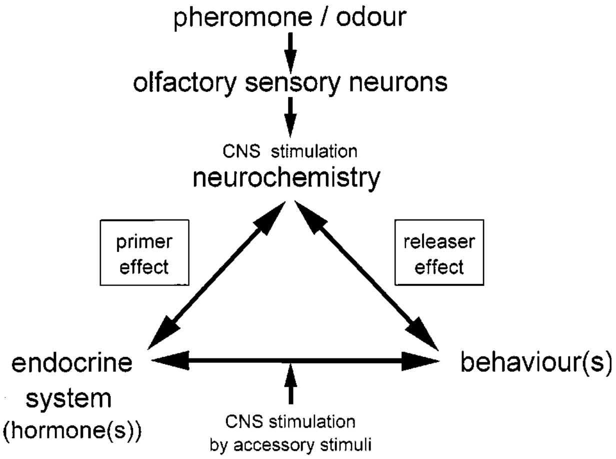

Fig. 1.10. Pheromones can be a stimulus leading to a prompt behavioural response by nerve impulses from the brain (CNS, central nervous system) (**releaser effect**) or can act indirectly by stimulation of hormone secretion resulting in physiological changes, 'priming' the animal for a different behavioural repertoire (**primer effect**). A given pheromone can of course act as a primer or releaser at same time or in different contexts. The distinction between primer and releaser pheromones has become blurred as we understand more about the links, interactions, and feedback loops in the sequence from odour to behavioural and endocrine effects. Hormonal effects can be rapid, and memories, sometimes facilitated by local neurochemistry changes, can be long lasting (see Fig 9.10 for an example using maternal learning of the odours of her lamb by a sheep). Diagram brings together ideas from figures in Wilson & Bossert (1963) and Sachs (1999).

the group. This redundancy in signal can make dissecting the role of pheromones much more difficult (Chapter 2). While this complexity is perhaps characteristic, and perhaps even the rule, of many signals in mammals, there are also many invertebrate examples of modulation of pheromone signals by other stimuli. For example in the desert ant *Novomessor*, recruitment of nestmates to a new food source is faster when release of pheromone is accompanied by stridulation sounds from scouts (Chapter 7). In the snapping shrimp *Alpheus heterochaelis,* male responses to visual threat signals are changed if these are accompanied by female pheromones (Hughes 1996). Successful courtship by male *Drosophila melanogaster* fruit flies requires a combination of chemical and visual stimuli from the female; pheromones are necessary but not sufficient alone (Chapter 3) (Greenspan & Ferveur 2000).

1.8 Primer and releaser pheromones

Most of the phenomena described so far have been of **releaser pheromones**, with immediate effects on the behaviour of the receiver. An equally important group of pheromones, **primer pheromones**, have longer term physiological

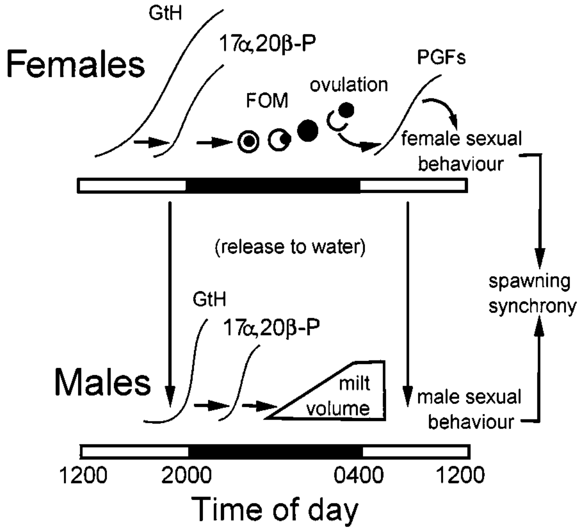

Fig. 1.11. Primer and releaser pheromones, evolved from hormones, coordinate reproduction in the goldfish, *Carassius auratus* (Sorensen & Stacey 1999).

Preovulation primer pheromones: In the evening while the female matures her eggs before release, rising levels of the steroid 17,20β-P in her blood leak into the water. The male's olfactory system detects the pheromone and stimulates his brain to release male gonadotropic hormone (GtH) which in turn stimulates testicular 17,20β-P synthesis and promotes increased milt (sperm and seminal fluid) production.

