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PHEROMONES: CONVERGENCE AND CONTRASTS IN INSECTS AND VERTEBRATES¹

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1. INTRODUCTION

Chemical signals or pheromones are the most important signals for most of the animal kingdom. The organization of the olfactory system and brain, independently evolved across many taxa, makes it almost inevitable that chemical communication will evolve as animals are selected to respond to their chemical environment (Wyatt, 2003). As might be expected, pheromones play key roles in the lives of insects and vertebrates. However, the literature tends to separate these taxonomic groups rather than emphasising the similarities in the ways they use pheromones. For example, small molecules can be important in vertebrate signaling as well as in insects, though in terrestrial vertebrates these may be associated with proteins. In this chapter I would like to discuss the molecules used as pheromones, the paradox of signature odours in social insects and social mammals (where differences are the message), and finally the possible signal role of pheromones in complex social groups in mammals and social insects where only one female reproduces.

2. THE MOLECULES USED AS PHEROMONES

Elephants and moths are unlikely mates, so scientists and the general public were surprised when it was discovered 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. The shared use of a compound as a signal illustrates a relatively common phenomenon of independent evolution of particular molecules as

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signals by species that are not closely related (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 2.2). 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).

The importance of small molecule pheromones in vertebrate communication should not have been a surprise after the work over many years on the role of molecules such as brevicomin in mice by Novotny and others (Novotny et al., 1999; Leinders-Zufall et al., 2000). Similarly, the crested auklet (*Aethia cristatella*), a monogamous seabird, has recently been shown to produce a distinctive tangerine-like scent in the breeding season, of the volatile molecules *cis*-4-decenal and octanal (Hagelin et al., 2003; Jones et al., 2004). The possible importance of smell for bird courtship was long ago highlighted by Darwin (1871), reporting observations of the musk duck *Biziura lobata* in Australia. These examples are an important illustration that, like insects, mammals and other vertebrates 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 but this does not necessarily mean that their pheromones are more complicated.

However, unlike small molecule pheromones in terrestrial invertebrates such as moths, many terrestrial mammals may increase the activity of their small molecule pheromones by interaction with carrier proteins. For example, in mice the small volatile molecules are presented as ligands of Mouse Urinary Proteins (MUPs). The MUPs provide a slow release of the volatile signal and the highly variable MUPs may also provide individuality to the signal (Hurst et al., 2001; Beynon and Hurst, this volume; Hurst and Beynon, this volume). As far as I know, there are no examples among the invertebrates of combining small molecules with proteins.

Whereas volatility is a key signal design feature of pheromones in air, solubility of molecules is perhaps the functional equivalent in water – and many soluble peptides are pheromones in their own right. 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 and barnacle egg hatching pheromone. 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 is a large cation. Many other aquatic animals use polypeptides as chemical signals. The first peptide pheromone to be identified in a vertebrate was the decapeptide, sodefrin, in the Asian red-bellied newt (*Cynops pyrrhogaster*) (Kikuyama et al., 1995) and the first peptide pheromone in anurans, splendipherin, the male aquatic sex pheromone of the tree frog *Litoria splendida* (Wabnitz et al., 1999; Apponyi and Bowie, this volume). Aquatic invertebrates also use peptides as sex pheromones, for example in the sea-slug mollusc *Aplysia* (Painter et al., 1999). Barnacle larvae settling out of the plankton ensure they settle in good sites by having a very specific response to certain peptides of their adult conspecifics.

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 social interactions. 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. There is also evolution in the sensory systems 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; 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.

4. SPECIES SPECIFICITY

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). 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 multicomponent 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 dehydro-*exo*-brevicommin and 2-*sec*-butyl-4,5-dihydrothiazole (Novotny et al., 1999), each of which is inactive alone. Similarly, in the goldfish, while each of two female prostaglandin pheromones, F2 α (PGF2 α) and 15-keto-PGF2 α , have similar effects on male behaviour when presented singly, both are needed together to stimulate a gonadotropin surge in males (Stacey and Sorensen, 1999). It is possible that other pheromone components add species specificity in these fish.

