Sociobiology of Communication

An interdisciplinary perspective

EDITED BY

Patrizia d'Ettorre and David P. Hughes

The extended phenotype within the colony and how it obscures social communication

David P. Hughes

10.1 Introduction

'This is a work of unabashed advocacy.' So Richard Dawkins began his seminal contribution to evolutionary biology entitled *The Extended Phenotype* (1982). So too, in a way, is this chapter. I do not wish to advocate the central theorem of the extended phenotype because that, in the intervening 25 years, has gained general, if not universal acceptance (Dawkins 2004). Rather, what I want to advocate is that the topic of this book, social communication, may be a misnomer if one 'individual' in a communication **network** is a chimera of two that have widely diverging interests. What this chapter is about is the intra-organismal **conflict** resulting from **parasitism** and how the phenotype, which is the originator of **signals** in all social communication, may in fact be an extended phenotype of the parasite. If so it will impact upon, and ultimately obscure, social communication.

I will advocate that if we reconsider the phenotypic features involved in social communication, be it bird song or the honeybee waggle dance, in the context of parasite extended phenotypes we will gain a greater understanding about how conflict within organisms shapes social communication among organisms. In order to do this we will need to view familiar phenomena from unfamiliar angles. Thus, I fall in step with Dawkins, whose book was not a laying down of facts to convince his audience of the generality of his theory; in fact it wasn't even a theory, but a *way to view facts* that he advocated.

I begin by defining the extended phenotype and provide examples both from biology generally and from the social insects specifically. Quite apart from the need to reacquaint readers with the extended phenotype we will need to precisely define our subject matter because of recent developments in evolutionary biology that centre on the extended phenotype. I will also briefly detail key information relating to the evolutionary biology of social insects which includes the ways in which they communicate. Once that is achieved I will encourage an alternative view of a colony of social insects as a single superorganism. This much maligned term has experienced a renaissance of late, and here I will discuss its usefulness for social communication.
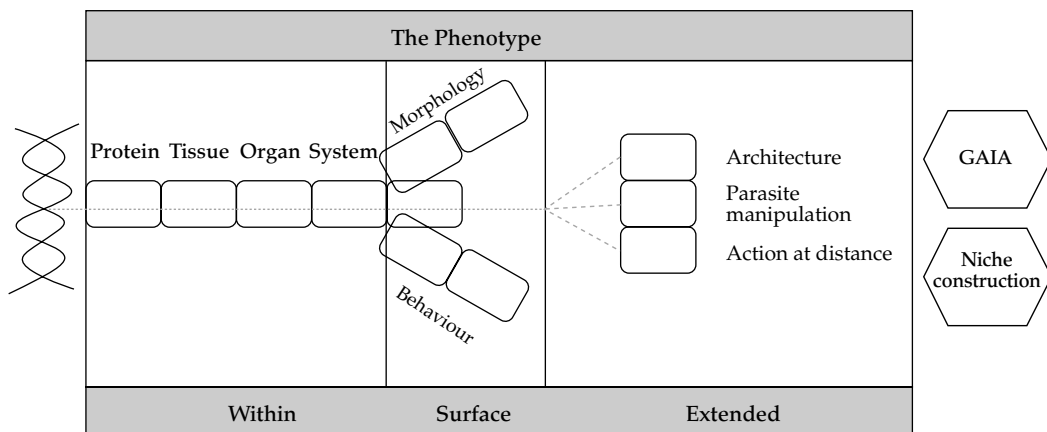
10.2 The extended phenotype

The paradigm of the gene as the unit of **selection** emerged during a period of much debate between advocates of individual and group level selection and through the work of Hamilton (1963, 1964a,b). It was subsequently developed as a transparent concept by Dawkins in his **selfish gene** approach (Dawkins 1976) and became the foundation for sociobiological theory (Wilson 1975). As an historical aside it was recently emphasized that Wilson's sociobiological stance leant more towards group rather than individual selection and that it is Dawkins who deserves the major credit for the current association between sociobiology and gene

level/individual selection (Segerstråle 2007). What the paradigm of the gene as the unit of selection states is that it is genes alone which are transferred between generations; the organisms in which genes reside and their phenotypes are the means by which transmission is secured. Organisms are vehicles and genes are replicators. **Natural selection** chooses among variation in phenotypes but the information encoding these phenotypes and, ultimately, the unit which is selected is the gene (see discussion by Mayr 1997).

The phenotype has principally been considered a trait of the individual organism. Examples are eye or flower colour, antler length, butterfly wing spots, behaviour, or chemical signals released into the air, to name just a few. But such foci only reflect the convenience with which we could study those easily visible attributes of organisms (Dawkins 1990). Increasing advances in cellular and chemical biology allow a fuller exploration of hitherto less obvious phenotypes of the organism such as the surface of cells, tissues, and organs (Chapter 12) or protein signatures in rodent urine (Chapter 6). Dawkins (1982) also advocated an additional level of the phenotype, but what was, and still remains, novel is that this additional level of phenotype is not physically attached to the organisms whose genes are encoding it, that is the

extended phenotype (henceforth EP; see Fig. 10.1). The first of the three EPs to be considered was animal architecture which Von Frisch (1974) called 'frozen behaviour'. The work of Michael Hansell gives an excellent insight into this little studied, but fascinating, component of behaviour (Hansell 1996, 2004). The example *par excellence* is the beaver dam which is a physical representation of beaver behaviour that increases the **fitness** of the genes encoding the building behaviour. The second EP is parasite manipulation of host behaviour. This topic was elegantly reviewed by Janice Moore (2002). An exemplar of this field is the suicidal behaviour of crickets infected by hairworms, whereby they jump into water so the adult worm can impressively exit from the thrashing body of its drowning host (Thomas *et al.* 2002). This behaviour is controlled by parasite, and not host, genes (Biron *et al.* 2006). The third and final EP is action at a distance, and here a parasite example was used which is the manipulation of host behaviour by cuckoo chicks. In this case the chick is not physically associated with the host, as in the case of hairworms, but influences the expression of its behavioural phenotype nonetheless. Dawkins further discussed how action at a distance need not be confined to parasite–host relationships but can occur elsewhere, such as between conspecifics,

Figure 10.1 The phenotype, extended out from the gene, showing three levels: within the organism, on its surface and extended away from the organism. The dotted line links them all to the gene. Examples of morphology are colour and size and examples of behaviour are song and courtship dances. The box like representation communicates limits for the phenotype. Designations that have been illogically claimed as phenotypes are in hexagons outside the box.

as in **pheromone-**based social communication (Chapter 5).

The extension of the phenotype beyond the physical borders of the organism in which the encoding genes can be found is a logical one, just as examining other phenotypes that are inside the organism such as proteins, cells, tissues, and organs. There is a chain of phenotypes (Fig. 10.1) extending from the gene, and in this chapter I discuss the links that are beyond the organism's traditionally considered phenotype. Others in this volume (see Chapter 12) advocate moving backwards down through less obvious phenotypes within the organism such as proteins, cell products, and tissues. Yet despite its logic the language of *The Extended Phenotype* (Dawkins 1982) has not been universally adopted by biologists studying animal behaviour (Dawkins 2004). It has not, conversely, suffered from any sustained criticism of the fundamental positions. If anything it has recently gained increased general interest once more because of its suggested role in niche construction theory (Odling-Smee *et al.* 2003; Laland 2004; Laland and Sterelny 2006) (Fig. 10.1; and see also Chapter 15).