Postovulatory releaser pheromone: The next morning at ovulation, eggs within the reproductive tract stimulate the production of prostaglandins (PGFs), which act as hormones to stimulate female sexual behaviour. Metabolites of PGFs leak out and function as a releaser pheromone stimulating male sexual behaviour (Dulka 1993).

The sensitivity to the primer pheromones benefits male reproductive success (Sorensen & Stacey 1999). Males primed overnight are more aggressive in chasing other males away, spawn almost three times more often, and fertilise more eggs than males who were not primed. Figure redrawn from Dulka (1993).

effects on the receiver, in the original definition by stimulating olfactory sensory neurons that send signals to the brain to release the hormones of the endocrine system (Fig. 1.10) (Wilson & Bossert 1963). Studying primer pheromones is a challenge because the timescale for primer effects can be long and it may be difficult to associate a gradual physiological change with an earlier contact with a chemical signal.

Examples of primer pheromones include stimulation of sperm production in fish (see Fig. 1.11), termite caste determination, locust development rates, and menstrual cycles in humans and other mammals (Chapters 4, 6, 9 and 13).

The division into releaser and primer pheromone is only a rough classification, first, because many pheromones have both roles. For example, honeybee (*Apis mellifera*) queen mandibular pheromone attracts males on her nuptial flight but also has primer effects on worker reproduction (Chapter 6). Second, response to some endocrine-mediated pheromone signals can be rapid. For example, pheromones of oestrous females cause release of hormones into the blood in sex-experienced male rats, which give them erections and elicit sexual behaviours within minutes (Sachs 1999). Third, the mutual influences and feedback loops between hormones, olfactory centres and endocrine cells in the brain, are complex. For example, long-term behavioural effects can come from neuronal memories for odours, themselves modulated by hormones (e.g. sheep maternal behaviour, Chapter 9). Sachs comments that it may be more useful to view primer and releaser pheromones as acting on a continuum of physiological and behavioural pheromone-induced effects occurring earlier or later in a sequence (Fig. 1.10).

While the physiologies of mammals and insects are very different, there are parallels between the modes of action of primer pheromones in both. For example, in mammals, dominance hierarchies are reflected in blood gonadal hormone concentrations. In social insects JH (juvenile hormone) is often important in pheromone-mediated effects (Chapter 9).

It is sometimes argued that mammals do not have many releaser pheromones that elicit a particular behaviour. However, some have been identified and more are likely to be discovered. One example is the ‘standing behaviour’ of an oestrous pig (*Sus scrofa*) female in response to the steroid sex pheromones, 3α-androstenol and 5α-androstenone, of the male pig in his saliva (Chapter 12). Another is the rabbit nipple pheromone, which allows the young rabbit pup to find the nipple rapidly (Chapter 9). A third example is the vaginal pheromones attracting males and stimulating mounting in the golden hamster (*Mesocricetus auratus*) (Chapter 9).

You will have noticed that one group missing from the discussions so far are the birds (see Box 1.2).

1.9 | Cost of signalling

The metabolic cost of most pheromone signalling is low compared with that of other signals (Thornhill & Alcock 1983), in part because the quantities of material needed are so small. For example, the lifetime cost to a male boll weevil beetle (*Anthonomus grandis*) to produce its monoterpene sex pheromone is estimated at only 0.2% of its body weight (Hedin *et al.* 1974). In contrast, male crickets devote over half their daily respiratory budget to acoustic signalling (Prestwich 1994). Some of the advantages of chemical communication over sound relate to scale effects of signal production and the size of the organism: smaller organisms cannot make the lower frequency sound signals which travel further (Dusenbery 1992) (see Chapter 10). The costs of production are

Box 1.2 Birds and pheromones?