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5. DISTANCE FOR SIGNALS

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. In both vertebrates and invertebrates, 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 (Eisner and 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 and Reagan, 1990). Perhaps at the extreme of this continuum are the molecules passed, together with sperm, to the female during mating in many species: for example, the fruit fly *Drosophila melanogaster* and garter snakes (see references in Wyatt, 2003).

6. HONEST SIGNALS

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 (Eisner and Meinwald, 1995). 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 (LeMaster and Mason, 2002). In mammals, production of pheromone is directly related to hormone levels and so scent marks will tend to be honest (Ferkin et al., 1994). Animals such as mammals and lizards that scent mark their territories leave signals that are inherently reliable – only if the owner does own the territory will his marks exclusively cover it (Gosling and Roberts, 2001). 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 and Rich, 1999), the major cost may be that of maintaining the advertised status.

7. SOCIAL RECOGNITION – SIGNATURE ODOURS

One of the most important uses of odour signals in both mammals and social insects is as signature odours, chemical cues used for social recognition. Signature odours do not fit the original pheromone criterion of a defined chemical mixture eliciting particular behaviour or other response (Karlson and Lüscher, 1959). The cues used for social recognition of kin, clans, colony members and the like are complex, greatly varied mixtures of many compounds. The differences between the odour mixtures are the

message. The resulting chemical signatures of both mammals and social insects are complex and variable mixtures, giving a forest of peaks on a gas chromatograph trace, in contrast to the small number of defined peaks for the sex pheromones of moths and other insects. These complex mixtures reflect the overlaying of many different messages.

For example, the saddle-back tamarin (*Saguinus fuscicollis*) a South American primate, produces chemical messages which identify species, subspecies, individual and gender, and may also contain information on social status (Epple et al., 1993). Social insects carry a chemical message on their cuticle that includes information about their species, colony, caste, age and gender. In both mammals and social insects the cues giving reproductive status, in particular ovarian status, may be the key to the role of pheromones in reproduction in social animals. While signals of caste, gender, life stage or species may not vary much within the species and could thus be said to be anonymous (Hölldobler and Carlin, 1987), the variability of colony and kin recognition chemical signatures is what gives them their specificity. In the case of the honeybees, at the entrance to the nest there are guard bees with a specific and characteristic posture. They will challenge any bee trying to enter the hive and if only it has the right particular signature will it be let in; strangers are attacked and killed. And of course we are familiar with similar recognition phenomena using odour cues across the vertebrates, for example among beavers (Sun and Müller-Schwarze, 1999) and hamsters (Johnston, this volume) (incidentally, people are also good at recognising their own family by smell – see Wyatt, 2003 for review).

8. PHEROMONES AND REPRODUCTION IN SOCIAL GROUPS: CONTROL OR SIGNALLING?

In social insect and social mammal species such as honey bees and naked mole rats, only one female reproduces. In social insects, queen pheromone signals may be honest cooperative signals, not control. Might these ideas apply to social mammals?

Pheromones are important for the many species of mammal that live in social groups with animals sharing and defending the same territory and for species of social insect that live in colonies. In some societies of mammal and social insect, cooperation is taken a stage further, with a reproductive division of labour: some individuals (helpers or workers) do not themselves reproduce but instead help to rear the offspring of other group members, usually the helpers' sisters or mothers. In the social insects (ants, termites and some bees and wasps), this is termed eusociality. The reason that such altruistic reproductive behaviour can persist is kin selection, which allows the helpers to gain their inclusive fitness indirectly by rearing copies of their genes in their brothers and sisters (Bourke, 1997). Hamilton's rule for kin selection predicts that altruistic behaviour will be more likely to be selected for if the individuals are closely related (and thus more likely to share the helper's gene for helping) and if the decrease in the actor's personal fitness is relatively small compared with the increase in the recipient's fitness (Hamilton, 1964; Keller and Chapuisat, 1999).

One way of describing the sharing of reproduction in social groups is by the term reproductive skew, which describes how much the spread of reproduction differs from an equal share for each member of that sex in the group (Keller and Reeve, 1994). Reproductive skew for males or females in a group ranges between 'zero', with equal shares (where all group members of a sex reproduce, for example female spotted hyenas),

and 'one', in highly skewed animal societies in which effectively only one or a few members reproduce (for example, females in termites, ants, honeybees and the naked mole rat). Species with small colonies can be highly reproductively skewed, for example bumblebees, paper wasps, and the common marmoset.