10.3 Social insects and their extended phenotypes

The ants, termites, wasps, and bees are the taxa we think of as the social insects. The technical term is **eusocial**, which is defined as having overlapping generations, cooperative care of the brood, and division of labour that typically means a reproductive division with the majority of individuals being sterile (Wilson 1971). There have been other definitions of eusociality (e.g. Crespi and Yanega 1995). There are many other taxa besides ants, termites, wasps, and bees in which we find eusociality; examples are mites, spiders, shrimp, thrips, aphids, beetles, and naked mole rats (Wilson 1971; Crespi and Cho 1997; Bennett and Faulkes 2000; Costa 2006). Even humans and pilot whales have been called eusocial (McAuliffe and Whitehead 2005; Foster and Ratnieks 2005). In this essay I will restrict myself to the traditionally defined social insects (ants, termites, wasps, and bees) since I know these best, but my arguments are applicable to the other taxa. Also, for convenience, and in line with most authors, I will use the term social insects, rather than eusocial insects (see also Chapter 5).

Social insects live in family-based groups where a minority of individuals reproduce (queens and kings) and the majority (the workers) are functionally sterile and collect resources to provision the offspring of the reproductives. Such **altruism** is considered adaptive for workers since the offspring are usually their full siblings and by helping they gain indirect fitness benefits (Hamilton 1963). The role of **kin selection**, as it is called, in the evolution and maintenance of such societies was recently challenged by E. O. Wilson, one of its early supporters (Wilson 2005; Wilson and Hölldobler 2005) but the prevailing view is still that kin selection is essential (Foster *et al.* 2006). Social insects live in colonies that vary in size from 10 individuals in hover wasp societies (Turillazzi 1991) to more that 10 million in army ant societies (Hölldobler and Wilson 1990). They can occupy living spaces ranging in size from an acorn (*Temnothorax*) to 3 m high mounds (termites). A great deal of communication goes on inside societies, and studies of social insects have been instrumental to the development of communication theory (Hölldobler and Wilson 1990; Ross and Matthews 1991; Seeley 1995; Abe *et al.* 2001). Obvious examples are communication of status in the linear dominance hierarchy first discovered in paper wasps (Pardi 1948; Turillazzi and West-Eberhard 1996), pheromone communication developed extensively in ants (Wilson 1959; Hölldobler 1995), language among insects in the honeybee waggle dance (Von Frisch 1968; Seeley 1995), and teaching (Franks and Richardson 2006; Richardson *et al.* 2007). Social insects communicate with other members of the society: signalling identity (which colony they belong to); soliciting of food by larvae and adults soliciting nutritious regurgitations from larvae; individuals signalling their reproductive status and their position in a hierarchy (submissive posture, **badge of status**) or describing the location and quality of food (waggle dance). Individuals also communicate with other societies: signalling identity (nest of origin), aggressive displays signalling fighting ability and resource ownership. Collective actions involving many individuals also have communicative roles and usually towards potential threats: Asian honey

bees (*Apis dorsata*), which form a bee-curtain across their comb ripple *en masse* to confuse predatory birds (Kastberger and Sharma 2000), paper wasps (*Polistes)* dance *en masse* to threaten parasitoids (West-Eberhard 1969) and, most impressive of all to me, the production of sound up to 5 m away via cooperative wing beating (*Syanoeca surinama*, a wasp) against the inside of a corrugated carton nest to deter mammalian predators (Rau 1933). The latter report, which is anecdotal, has a recent parallel in African bees whose sound was shown to deter herds of elephants (King *et al.* 2007). So, social insects communicate in a wide range of modalities (**channels of communication**) among colony members, between colonies, and even towards predators and parasites.

This chapter is about parasites manipulating social insect behaviour and how that may affect the range of communication discussed above. But in a chapter about the EP (of parasites) I would be negligent if I didn't spend a few words on the EPs of the social insects themselves since they too are highly impressive. The first is animal architecture. The social insects are rivalled only by humans in their ability to construct artefacts. No bird's nest, spider's web, or caddis shell rivals the multifunctional cathedral mounds built by fungus-growing termites; these 3 m high, rock-like structures, standing in sun-baked desert brush, contain within them sophisticated natural air-conditioning units, crop-fungus-growing combs, brood nurseries, refuse piles, networks of passageways, and, at the centre, a rock-hard protective chamber in which the king and the 3000 eggs per day egg-laying machine that is the queen, reside (Abe *et al.* 2001). Even the multifunctional beaver dam with its homely lodge is merely a well-placed branch and hollowed out mound of dirt by comparison. A termite mound is all the more impressive when we recognize that the architectural feat exists as a greenhouse to grow a rainforest adapted fungus in such places as the dry savannah (Aanen and Eggleton 2005). The second of the EPs, that of parasite manipulation of host behaviour, does not have any examples among the social insects as none are internal parasites. But if we view the colony itself as a host, as it is correct to do because of **inclusive fitness** that merges the genetic interests of individuals with that the

whole colony through kin selection (Sherman *et al.* 1988, p. 263; Schmid-Hempel 1998) then there are examples of internal parasites of the colony causing behavioural changes. These are '**social parasites**' that, through chemical, morphological, and behavioural means induce workers to care for the parasite's offspring in preference to their own (Chapter 4). Finally, genetic action at a distance is an EP with many interesting examples among social insects. My favourite is among queenless ants (*Dinoponera quadriceps*) in which there is a hierarchy such that the alpha 'worker' reproduces but beta, gamma, delta, and so on do not (Monnin *et al.* 2002). An overly ambitious beta worker who challenges a fit alpha risks being dobbed with a droplet that signals to the others to immobilize the insurgent, sometimes effective in excess of 24 hours. The genes of alpha produce a phenotypic behavioural response among gamma and delta workers, at a distance (see also discussion of chemicals in social parasitism in Chapter 4 and pheromones in Chapters 5 and 7). Another example is the aforementioned production of sound by wasps and bees to deter predators.

10.4 Superorganism and communication

Having provided a short background to social insects and their EPs I now want to discuss the valid use of the metaphor of the colony as a superorganism, since it is especially useful for considering ways in which communication can be obscured because of parasite EPs. The large sizes of social insect societies, the multiple examples of collective action, and the ways in which society members are often behaviourally or morphologically specialized for certain tasks, together with the localization of the colony in a bounded structure that is built by multiple individuals, has led to the view that the whole colony is a superorganism (Wheeler 1911). This view, though intuitively appealing, lost favour for two reasons. The first was the supposed conflict it had with individual or gene-level selection. However, no such conflict exists so long as the superorganism is viewed within the levels of selection framework (Bourke and Franks 1995, pp. 64–66; Reeve and Keller 1999). In addition we

need to clarify the mechanistic/functional division in our approach (see Chapter 11). It is important to be clear and precise when adopting a metaphor, and it should be stressed that the superorganism, just like the organism itself, is not a replicator (Dawkins 1990). The second reason why the superorganism concept declined in popularity was the limitation of a primarily analogical approach (Hölldobler and Wilson 1990, p. 358). The concept was good, but not particularly useful when investigators proceeded to examine the fine details of colony life such as reproductive decision-making in the light of kin selection. That is because different individuals within a colony may have different goals. Colony members do not come into conflict over resource acquisition but can, and do, conflict over resource allocation (Boomsma and Franks 2006). A clear example is the conflict between workers and queens in hymenopteran societies over the sex ratio of the reproducing offspring; the former favour a 0.75 bias towards females and the latter an equal sex ratio (discussed extensively in Bourke and Franks 1995). There is also conflict between workers if one decides to reproduce, and here we see the evolution of policing behaviour (Ratnieks 1988) where workers 'police' the egg laying of other workers because it is in their genetic interests that only the queen reproduces. When examining such conflicts, the individual-level view is more useful than a superorganism view.