Birds are not famous for their pheromone communication . . . yet. Just as studies of mate choice in birds were transformed by the recent discovery that, unlike us, birds see ultraviolet (e.g. Bennett *et al.* 1997), pheromones could be important for birds. Most birds have a good sense of smell but we have been so attracted by bird songs and visual displays that the role of olfaction in reproduction and recognition behaviour has been little studied (see review in Roper 1999). All but a few species of bird have a uropygidial gland, at the base of the tail, which secretes lipids used in preening the feathers. The secretions differ between species. Darwin observed that sexually selected characters will be expressed differently in the sexes, at sexual maturity, and during the breeding season (Chapter 3). The uropygidial secretion in the female mallard duck (*Anas platyrhynchos*) meets all these predictions. It changes during the breeding season but during the rest of the year it is the same as that of males and ducklings (Balthazart & Schoffeniels 1979; Jacob *et al.* 1979). The sexual behaviour of male mallard ducks was reduced if their olfactory nerves were cut, although their other behaviour was apparently normal. Other potential secretory glands in birds include the sebaceous and anal glands.

Olfaction may play an important role in the navigation of adult procellariiform seabirds – 'tube-nosed' birds which include petrels and albatross, to colony sites and nesting burrows, marked in many species by notoriously smelly stomach-oil secretions (nestlings of the British storm petrel *Hydrobates pelagicus* recognise their nest by smell, Minguez 1997). Almost all the Procellariiformes have very large olfactory bulbs in the brain, although these may have evolved primarily for the location of patchy food resources in the ocean (see Chapter 10). In the Antarctic, petrels and albatrosses appeared within minutes at oil slicks scented with food odours (Nevitt 1999b).

Pheromone-mediated behaviour in birds is just as likely to be found in species with small olfactory lobes. The relative size of the olfactory lobe is not necessarily an indication of its importance: if the pheromones are used at close range there need not be large or specialised olfactory structures (female moths respond to male courtship pheromones despite having tiny antennae compared with the male – Chapter 3). Olfactory cues in courtship in ducks and other birds would be well worth investigating; this is another dimension of the world of birds to be explored.

probably similarly low for vertebrates (Chapter 3). For example, just 40 nanograms of the peptide pheromone of the magnificent tree frog *Litoria splendida* released into the water one metre from a female, will attract her to the source in minutes (Wabnitz *et al.* 1999). Nonetheless, pheromone signals in some mammals, such as mice, may be costly, as they secrete significant amounts of protein in their urine to make long-life signals (Chapter 5).

However, the costs of signalling in most animals are not limited to the simple cost of production. For example, in territorial animals, the time taken to maintain scent marks may be much more important (Chapter 5). Similarly, there are time and energy costs, in species which do not synthesise their pheromones themselves, of collecting plant materials used as pheromones or pheromone precursors (Section 1.4).

1.10 Pheromones in humans?

Sight and hearing are our most important senses, which makes us very untypical mammals. There are many exciting things going on around us just beyond our noses (although even the animals that do use pheromones extensively are usually only sensitive to their own; other odours pass them by). However, one of the intriguing possibilities emerging in recent research on human senses is that olfactory signals may be more important to us than supposed, at both conscious and unconscious levels. This is explored in Chapters 9 and 13.

1.11 Conclusion

Across the animal kingdom, more interactions are mediated by pheromones than by any other kind of signal. A wide variety of compounds are used as pheromones but there are many examples of the same compounds being used by different species. The design of the olfactory system makes evolution of pheromones very likely because there is selection for any odour cue that increases reproductive success or survival. There is less difference between vertebrates and invertebrates, in both the pheromones produced and in the range of behaviours that pheromones influence, than is often thought. Pheromones perhaps provide the supreme honest signals. Given the ubiquity of chemical communication among animals, chemical cues are likely to emerge as one of the key criteria animals use for choice of mate.

1.12 Further reading

For a general introduction to pheromones, written at a more popular level, there are two excellent books: Agosta (1992), in English, and Brossut (1996), in French. A stimulating discussion of the definition of pheromones in both invertebrates and vertebrates is given by Johnston (2000) (see also Müller-Schwarze 1999). Dusenbery (1992) offers a comprehensive and very readable discussion of sensory ecology. For pheromones in particular taxonomic groups see Johnston *et al.* (1999) and Marchlewska-Koj *et al.* (2001) on vertebrates, Hölldobler & Wilson (1990) on ants, Cardé and Minks (1997) largely on moths, and Hardie & Minks (1999) and Cardé & Bell (1995) for other insects.

In this book I have not attempted a review of animal communication as this has been done excellently by Bradbury & Vehrencamp (1998).