Using reproductive skew as a measure, one can envisage social animals of all kinds placed on a eusociality continuum from no skew to high skew (Lacey and Sherman (1997), but see counterexamples of Crespi and Yanega (1995) and Crespi and Choe (1997)). At the high skew end, eusocial species show cooperative care of the brood, overlap of adult generations (with offspring helping parents) together with reproductive division of labour, with some individuals specialised for reproduction (called queens or kings in social insects), and other more or less sterile individuals showing reproductive altruism (Wilson, 1971). In addition to the well-known highly eusocial insects among the Hymenoptera (wasps, bees, and ants) and Isoptera (termites), and among mammals (naked mole rats), there is a growing list of other eusocial animals, with species of eusocial spiders, aphids, gall thrips and coral reef shrimps all now recorded.

Eusocial societies have cooperative broodcare but in even the most cooperative societies, genetic conflicts of interest are inevitable (Emlen, 1997). In particular, group members will compete over who gets to reproduce. In most mammalian societies and in those social insect species in which almost all individuals could potentially reproduce, fierce fighting determines who reproduces. Perhaps surprisingly at first sight, in some of the most skewed societies, with the greatest morphological differences between the queen and workers, and in some mammals, pheromones produced by the dominant female 'settle the dispute', by appearing to stop subordinate females from reproducing. In social insects this phenomenon was traditionally viewed as pheromone control by the queen. An alternative view is gaining ground: that the queen's pheromones are cooperative signals, not control by a form of chemical aggression. The proposals were outlined first for social insects so I describe these first, but the same or similar points probably apply to cooperatively breeding (eusocial) mammals (Section 4.2).

9. SOCIAL INSECT QUEEN PHEROMONES

The coordination and integration of colony activities, in particular recruitment for foraging and defence, has been an essential contribution to the success of social insects: the road to sociality was paved with pheromones (Blum, 1974). Pheromones play a central role in these activities and in other functions such as recognition (of caste, sex, kin, colony, and species), caste determination, trophallaxis (mouth-to-mouth transfer of food), nest entrance marking and colony reproduction (Winston, 1992). Termites show convergent evolution of chemical signaling with the eusocial Hymenoptera.

Eusocial insect colonies are characteristically divided into two castes, reproductives and workers: a few individuals, queens or kings, are reproductive and workers reproduce little or not at all. The kin conflict between workers and the queen within social insect colonies can be over the level and timing of resources put into rearing reproductives, their sex ratio, and egg laying by workers (Keller and Reeve, 1999). However, despite the conflict, dominance with open aggression by the queen is virtually absent in more advanced insect societies, which have effectively sterile, morphologically distinct, worker castes (Wilson, 1971, p. 302). As colonies increase in size, it is hard to see how physical domination could work for more than a few tens of animals let alone the 500,000

individuals in a weaver-ant colony, controlled by a single queen (Wilson, 1971, p. 432; Hölldobler and Wilson, 1977). Instead, in advanced insect societies, pheromones take the place of fights. The phenomenon of queen pheromone influence within social insect colonies is clear in advanced ants, wasps, and bees. Pheromones play a similar role in termites. The queen's primer pheromones affect the colony production of reproductives by influencing the behaviour of workers; this is important both for maximising her reproductive fitness and that of the colony (Winston, 1992). Her pheromones also appear to cause the workers not to develop their ovaries.