But in many activities individuals do cooperate and appear to be maximizing something that is usually colony survival or colony propagule production (Queller and Strassmann 2002). So, for example, in seasonally flooded Argentinian habitats, fire ant colonies make a raft of interlinked workers and float to safety; in choosing a new home, swarming bees migrate *en masse* as a single unit; and in rearing its crop fungus leaf-cutting ants have distinct morphological and behavioural castes that transport leaves from the forest to the food fungus in a 'Henry Ford factory-like' manner and then process the waste in an extraordinarily efficient division of labour (Anderson *et al.* 2002). In these cases multiple individuals cooperate because of shared interests and produce phenotypes that cannot be achieved individually. That is, the colony-level phenotype. Since the organism is neither the object of selection

nor the replicator, but rather comprises cooperating genes that have resolved potential conflicts because of shared interests in gamete production (in which genes are packaged (Dawkins 1990); see also Chapters 12 and 13), then the apparent unity of the superorganism can be explained because it helps genes lever themselves into the next generation (see also Queller and Strassmann 2002).

Why do I want to use a term that is, for many, either a throwback to the bad old days of group selection or an extension too far of the phenotype (Dawkins 2004; Jablonka 2004; Laland 2004)? The fact is the colony has, at times, its own phenotype, such as self-assemblages, to perform tasks that are not possible for individuals (Oster and Wilson 1978, p. 10; see also Chapter 11). These include collective phenotypes such as rafting, choosing nest sites via **quorums**, thermoregulation through combined fanning, killing predators, and collecting large food items. In a review of this topic Anderson *et al.* (2002) identified 18 such self-assemblages. There is undoubtedly a genetic basis for this and no doubt natural selection acted upon variations in rafting ability, for example, to produce an optimal response to seasonally flooded habitats. This phenotype is not an extended one like the physical, abiotic nest walls but rather it is a cumulative effect of the coordinated actions of individuals. The colony-level behaviour we see is 'more than the sum of its parts' (Oster and Wilson 1978, p. 10). It has synergy (Chapter 11). In order to produce effective responses to collective goals (e.g. colony survival) individuals must cooperate irrespective of any gene-level conflicts they may have. They may be in conflict later on in the colony cycle (at the timing of reproduction) but when necessary for collective survival the cooperation is necessary and observed (see below the grey boxes in Fig. 10.2a,b). The desiderata, or interests, of the distinct members are aligned for a period of time (Dawkins 1990). Such cooperation requires communication among members of this kin-based network of individuals. But as emphasized already, members of a network may be chimeras of both social insect and parasite. Here conflicts are predicted because their goals are diametrically opposed. Some parasites have little interest in whether or not the colony to which its host belongs will survive or not; all it is
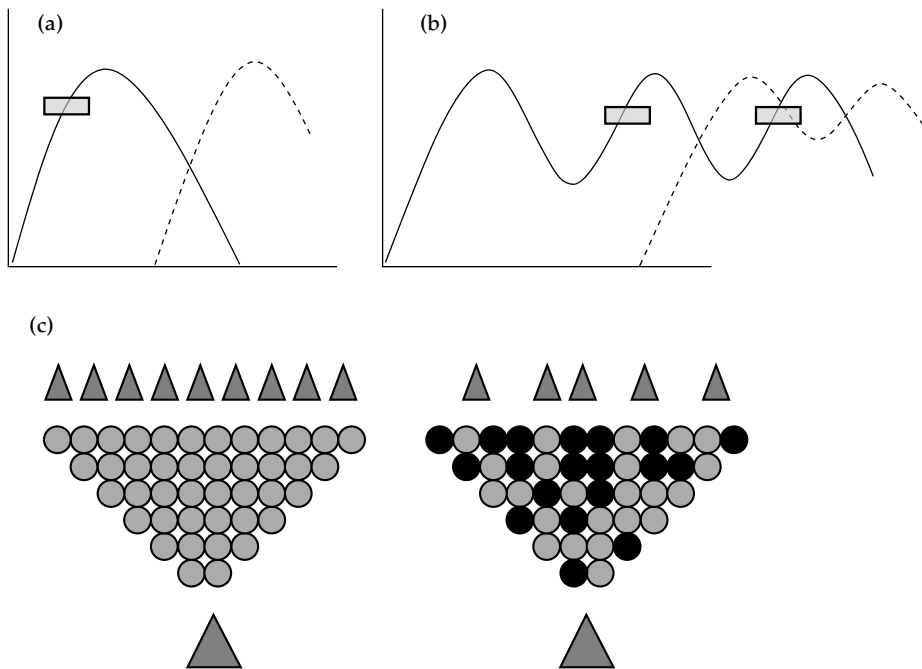
Figure 10.2 An idealised, bang-bang, mode of colony production for an annual a) and perennial b) social insect colony. Worker numbers (solid line) increase along y-axis until sufficient numbers are reached to achieve a switch to production of reproductives (dotted line). The difference between annual and perennial colonies is that worker numbers do not increase after production of reproductives (i.e. the colony dies) and that in the latter a few years may pass before reproductives are produced. Time (no units given) in on the x-axis. The grey box indicates the idealised switch point when worker numbers, sufficient for the production of sexuals, is made. Below this point the interests of colony members (queen and workers) are aligned and conflicts are not predicted except in special cases. In c) the number of workers (circles) builds up in an inverted pyramid fashion to produce new reproductives. The presence of chimeric individuals, workers infected by a manipulating parasite, is shown by black circles. These do not work but their presence in the colony will be detected their contribution to the production of reproductives (triangles) will not be realised, i.e. fewer triangles in the right hand panel of c).

trying to do is maximize is its own survival. Given that many of these colony-level activities (house-hunting, foraging, defending against predators) are risky pursuits (e.g. Schmid-Hempel and Schmid-Hempel 1984) then the conflict is more apparent. Whereas we generally do not see conflict in insect societies over resource acquisition (collecting food), but rather over resource allocation (to male vs. female larvae, to own vs. queen reproduction) (Boomsma and Franks 2006) the presence of parasites establishes a conflict scenario over resource acquisition since it entails an appreciable risk. The superorganism concept is therefore good because is forces us to remember the alignment of interests among non-infected colony members while at the same time erecting a category of aligned members into which the infected individuals may not always fit because of diverse desiderata of parasites within them. Parasitized individuals in the colony are the ultimate 'cheaters' of the cooperative hive but of course, unlike the more well-known selfish individuals that want to pursue their own interest (e.g. laying their own eggs), the infected individuals are vehicles for parasite genes. In the next section, I review what behaviourally modifying parasites these chimeric individuals contain.

10.5 Behaviourally modifying parasites of social insects

Among all the possible phenotypes expressed by the genes of social insects it is their behaviour that
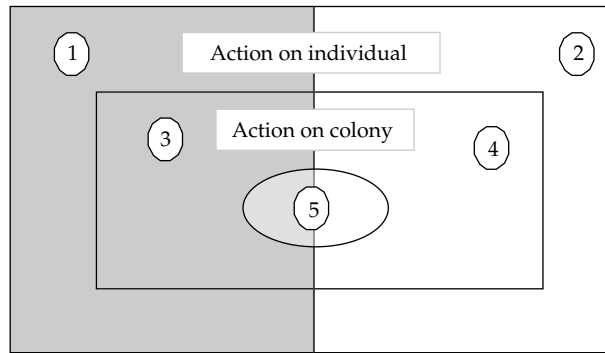
Figure 10.3 The dual host nature of social insects showing where the obvious effects of parasite manipulation can be on the individual (outer box) or on the colony (centre box). The shaded zones are interactions where the parasite benefits from manipulation and the un-shaded zones are where the host benefits. The innermost box represents the category of 'boring by-product' that are changes accompanying parasitism but which are not evolved manipulations by parasites or defence by hosts. Examples from each of the categories are 1) Nest desertion by individuals to promote parasite dispersal (e.g. Strepsiptera), 2) Nest desertion by individuals to retard parasite dispersal (e.g. Conopids), 3) Colony wide social confusion due to parasite presences and or manipulator compounds (ant warfare engineered by parasitoid) 4) Collective defence against parasite (wasp dancing against ovipositing parasites) 5) reduced individual activity and thus colony productivity if parasitism prevalence is high enough due to parasite induced lethargy (gregarines in ants).

is the most important when one considers sociality. Colonies do have fortified walls and individuals have an armoured cuticle and a battery of defensive compounds, but it was behaviour, and specifically altruistic behaviour, that seeded the growth of loosely banded individuals into colonies. Here I echo an important, though surprisingly neglected, assertion of behaviour as the evolutionary pacemaker (Baldwin 1896; Wilson 2000; West-Eberhard 2003) (see also Chapter 8). And behaviour remains the most important phenotype in the colony through such actions as division of labour, cooperative care of the brood, defence of the nest, and communication. Thus, in considering the EPs of parasites I will consider those parasites that alter the behaviour of their social insect hosts. I could have chosen parasites that cause colour changes (Trabalon *et al.* 2000) or size difference in infected individuals (Maeyama *et al.* 1994); but the effect on communication is less clear.

