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Tristram D. Wyatt
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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

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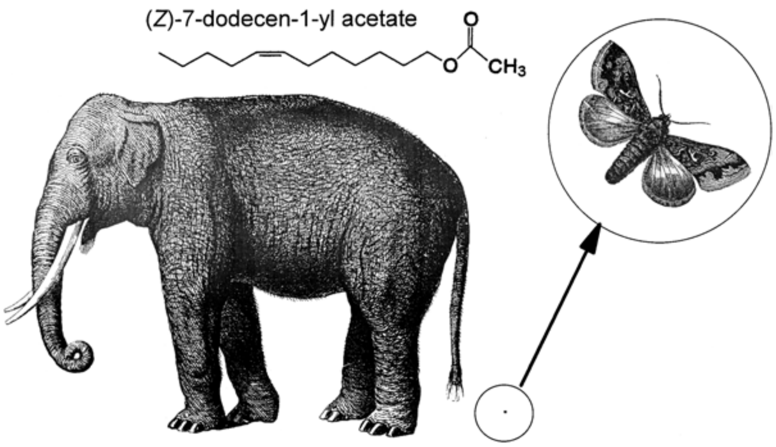

Fig. 1.1. The Asian elephant *Elephas maximus*, shares its female sex pheromone, (*Z*)-7-dodecen-1-yl acetate (top), with some 140 species of moth (Rasmussen *et al.* 1996). Animal figures from Harter (1979).

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).

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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).

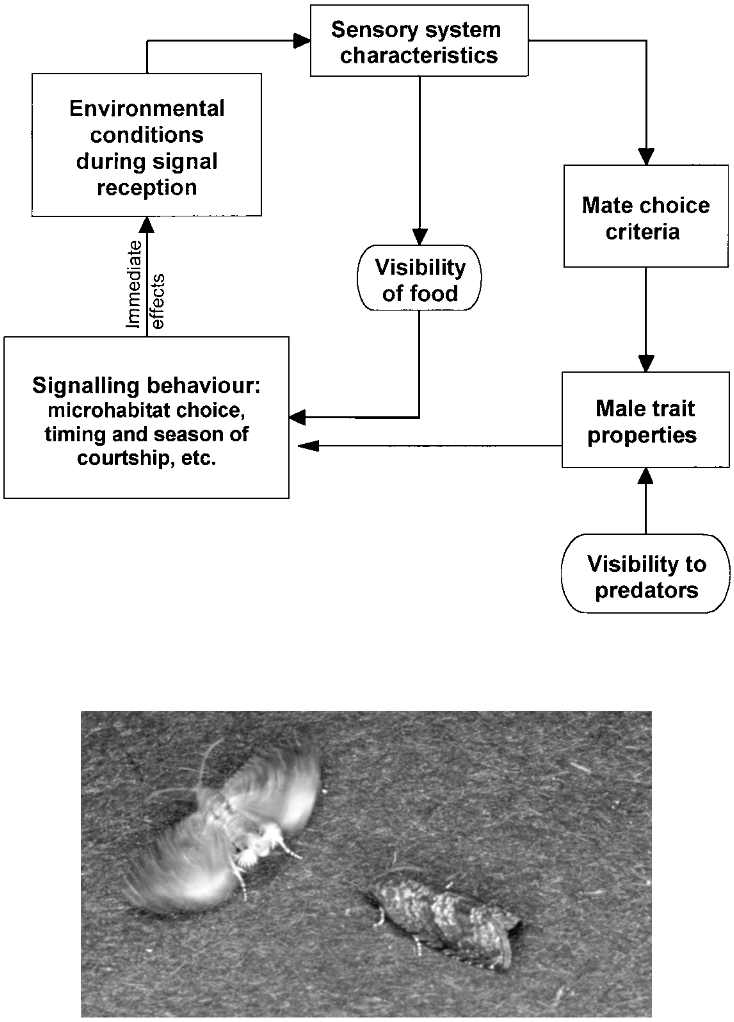

Fig. 1.2. Sensory drive. (Left) Signals that exploit the existing senses of the receiver will be selected for: this is the phenomenon of sensory drive. In the diagram, arrows indicate evolutionary influences (except for the one labelled 'immediate effects'). Predators can have a counter-selection pressure 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.

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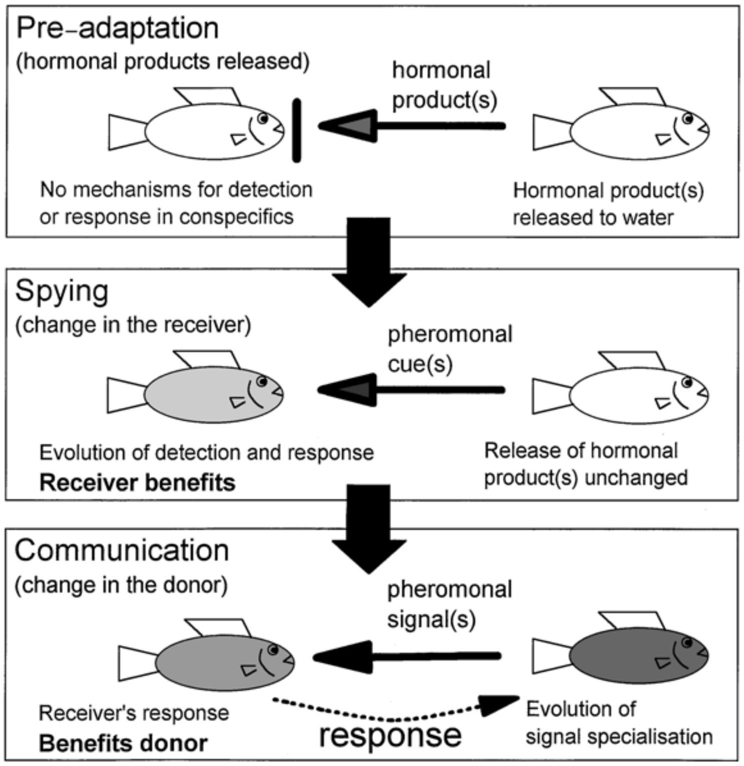

Fig. 1.3. Proposed stages in the evolution of a communication function for hormonal pheromones from pre-existing hormones by intraspecific eavesdropping or spying. In the 'spying phase' only the receiver benefits. The transition to bilateral benefit to both sender and receiver could occur later if there 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

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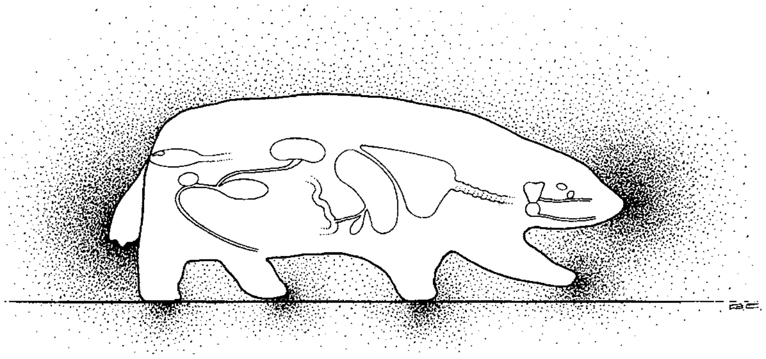

Fig. 1.4. A summary diagram of an imaginary mammal illustrating a variety of possible odour sources. The stippling indicates a potential distribution of odorants in the immediate environment. The following are shown: salivary glands and glands associated with the eye (e.g. preorbital glands); the lungs 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.