News of the health of the queen is continually spread throughout a colony of social Hymenoptera, mediated by the queen's pheromones passed from one colony member to another (Winston and Slessor, 1992). The queen is surrounded by a retinue of eight to 10 workers, which constantly change as new workers approach and lick or touch her with their antennae. After picking up the queen mandibular pheromone (QMP), these workers groom themselves and then act as messengers by running through the rest of the colony for about 30 minutes, making frequent reciprocal antennal contacts with other workers, and passing on the QMP by contact, as if playing chemical tag (Seeley, 1979). These queen pheromone effects can be dramatically demonstrated by removing the queen and seeing the rapid changes in worker behaviour and physiology; these can start in as little 30 minutes in honeybees (*Apis mellifera*). Without the queen pheromone, workers start to rear new queens. Keller & Nonacs (1993), following Seeley (1985) and others, argue that the pheromone effects are not the consequence of pheromone control by the queen but instead that workers are using the queen pheromone as an honest signal that the queen is there and that the workers' response to the pheromone increases their inclusive fitness as much as that of the queen. The queen could perhaps control the colony by deception, fooling workers to act in her interest rather than theirs, but Keller and Nonacs (1993) argue that dishonest signalling in the colony is unlikely to be evolutionarily stable and conclude that queen-produced pheromones are honest messages of queen activity or presence. There are possible scenarios for the evolution of control by pheromones (Bourke and Franks, 1995, p. 239) but, nonetheless, if it was not in their interest to respond, workers or subordinate queens would evolve to ignore queen pheromones. The genetic variation in worker sensitivity to queen pheromones, on which selection could act, has been demonstrated in honeybees (Slessor et al., 1998). Similarly, there will be selection for queen behaviour that avoids costly queen-worker conflict that reduces colony productivity (Keller and Nonacs, 1993). Evolutionary solutions in the eusocial nest may be most stable where benefits are shared between workers and queen, pulling in the same direction (Seeley, 1995, p. 11). If queen pheromone is a signal to say that 'I am laying eggs' then one should expect the time course of pheromone production to match egg laying and to correlate with fecundity, which it does in honeybees and fire ants (Winston and Slessor, 1992; Vargo, 1998; Vargo, 1999). A honeybee queen's queen mandibular pheromone blend changes with age (Winston and Slessor, 1992). The full blend, including the aromatics, is only produced after mating and when she begins to lay eggs.

The reason that physical fights do not occur is not because the pheromone controls the workers but because their interests often match those of the queen. The strong morphological specialisation of the queen as an egg and pheromone factory and of the workers for their many colony-sustaining roles means that an individual worker gains more by helping to rear the queen's eggs than by laying its own. With specialised morphological castes, the queen pheromone may be a relatively low-cost cooperative

signal (Keller and Reeve, 1999). In a cooperative signal, with benefits to both sides, evolutionarily stable signals do not have to be differentially costly to signalers with high values of the signalled attribute (which is the central assumption of the Zahavi handicap model for signals) (Keller and Reeve, 1999). A further pheromone-mediated effect is the way that any eggs that *are* produced by workers are destroyed by other workers, termed 'worker policing'. Worker honeybees have ovaries and although they cannot mate, they can lay unfertilised eggs which become males. Workers destroy the eggs laid by other workers because if the queen is multiply mated, workers are on average more related to the sons of the queen than to the sons of other workers (Ratnieks, 1993). Worker policing is made possible because the queen's eggs can be recognised by a pheromone mark from her Dufour's gland (Ratnieks, 1995). In nests with a queen, almost all the eggs produced by workers are destroyed (Ratnieks and Visscher, 1989). Workers also attack workers with well-developed ovaries (Visscher and Dukas, 1995). A genetic basis for worker policing has been found in honeybees (Montague and Oldroyd, 1998). Worker policing is evolutionarily stable because it benefits the queen *and* the average worker (Vander Meer and Morel, 1995; Bourke, 1997). Even in once-mated single queen colonies, in which workers would be more related to their own sons than to the queen's sons (Bourke, 1997), workers might not reproduce if it reduces the efficiency of the colony.

10. PRIMER PHEROMONES AND REPRODUCTION IN SOCIAL MAMMALS

It is in social mammals, those living in groups on shared territories and especially those breeding cooperatively, that mammal primer pheromone interactions have reached their greatest complexity and subtlety. Pheromone stimuli in social mammals can induce hormonal changes, affect the success of pregnancy, alter the course of puberty, modulate female cyclicity and ovulation, and modulate reproductive behaviour and aggression. These physiological effects include the Bruce and Whitten effects in mice.

Cooperative breeding, with alloparental care in which members of the social group assist in rearing young that are not their own, is common in some mammalian taxa, in particular rodents and canids. For example, cooperative or communal nesting and care of young have been reported for 35 species and from nine of 30 rodent families (Solomon and Getz, 1997). Cooperative breeding covers a wide range of behaviour depending on reproductive skew in the species, from plural breeders with all females reproducing through to singular breeders, social groups in which only one female breeds together with 'helpers-at-the-nest' (Solomon and French, 1997).