Parasites of social insects have provided prominent and compelling examples of parasite EPs where host behaviour is manipulated. The best known example is the 'brain-worm', which is a trematode that induces its intermediate ant host to leave the colony and climb blades of grass and bite hard (Carney 1969, references on pp. 55–57; Moore

2002). The final host is a grazing animal such as a sheep which is presumed to ingest ants along with the grass it is eating. So emblematic is this example that it 'made the cover' of Janice Moore's excellent review entitled *Parasites and the Behaviour of Animals* (Moore 2002). (Another manipulating parasite, the fungus *Cordyceps*, that also causes ants to bite onto vegetation similarly adorned the cover of Paul Schmid-Hempel's book, *Parasites in Social Insects* (Schmid-Hempel 1998).)

In reviewing here the range of parasites causing behavioural changes among the social insects it will be useful to introduce a schema (Fig. 10.3). There are five categories of behavioural modification in social insects:

1. The first is adaptive manipulation of individual host behaviour that favours parasite genes. The above-mentioned brain-worm is an example. For many horizontally transmitted or trophically transmitted parasites (i.e. where predation of the host is a necessary requirement for transmission) it is obligatory for the individual host to leave the colony, and in these cases nest desertion is the EP of the parasite: conopids, Strepsiptera, trematodes, cestodes, mermithid and rhabtid nematodes, Entomopthoralean and Clavicipitalean

fungi (parasite associations with social insects was extensively reviewed in Schmid-Hempel (1998) so a full list of references is not presented here due to space constraints). In all cases the manipulation is a multistep process. Once outside the colony the host is often directed to a particular location where it performs a stereotypical activity: biting vegetation (fungi, trematodes), suicide in water (mermithid nematodes), digging to provide a diapause site for the parasite pupa (conopids), or inactivity in a prominent place to facilitate parasite mating (Strepsiptera) or predation by final host (cestodes, trematodes). In each of these cases the biology of the parasite and its mode of reproduction is such that nest desertion is interpreted as adaptive to the parasite: remaining in the nest would not lead to infection of other colony members because the parasite is not infective without that necessary departure outside the colony where it either mates or develops in a manner not possible in the colony (e.g. fungi growing through the cuticle or trematodes causing ants to bite).

2. The second category is adaptive manipulation of more than one individual (i.e. the colony) that favours parasite genes. The entry of social parasites into the colony can be accompanied by the release of chemicals that induce confusion among workers and prevent parasite exclusion (these propaganda signals are discussed in Chapter 4). Because the parasite is not internal to the individual host then we may view this as the action at a distance EP like the familiar example of cuckoo chicks manipulating their hosts to feed them. Indeed, the social parasites are often are called cuckoo wasps and ants. Recall the justification in considering the colony as a host, in addition to the individual (Sherman *et al.* 1988, p. 263; Schmid-Hempel 1998) which in this example means the EPs action at a distance and parasite manipulation of host behaviour can be used.

3. The third category switches the benefits of the parasite-associated behavioural change from the parasite to the host and into defensive behaviours. Individual social insects have a very large repertoire of defensive behavioural reactions against parasites. Most mundane, but evidently important for colony-level defence, is self-grooming, allogrooming, and, in the case of crop-rearing ants,

grooming, or 'weeding', their **mutualistic** fungus (Cremer *et al.* 2007). More dramatic is cold-seeking behaviour by bees infected by conopid flies to retard parasite development; every night they move outside the high-temperature nest (Muller and Schmid-Hempel 1993). Conopid larvae live inside bees and cannot infect the siblings of the bee they are infecting, so this nightly self-exclusion is defensive in that it retards the parasite's growth and facilitates a longer working life for the infected individual.

4. The fourth category is also a defensive behaviour against parasites, but here it requires the coordinated action of multiple individuals to succeed. The 'dancing behaviour' of paper wasps in response to the presence of an ovipositing Ichneumonidae wasp is a good example (West-Eberhard 1969). Another example is construction behaviour where individuals cooperate to build satellite nests (Jeanne 1979) or walls to quarantine infected areas of the colony (Schultz *et al.* 2005) and even infected siblings (Epsky and Capinera 1988). The last one, that of construction, is an EP of ants and wasps as a defence against parasites and has nice parallels with avian construction such as oven and weaver bird nests as a defence against predators such as snakes (Hansell 2004).

5. The fifth category does not interpret the behavioural change as an adaptive trait of either the parasite or the host but rather as a 'boring by-product' of infection (coined by Dawkins 1990; see also Poulin 1994, 1998, 2000). This category, though important when considering the EPs of parasites, is often the least satisfactory: it is commonly the one advanced in objection to the adaptationist explanations (this point is touched upon by de Sousa in Chapter 16 when discussing the infamous Spandrels of San Marco by Gould and Lewontin 1979). We can think of lethargy or reduced flying ability when infected as possible examples (Kathirithamby and Hughes 2005). However unsatisfying to an adaptationist (Pigliucci and Kaplan 2000; Gardner *et al.* 2007), this category is very important because it can obscure communication.

So these are the five categories of behavioural changes among social insects due to the presence of parasites. I will now move onto the central thesis

of this chapter, which is that such changes can significantly impact upon social communication. Recall that I said this is advocacy. We know that social insect nests are literally hives of complex communication and that this can be a phenotype at both the individual and the colony level. Now you are aware that parasites are imbedded in the bodies and chambers of both the nest occupants and the nest itself. I advocate viewing the nest from the perspective of the parasite's genes and asking what utility is there within this social communication network?

10.5.1 Scenarios where communication channels are potentially obscured

We have seen the ways in which behaviour can be changed at both the individual and the colony level; and to benefit either parasite or host (or neither in the case of boring by-products). There is no shortage of examples, and documenting behavioural change is particularly easy for social insects because as **central place foragers** with precisely defined roles within a kin-structured society any behavioural deviations from the norm are easily observed. For example, desertion; 'workers' not working or young workers performing tasks, or occupying areas, usually ascribed to older individuals and vice versa. The value of studying parasite EPs is not found in describing or cataloguing the behaviours but in understanding their consequences for both host and parasite fitness (Moore *et al*. 2005; Thomas *et al*. 2005). I have previously suggested that the complexity of insect societies offers rich rewards when studying the evolutionary consequences of manipulation (Hughes 2005). For example, recognizing that behavioural changes are surrogates of virulence (Read 1994) we could examine the cost of manipulated workers (or the cost of behavioural defence) on colony fitness (represented by the reduced output of reproductive individuals; see Fig. 10.2c). We could also ask what are the proximate-level mechanisms by which parasites exert such fine detailed control? And have the widely different taxa of parasites convergently evolved similar mechanisms to affect a common behaviour such as nest desertion? I mention these directions only in passing as profitable lines of research and

now turn my attention to social communication. I will examine four scenarios where communication within the colony is potentially obscured and close with a fifth scenario concerning communication outside the colony.

10.5.1.1 Altruism

Despite the very obvious differences, to our eyes, between a cuckoo chick and its host chick, the cuckoo is provided with food. Clearly the host bird (a fairy wren for example) is losing out. Among social insect species the equivalent scenario would be interspecific social parasitism where one social insect, a cuckoo wasp, *Polistes sulcifer* for example, takes over the nest of another, *Polistes dominulus*, and the workers accept this alien queen (Cervo and Dani 1996). This type of parasitism, also called social parasitism, even occurs between orders with parasitic lycaenid caterpillars infecting ants nests and either being fed like cuckoo chicks or simply eating the ant brood (Pierce 1995; see also Chapter 4 and Pierce *et al*. 2002). In the case of cuckoos, cuckoo wasps, and parasitic caterpillars there is communication between host and parasites. Notwithstanding the Mafia hypothesis, where hosts 'cooperate' with parasites or face retaliatory behaviour (Zahavi 1979; Ponton *et al*. 2006; Hoover and Robinson 2007) it is not an adaptive strategy for hosts to feed parasites. The reason why hosts do feed alien chicks boils down to selection pressures on recognition mechanisms that are related to the prevalence of infection in the population at large (Winfree 1999). The communication system that exists is one of deception with the parasite either mimicking, camouflaging, appeasing, or over-stimulating the host (discussed at length in Chapter 4; see also Chapter 16 for a discussion on camouflage). For the social insects the external parasite (external that is to an individual host) may eventually come to 'look' like its host through camouflage or mimicry, which typically means either adopting or synthesizing the colony odour so as not to be discovered. But an external parasite is always different, and especially so from the start of the relationship when it just enters the colony. Thus the signal must be deceptive. What is important to understand is that the colony member which contains an internal parasite (category 1, Fig. 10.3)

was not always infected. For the majority of its life it was a normal, uninfected, colony member, and kin selection favours cooperation, which for workers means feed a related individual until it is big enough to work and contribute, cooperatively, with similarly aged individuals to colony productivity. But once the individual is parasitized, i.e. becomes a chimera, then altruism directed towards it is the same as feeding a cuckoo chick. I will not discuss why colony members don't immediately recognize this changeling, but it is likely to be related to fitness costs, at the colony level, of lost investment, zero return because of no work and costs of discrimination. What is interesting to consider in the present context is communication.

Is an infected individual signalling? Just before it became infected the answer was yes. It signalled its status (larva, worker, male, queen) and, if an adult, its position in the hierarchy through chemical (e.g. Turillazzi and West-Eberhard 1996) and even visual modalities (Tibbetts 2002). Via pheromonal **cues** it can signal its reproductive status (Chapter 7). As a worker it signalled its task and in many cases information about colony and environmental resources (by orally exchanging liquid, called trophallaxis, colony members communicate if and where they have foraged, or if they are hungry). It also signalled to its nestmates and foreign colony members its colony of origin via the chemical odour present on its cuticle (see Chapter 5). All such signals were likely to be honest and to benefit all parties because the sender and the receivers had aligned interests (colony productivity). The parasitized individual, however, no longer has completely aligned interests with other colony members because many activities in the social insect life history are risky, such as working (Schmid-Hempel and Schmid-Hempel 1984), mating (Boomsma *et al*. 2005), or defending. If not risky then tasks are energetically costly. A parasite that is not transmitting itself, or reproducing, should not want its host to engage in risky tasks such as defending the nest, foraging, or mating; nor waste energy contributing to colony reproduction. A general effect of parasites is castration where hosts are prevented from reproducing while parasites channel resources into their own development (Poulin 2007). Because most individuals in societies are workers, and these are

functionally sterile, then castration is not achieved by preventing workers from reproducing, which they wouldn't do anyway, but by preventing them from working since division of labour in the colony (superorganism) is the method by which reproduction is achieved using the reproductive castes. Parasitic castration of social insects is preventing the worker caste from working (but may involve associated physiological reduction of gametes which some workers can possess, but to my knowledge this has only once been investigated; Strambi *et al*. 1982). Castration, by behavioural modification, will benefit parasite fitness by (1) reducing the risk to the parasite vehicle and keep the parasite out of danger or (2) not wasting valuable energy. Whether this form of behavioural parasitic castration will reduce colony fitness (and the fitness of the individual that is parasitized through indirect effects) probably depends on how many other workers are likewise behaviourally castrated.

That parasites should not allow their vehicles to go outside the colony and engage in expensive tasks that divert resources away from parasite development is especially probable if we remember that the a mature colony is a protected fortress where predation is essentially zero (Keller and Genoud 1997). There are very few studies that have set out to test whether infected individuals do in fact work (Schmid-Hempel and Schmid-Hempel 1990; Schmid-Hempel and Muller 1991; Hughes *et al*. 2004a,b) and more data are required. Even if individuals do work and do repay the colony for its investment then it may transpire that they do so less efficiently, as in the case of parasites of bumblebees that affect flower choice and pollen load (Schmid-Hempel and Schmid-Hempel 1990; Schmid-Hempel and Muller 1991; Shykoff and Schmid-Hempel 1991; Schmid-Hempel and Stauffer 1998). The details are sure to vary with parasite taxa and ecological conditions but it is reasonable to suspect that parasitism prevents altruism towards other colony members and that the infected individual, by consuming colony resources for its growth and that of the parasite, is expressing the EP of the parasite at the expense of the society.

Let us realistically assume that infected individuals do not work, or that they are less efficient if they do work. We expect from evolutionary theory

that non-cooperating individuals, i.e. cheats, are sanctioned (Chapter 2). One could speculate that in addition to expressing the extended phenotype of cheating behaviour (i.e. make your social insect host a lazy, non-working member of the society, because that is the safer and less energy-demanding course), the parasite has an additional agenda, which is to signal to colony members that its vehicle is not in fact a lazy individual but rather a productive member of the society. That is, do internal parasites deceive colony members at a distance as we know social parasites do (Chapter 4)? At the proximate level signals are being sent, and whether these are exact copies of signals normally transmitted between uninfected colony members or some *de novo* deceptive signal requires study. Besides the signals being sent (such as 'feed me even though I am actually a wolf in sheep's clothing') there potentially exists cues that could be used by non-infected colony members to decide the infection status of others. Such things are the aforementioned non-working behaviour, lethargy (Trabalon *et al.* 2000 and references therein), body distortions such as enlarged abdomens, and smaller wings in reproductives, following nematode infection (Maeyama *et al.* 1994), extruded pupae of Strepsiptera in ants (Hughes *et al.* 2003), or changes in hair growth pattern in wasps and bees making 'intersexes' (Salt 1927, 1931; Wcislo 1999). We know from other cooperative systems such as fish shoals that infected individuals can be easily recognized by the group via phenotypic assortment (Barber *et al.* 2000). If such cues have a realistic chance of evolving into a signal ('I am your kin but I am now infected and therefore non-working') then we would expect selection acting on the parasite to evolve deceptive signalling, such as camouflage. (With the obvious assumption that the prior cue resulted in sanctions against infected individuals, which, I suspect, would not always be the case. But that is beyond the present scope.) An interesting test of this would be determining whether the extruded pupa of internal strepsipterans (insects) infecting ants mimics the cuticular profile of the host because infected ants remain inside the nest even once the parasite has extruded through the cuticle, which means a large area of extruded parasite could be detected. This could be compared to the chemical profile of the extruded pupa of strepsipterans infecting wasps where the parasite extrudes the pupa only after the wasp has left the nest and thus the necessity of deceiving kin is gone (Hughes *et al.* 2003, 2004b). To conclude this section on altruism, is clear is that internal parasites disrupt the altruistic actions of the individuals they infect and this probably involves the evolution and transmission of signals that obscure social communication over who receives the benefits of altruism.