Most of the pioneering work on mammal primer pheromones was on social rodents such as house mice which are plural cooperative breeders (all females breed, although not all males). Female house mice suckle each other's young and cooperatively defend the nest. Characteristic of these societies is an interplay of dominance (in particular between males), sex, and population density.

In plural breeders, the effects of females on each other are mutual, but in singular cooperative breeding species, such as beavers, prairie voles or the common marmoset, the dominant female suppresses reproduction by the subordinate females. The parallels between social organization in these species and social insects are explored in Section 4.5. It is worth noting that some of these social effects, such as influences on puberty timing, are also seen in solitary rodent species under some conditions.

11. REPRODUCTION IN SINGULAR COOPERATIVELY BREEDING MAMMALS WITH HIGH REPRODUCTIVE SKEW

Reproductive suppression is common in singular cooperatively breeding mammals in which typically only one dominant female breeds. As in many social insects, the subordinate females are often her daughters, and in mammals, as in social insects, signals affecting the reproduction of subordinates range, in different species, from physical dominance to pheromones. Most mammal social groups do not use pheromones for this. For example, in the most eusocial mammals, naked mole rats (*Heterocephalus glaber*), with colonies of up to 300 non-breeding workers, the suppression of worker fertility by the queen is not pheromonal (Faulkes and Abbott, 1993). Instead, the queen, which is larger than other colony members, exerts her reproductive suppression on the non-breeding workers by physical dominance, 'shoving' and pushing subordinates down the tunnels (Bennett et al., 1999). In singular breeding canids the mechanism has only been identified in the grey wolf (*Canis lupus*): subordinates could reproduce but do not because their mating attempts are interrupted by their parents (Asa, 1997).

It is in some of the singular cooperatively breeding rodents and the New World primates that there are strong pheromone parallels with advanced social insects (Solomon and Getz, 1997; Carter and Roberts, 1997; Abbott et al., 1998). We know most about the reproductive biology of prairie voles (*Microtus ochrogaster*) and the common marmoset (*Callithrix jacchus*). In both species, many of the effects are mediated by odours for recognition, signal or primer pheromones.

In prairie voles, monogamous pairs and their offspring form the core of a communal breeding group. Continued breeding by the original pair and concurrent inhibition of reproduction of other members of the group is promoted by reproductive suppression of offspring, incest avoidance, social preferences for the familiar sexual partner and active defence of territory and mate (Carter and Roberts, 1997). Almost two-thirds of prairie voles young remain in their parents' nest (philopatry). These non-breeding subordinates engage in all parental behaviour except nursing (Solomon and Getz, 1997).

The young of the common marmoset also stay within their natal group into adulthood and do not breed. All group members, of both sexes, contribute to infant care, and may groom, tend (babysit) and transport young, but in addition may help with post-weaning feeding of infants (Tardif, 1997; French, 1997). The evolution of cooperative breeding may be a two-step process (Lacey and Sherman, 1997). The first step is the presence of ecological conditions that encourage natal philopatry: staying on the parental territory rather than trying to breed on one's own. This could be because of high costs, or low success, of independent breeding or dispersal, and would lead to groups containing two or more generations of related adults. The second step is the evolution of alloparental care, depending on the benefits to kin and ultimately on inclusive fitness. Long-term studies of the costs and benefits of helping in mammals and birds give widespread confirmation that helpers frequently do gain large indirect genetic benefits by helping to rear collateral kin (Emlen, 1997).

For prairie voles, indirect benefits from alloparenting could include better survival of sibling pups, faster pup development and reduced workload for parents, thus allowing the parents to produce more litters (Solomon, 1991; Wang and Novak, 1994). For common marmosets, the initial benefits of alloparenting might originally have been increased survival of young, but once set on the path of helping, it has become a requirement as the

energy costs of breeding are so high that a lone pair is effectively incapable of reproducing successfully (French, 1997). Cooperation between animals may also be needed for the successful founding of new marmoset groups (Abbott et al., 1998). The importance of ecological factors for the fine balance of benefits and costs to helpers is shown by the patchy distribution of singular and plural cooperative breeding across related genera. Even in the same genus there may be species that are singular breeders and others that are plural breeders, for example prairie voles, and common voles respectively. Populations of the same species in different places, for example prairie voles (Roberts et al., 1998), may show more or less alloparental care according to local ecological conditions.