10.5.1.2 Misdirected altruism

When colonies of the Asian army ant, *Leptogenys distinguenda*, move home (a regular occurrence for such nomadic ants) they pick up a molluscan parasite of their colony in preference to their brood stage siblings (Witte *et al.* 2002). It appears that the mollusc produces an irresistible foam mass that the ants find very attractive (V. Witte, pers. comm.). This sort of super-normal signal (Dawkins and Krebs 1979) appears to be a common strategy among social parasites (see details in Chapter 4). It is also the situation to be found among brood parasites such as cuckoo chicks where 'cuckoos should be selfish because their greed is unconstrained by kinship' (Kilner and Davies 1999) A colony member responding to such signals by a social parasite is misdirecting altruism and deceptive communication is the explanation. But let us again consider the more subtle phenomenon of internal parasites of social insects (internal to individual social insects). A nursing worker that gives food items to brood members will be faced with situations of chimeric individuals. There are then two important points to consider. The first is whether increased begging is observed and the second is whether any non-parasitized individuals respond? We have no evidence at all for increased begging by infected brood and the only study to address this found no differential mass loss between infected and uninfected wasp brood, demonstrating that the parasite was not placing a high demand, but since the parasite was a strepsipteran that requires a morphologically intact adult wasp for future transmission then the absence of a high cost at the larval stage is reasonable (Hughes and Kathirithamby 2005). Begging responses of their

hosts should be investigated in parasites that only infect larva or adults (but not both sequentially such as Strepsiptera).

The field of brood sibling rivalry has not been developed for social insects in the same way as for birds (Mock and Parker 1997). In general we might speculate that full siblings in hymenopterans societies with high relatedness (0.75, due to haplodiploidy) will not be selected to compete for food in quite the same way as 'normal' diploid siblings do. However, infected individuals no longer have aligned interests and should solicit more food without considering the kin of the vehicle they inhabit. Since the decision to feed a larva follows from communication of need by that larva, then parasitized larvae may send an honest signal but the receiver is duped because it is not feeding just a sibling, but also the parasite. The question, again, is not whether natural selection should allow nurses to recognize infected brood but rather whether communication has been obscured in cases where parasitism is obviously not detected? (Non-detection is evidenced by the fact that the infected individual has not been removed.) The answer would appear to be yes, and I will discuss the significance later.

Providing food to a begging larva is not the only form of altruism. Simply allowing an individual to reside within a cell is altruism and in cases of stress and low food availability nursing workers will remove and eat young individuals but allow older individuals to stay alive because of the higher investment in the latter (Hölldobler and Wilson 1990). In many cases where cells are used to rear brood (wasps and bees) the cell can be occupied by a parasite which often has completely consumed the former occupant (e.g. Ichneumonidae wasps and chalkbrood fungi are examples). Usually the parasite allows the host larvae to spin a silken cap and this seals off the cell (which precedes pupation in uninfected individuals). In some cases a behavioural defence is uncapping, where bees uncap the cell and remove the infected individual as we see in fungal infections (Schmid-Hempel 1998). However, no evidence exists that wasps uncap cells infected by Ichneumonidae wasps. Does this imply that the parasite within is signalling to the nurses that the cell is not parasitized?

10.5.1.3 Reproductive decision-making (because of cheaters)

There are three principal modes of colony development. The first is an annual cycle (Fig. 10.2a). For example, a bumblebee queen begins a nest in springtime after winter diapause. Her first eggs become workers and she feeds the subsequent larvae with metabolized body stores until they become adults and can take over the foraging, nursing, and building tasks of the colony, leaving her to the job of egg laying. When the workforce has built up to a sufficient level to ensure adequate resources the colony begins producing reproductives (males and females) that leave to mate with the new queens and overwinter before the cycle begins again. A second mode also involves this solitary founding but here the colony lasts many seasons; it is perennial (Fig. 10.2b, e.g. ants, termites, some wasps, and bees). The production of reproductives may not happen for several years as the colony builds up a sufficient number of workers. In both modes the colony can start from a single female and male (in hymenopterans the vehicle for male genes is sperm stored inside the female, while in termites the vehicle is a whole male), or with multiple females/males. The third method of colony development is to simply split a big colony in two just like a fissioning yeast cell (this happens in honeybees and army ants, for example). The benefit of colony fission is that during the early days of the new colony it already has a very large workforce. By contrast solitary founding is very risky and estimates of up to 99% failures are not unrealistic (Hölldobler and Wilson 1990).

Whatever the method of its beginning the goal of the colony is to produce reproductives, and at some point in the life of each colony the decision about when the time is correct will be made (Fig. 10.2). We know very little about the optimal decision-making process or what cues are used. The standard model is the 'bang–bang' mode where investment in reproductive workers begins within 'one half the lifetime of the last cohort of workers' (Oster 1976; Oster and Wilson 1978). That is, workers and reproductives are not produced synchronously but rather sequentially. The decision to begin sexual production can be viewed either as one by the queen who produces queen- or male-destined eggs; or by the workers who feed

larvae either special food, or simply more food, thereby switching them from a worker-destined pathway to a queen-destined pathway. There are many taxon-specific details but the essential point is that the colony begins producing reproductives when the workforce is judged to be of sufficient size or when there are enough resources. To make this judgement must require some sort of internal communication and it is probably similar to **quorum sensing** in bacteria where a new action or phenotype occurs once bacterial numbers get over a set amount (Chapter 2).

What will be the role of chimeric individuals inside the colony for reproductive decision-making? They will not be collecting resources, and from the available evidence not tending the developing brood. Since the presence of the parasite divorces the infected colony member from its previously held common interests with its siblings, we are not surprised by this ensuing lack of altruism (Section 10.5.1.1 above). But it is unlikely that non-infected siblings know the infection status of each member of the colony due to the force of selection on evolving foolproof recognition systems (discussed above). More likely, infected individuals are recognized for what they are, another body in the colony that is expected to be collecting resources, tending brood, defending the nest, or acting as a reserve member for other tasks. Since the production of reproductives is a colony-level trait that is in the interest of all members, we would expect the signalling to be honest. I suggest that the presence of infected individuals changes the accuracy of information available preceding the decision to switch to producing reproductives. Let us realistically assume that the switch is a numbers game and relies upon a simple rule such as an encounter rate above a threshold value that will switch the colony into a reproductive phase (see Fig. 10.2c). Such a rule underlies quorum-based house-hunting in ants (Pratt *et al.* 2002) and bees (Seeley 1995; Seeley and Buhrman 1999; Seeley *et al.* 2006), and foraging decisions in ants (Greene and Gordon 2003) (see also Chapter 11). A colony above a certain size should switch to sexual production since the number of individuals obviously correlates with eventual resource acquisition and the transfer of those resources into reproductives. The presence

of infected, non-working individuals, means that the information guiding the switch is not accurate and thus communication is obscured.

To sum up this section, there is increasing attention to colony-level decision-making in social insect evolutionary biology (Boomsma and Franks 2006), and hopefully further studies will begin to elucidate the cues, signals, and timing of reproduction by the colony. The presence of chimeric individuals and their effect on colony communication preceding reproductive switches should be taken into account when considering colony-level decision-making processes.

10.5.1.4 Colony-level decisions (defence, house-hunting, swarming)

In the previous section I briefly mentioned house-hunting by ants and honeybee colonies, which are excellent examples of a complex superorganism-level phenotype that is generally called collective decision-making or self-organization (see Chapter 11). It is similar to self-assemblages such as the rafting fire ants I also discussed above. The term self-organization refers to the observation that complex patterns of behaviour can be observed when multiple individuals cooperate, and that these behaviours are not expressed by single individuals that are alone. The 'whole is greater than the sum of its parts' (Oster and Wilson 1978, p. 10), meaning there is synergy (Chapter 11). There has been an increasing level of attention focusing on self-organisation, not just among social insects but other taxa such as locust marching behaviour, fish shoaling, and even the coordinated clapping of opera audiences (Camazine *et al.* 2001; Sumpter 2006; Garnier *et al.* 2007). Such phenomena can be adaptive at the individual level (selfish herd) and the group level (coordinated defence) or just an emergent phenomenon that is a by-product of coordinated actions (opera audiences). For social insect societies the self-organizing behaviour we see, and that includes self-assemblages, is a colony-level phenotype shaped by natural selection (Queller and Strassmann 2002). Quorum sensing-based house-hunting in ants and bees is obviously an optimal way to choose among nest sites of varying quality (Seeley *et al.* 2006; Visscher 2007). Other examples of collective behaviour, such as thermoregulation

via coordinated movements, coordinated defence against invertebrate attackers, making trails, or coordinated efforts requiring multiple individuals physically linking together (building bridges, pulling chains, ladders, and bivouacs), would all appear to be colony-level phenotypes (Anderson *et al*. 2002).

To date studies have focused on a proximate-level, rather than ultimate, understanding of self-organization in biology generally and social insects specifically (Camazine *et al*. 2001; Boomsma and Franks 2006). This reflects the influence of mathematical and physical principles in developing algorithms that can explain the observed phenomenon (Sumpter 2006; see also Chapter 11). In my opinion, this lack of a functional-level approach has meant cheaters that benefit from the collective phenotype without investing in its production have not been considered deeply. Of course that is not a fault, and we need to consider many variants of non-cooperating individuals, whether because of parasitism or not, to better understand the fundamental question of how cooperation exists in the first place (see Chapter 2 and references therein). Obviously if cheating exists and it threatens a colony-level phenotype then one would expect punishment measures to evolve, as happens in the previously mentioned case of worker policing which is a colony-level defence to prevent selfish workers laying eggs against the collective interest (Ratnieks 1988; Wenseleers and Ratnieks 2006). But cheaters of course raise the important, though tautological, point that collective behaviour is the result of multiple individuals cooperating and these individuals are not all the same (Sumpter 2006). Recently, and perhaps for the first time, inter-individual variation was explicitly considered (Garnier *et al*. 2007) as a source of perturbation that could affect the outcome of self-organization. The authors imagine perturbations coming from outside or within the colony. Obviously, a within-colony source of variation among individuals that cooperate in collective behaviours is whether some of those individuals are chimeric and contain both parasite and social insect.

Two interesting examples can be considered here. In a swarm-founding nocturnal hornet from Southeast Asia (*Provespa anomala*) individuals infected by strepsipteran parasites (an internal parasitoid) were never found in swarms, though they were found in non-swarming stages of the colony (Matsuura 1999). Thus it appears that infected individuals don't participate in swarms. By contrast, in the collective defence of honeybee colonies against predatory hornets it is the virus-infected individuals that take the lead (Fujiyuki *et al*. 2004). Usually defence is a task performed by the oldest workers because they are the most expendable, so it is interesting that when honeybee colonies were presented with a predator (a hornet wasp) it was the middle-aged workers that would attack and these individuals had viral infections in their brain. The virus, called *Kakugo* meaning 'ready to attack' in Japanese, belongs to the same group as rabies so perhaps the high level of aggression in some way aids transmission (Fujiyuki *et al*. 2004). These two examples are tantalizing, but what is obviously required is many more data on the occurrence of infected individuals in collectively organized behaviours. Meanwhile, I feel the following two perspectives should be considered.

The first is whether or not infected individuals take part in collective activities. It will probably transpire that they do so long as it doesn't conflict with the desiderata, or desires, of the parasite within (Dawkins 1990). Clearly if the collective action is risky then we would not expect infected individuals to take part unless it facilitates transmission as in the probable case of the *Kakugo* virus above. The second and more interesting starting point is asking what communication occurs in collective organization and whether chimeric individuals can disrupt it? In most cases the answer will be probably be that chimeric individuals do not affect self-organization communication pathways because they do not assume the lead roles in self-organizing behaviour. For example, these lead roles are the scouts who search for nest sites, assess their suitability, and eventually communicate the location or quality of such sites (e.g. waggle dancing or laying pheromonal trails or physically leading individuals to the new site; see Chapter 11). But once a suitable location has been found through quorum sensing then the whole colony must move, and this requires communication between those who know the location of the new nest and those

who communicate that knowledge (Seeley *et al*. 2006; Visscher 2007). Amazingly, ants actually teach others the location (Franks and Richardson 2006). In the latter situation an obvious question is how teaching varies when 'students' differ in their individual capability to learn? Can chimeric individuals learn the way to the new location? Do instructors give up if their students are lethargic zombies? Does this negatively feed back upon an individual's stimulus to teach since we typically assume that this self-organization behaviour is a set of simple rules coupled with negative and positive feedback (Chapter 15). All of this is speculation, but as we start to develop a better understanding of the optima of self-organization behaviour then the role of these chimeric individuals is worth considering because they may be key to understanding the rules of thumb present. Ultimately it will probably come down to a numbers game again (Fig. 10.2c). The effect of chimeric individuals is not observed in colony-level phenotypes such as house-hunting when their numbers are low. When infected individuals occur at high levels the collective breaks downs. A clear example of this it the parasitic Cape honeybee (*Apis mellifera capensis*) that can reproduce parthenogenetically inside African honeybee nests (*Apis mellifera scutellata*) and behave like a cancerous line that eventually destroys the colony (Martin *et al*. 2002). However, whether or not the effect on colony phenotype or colony fitness is felt the existence of chimeric individuals has the possibility to obscure social communication during collective behaviours.

10.5.1.5 Extra-nidal activities

In the last example of potential ways in which communication is obscured by the extended phenotype of parasites I consider activities outside the nest. Social insect workers leave the colony to forage for food, water, building materials, and when defending the fortress. Reproductives leave the colony to mate and establish new colonies (or in some cases re-enter their natal colony). 'Workers' possibly leave the colony to become reproductives (Reeve *et al*. 1998). The communicative behaviour of non-infected individuals away from the nest is little studied. For the most part it deals with the interactions among and between individuals at the colony

boundaries (Hölldobler and Wilson 1990; Ross and Matthews 1991; Bourke and Franks 1995; Seeley 1995; Abe *et al*. 2001). Impressive examples are the 'border patrols' (Hölldobler 1979) and ritualized tournaments (Hölldobler 1981) where opposing colonies display their colonies' fighting abilities. Another example of colony boundary activity is the communication between individuals returning from foraging and those waiting to determine if they should forage following the transfer of chemical information (Greene and Gordon 2003). Definite extra-nidal activities are orientation either away from the nest or back to it as well as choice of food. When ants and bees navigate they pick up cues to allow them to return home or lay trails. Many EPs of parasites involve nest desertion (Fig. 10.3), and though this is pure speculation in the absence of any data it would appear likely that deserting individuals do not record landmark features or lay trails, since they do not intend to return. For food choice we do know that infected social insects can behave differently; for examples parasites of bumblebees can affect flower choice and pollen load (Schmid-Hempel and Schmid-Hempel 1990; Schmid-Hempel and Muller 1991; Shykoff and Schmid-Hempel 1991; Schmid-Hempel and Stauffer 1998).