12. INHIBITION OR SUPPRESSION OF SUBORDINATE REPRODUCTION

The size of social groups is not the deciding factor for the transition to pheromonal control in mammals, as species that use pheromones in reproductive suppression tend to have small family groups. More species of cooperatively breeding mammals may turn out to use pheromones than is currently realised. Two effects keep subordinate female prairie voles pre-pubescent (Carter and Roberts, 1997). First, they delay puberty as long as they are exposed to only familiar males (father or male sibs) recognised by odour. Second, the stimulatory effect of urine from an unfamiliar male is overruled by inhibitory pheromones in the urine of their mother and sisters. Subordinate females thus remain functionally pre-pubescent and provide support to the communal family. The suppression of subordinate males is likely to be behavioural as they still produce sperm but do not mate. Suppression of ovulation in subordinate common marmoset females is by a combination of olfactory, visual and behavioural cues but once reproductively suppressed, this can be extended by odour alone: if a subordinate female is taken from the group, she will start her ovarian cycle but disinhibition is delayed by about 20 more days if she is exposed to the scent marks of the dominant female. A feature of reproductive suppression in mammals is the variety of mechanisms controlling singular cooperative breeding, even in closely related species. For example, unlike the case of the prairie vole, pheromone cues are not sufficient to suppress oestrus in the pine vole (*Microtus pinetorum*) (Brant et al., 1998). Similarly, in the golden lion tamarin (*Leontopithecus rosalia*), a member of the same family as the marmosets, subordinate females ovulate and are physiologically capable of mating but do not do so (French, 1997).

13. PARALLELS BETWEEN SOCIAL MAMMALS AND SOCIAL INSECTS

The response of subordinates in marmosets or prairie voles may be an adaptive response to signals from the principal female, analogous to the worker responses to signalling by social insect queen pheromones (Keller and Nonacs, 1993). Subordinates in marmosets, prairie voles and social insects may have evolved specific, adaptive responses to signs of subordinate status that lead them to respond with alloparental and other behaviour that increases their inclusive fitness by helping the society or family group (Abbott et al., 1998). Like workers in social insect colonies, subordinate female marmosets show many behavioural, neuroendocrinological and physiological differences from dominant females (Abbott et al., 1998). The differences include both the

alloparental tasks undertaken by subordinate marmosets and also their physiological responses to pheromones and other cues from the dominant female. Abbott *et al.* (1998) suggest that the behaviour and physiology of subordinates seem to be a stable alternative to dominant status, not a state of generalised stress imposed by the dominant female and endured by the subordinates to their physiological detriment (there is no elevation in the circulating hormones, cortisol or prolactin, associated with stress).

A further parallel comes from developmental pathways. The spontaneous alloparenting behaviour and high likelihood of remaining in the parental nest (philopatry) of subordinate prairie voles are influenced by their prenatal hormonal environment in the uterus (Roberts *et al.*, 1996). I wonder how different this is from developmental influences on social insect larvae as they are directed to worker or queen roles?

The roles of pheromones in influencing who reproduces in social groups of both insects and mammals are clearly complex. The interplay between pheromones and hormones, and the way that closely related species achieve similar ends by either a pheromone or behavioural dominance route, should make us reconsider rigid categories. What pheromones and behavioural dominance share in their mechanism of action is, ultimately, an effect on hormone release from the hypothalamus in mammals, and from the corpora allata in insects (Wyatt, 2003). Could one argue that pheromones and behavioural dominance are equivalent at the ultimate physiological level?

14. CONCLUSION

The individuals in animal societies interact via a complex web of semiochemical signals. Eusocial species of social insects and social mammals are characterized by reproductive division of labour. In some species, group members fight to establish which animals will reproduce. Other species use pheromones that act as signals rather than as coercion. The mechanisms used in social insects and in mammals have many similarities.

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