In the context of communication what is interesting is if non-infected individuals interact at all with chimeric individuals when performing extranidal activities. Currently, due to a lack of data, we are not in a position to discuss how chimeric individuals may or may not impact upon competition between conspecific individuals away from the nest. But taking a cue from parasitological research among non-social taxa (such as trematodes in snails) the interactions between infected and non-infected social insects at feeding sites may be of great general interest. In the snail–trematode system uninfected individuals directly competed with parasitically castrated snails in intertidal mud flats leading the authors (Miura *et al*. 2006) to propose that we should view foraging ecology on mud flats as a battle between snails and trematodes (in snail bodies). This parasite's eye view is of course generally lacking in behavioural ecology (Poulin 2007), but foraging arenas, where competition is to be expected, are likewise areas

of intense communication and the chimeric individuals (whether snail or social insect) can, once more, offer insights to general mechanisms in communication.

10.6 Conclusion

The social insects have been the subjects of pioneering work in communication and continue to be leading models systems in proximate and functional studies of communication, as a number of chapters in this volume attest (Chapters 4, 5, and 7). The rules that have been elucidated through their study have now been tested in diverse taxa from microbes to monkeys (Strassmann *et al.* 2000; Flack *et al.* 2006). But of course there are many details of communication in social insects that remain to be understood, and in particular a proximate-level understanding is lacking. One commonly applied approach when examining communication in diverse systems has been the use of naturally occurring or experimentally induced mutants, and a number of authors in this volume have discussed this: Haig when discussing inter- and intra-organismal communication (e.g. Prader–Willi and Angelmann syndrome, Chapter 12), Crespi when discussing language evolution (autism and affective psychotic spectrum, Chapter 13), Hurst and Benyon when discussing relevant contributions to scent marking (knockout mutants, Chapter 6), and Diggle *et al.* when discussing quorum sensing in bacteria (also knockout mutants, Chapter 2). In social insect research the use of 'knockouts', where part of the colony has been removed in what Wilson terms a sociectomy (Wilson 1985), has been a useful tool for examining effective colony-level phenotypes such as optimal caste ratios and foraging (Wilson 1983). The use of such a knockout approach has not, to my knowledge, been done specifically to examine inter-individual communication, but has recently been pioneered in social primates (Flack *et al.* 2006). It strikes me that the chimeric individuals I have discussed in this chapter, and the accompanying parasite EPs, are naturally occurring mutations in a highly complex communication network. Therefore, understanding the functional and proximate details of such obscured communication could offer multiple insights into

general principles of communication; the goal of this volume.

Summary

Societies of social insects are paragons of communication. Multiple channels exist between different members and the transmitted information ranges from specifying the location of foraging areas to who controls reproduction. Whole colonies can also communicate with other colonies or even vertebrates. But what if the individuals within a society are not, in a word, themselves? Here I explore how adaptive manipulation of host behaviour by parasites, i.e. the extended phenotype of parasites, obscures social communication, and ask how it influences other members of the society. Since manipulated kin are at best cheaters and at worst potential infective agents can the society recognize them? Knowing how a highly complicated example of social communication is broken or subverted by parasites can provide considerable insight into the evolution of communication. I discuss conflict and communication in this system in the context of the debate over the nature of the organism.

Acknowledgements

References

Aanen, D.K. and Eggleton, P. (2005). Fungus-growing termites originated in African rain forest. *Current Biology*, **15**, 851–855.

Abe, T., Bignell, D.E., and Higashi, M. (eds) (2001). *Termites: Evolution, Sociality, Symbiosis, Ecology*. Kluwer Academic Publishers, Dordrecht.

Anderson, C., Boomsma, J.J., and Bartholdi, J.J. (2002). Task partitioning in insect societies: bucket brigades. *Insectes Sociaux*, **49**, 171–180.

Baldwin, J.M. (1896). A new factor in evolution. *The American Naturalist*, **30**, 441–451, 536–553.

Barber, I., Hoare, D., and Krause, J. (2000). Effects of parasites on fish behaviour: a review and evolutionary perspective. *Reviews in Fish Biology and Fisheries*, **10**, 131–165.

Bennett, N.C. and Faulkes, C.G. (2000). *African Mole-Rats: Ecology and Eusociality* Cambridge University Press, Cambridge.

Biron, D.G., Ponton, F., Marche, L. *et al.* (2006). 'Suicide' of crickets harbouring hairworms: a proteomics investigation. *Insect Molecular Biology*, **15**, 731–742.

Boomsma, J.J. and Franks, N.R. (2006). Social insects: from selfish genes to self organisation and beyond. *Trends in Ecology and Evolution*, **21**, 303–308.

Boomsma, J.J., Baer, B., and Heinze, J. (2005). The evolution of male traits in social insects. *Annual Review of Entomology*, **50**, 395–420.

Bourke, A.F.G. and Franks, N.R. (1995). *Social Evolution in Ants.* Princeton University Press, Princeton, NJ.

Camazine, S., Deneubourg, J.L., Franks, N.R., Sneyd, J., Theraulaz, G., and Bonabeau, E. (2001). *Self-Organization in Biological Systems.* Princeton University Press, Princeton, NJ.

Carney, W.P. (1969). Behavioral and morphological changes in carpenter ants harbouring dicrocoeliid metacercariae. *American Midland Naturalist*, **82**, 605–11.

Cervo, R. and Dani, F. (1996) Social parasitism and its evolution in *Polistes*. In: S. Turillazzi and M.J. West-Eberhard (eds), *Natural History and Evolution of Paper-wasps*, pp. 98–112. Oxford University Press, Oxford.

Costa, J.T. (2006) *The Other Insect Societies.* Harvard University Press, Cambridge, MA.

Cremer, S., Armitage, S.A.O., and Schmid-Hempel, P. (2007). Social immunity. *Current Biology*, **17**, R693–R702.

Crespi, B.J. and Cho, J.C. (eds). (1997). *The Evolution of Social Behaviour in Insects and Arachnids.* Cambridge University Press, Cambridge.

Crespi, B.J. and Yanega, D. (1995). The definition of eusociality. *Behavioral Ecology*, **6**, 109–115.

Dawkins, R. (1976). *The Selfish Gene.* Oxford University Press, Oxford.

Dawkins, R. (1982). *The Extended Phenotype.* W.H. Freeman, Oxford.

Dawkins, R. (1990). Parasites, desiderata lists and the paradox of the organism. *Parasitology*, **100**, S63–S73.

Dawkins, R. (2004). Extended phenotype—but not too extended. A reply to Laland, Turner and Jablonka. *Biology and Philosophy*, **19**, 377–396.

Dawkins, R. and Krebs, J.R. (1979). Arms races between and within species. *Proceedings of the Royal Society of London Series B: Biological Sciences*, **205**, 489–511.

Epsky, N.D. and Capinera, J.L. (1988). Efficacy of the entomogenous nematode *Steinernema feltiae* against a subterranean termite, *Reticulitermes tibialis* (Isoptera, Rhinotermitidae). *Journal of Economic Entomology*, **81**, 1313–1317.

Flack, J.C., Girvan, M., de Waal, F.B.M., and Krakauer, D.C. (2006). Policing stabilizes construction of social niches in primates. *Nature*, **439**, 426–429.

Foster, K.R. and Ratnieks, F.L.W. (2005). A new eusocial vertebrate? *Trends in Ecology and Evolution*, **20**, 363–364.

Foster, K.R., Wenseleers, T., and Ratnieks, F.L.W. (2006). Kin selection is the key to altruism. *Trends in Ecology and Evolution*, **21**, 57–60.

Franks, N.R. and Richardson, T. (2006). Teaching in tandem-running ants. *Nature*, **439**, 153–153.

Fujiyuki, T., Takeuchi, H., Ono, M. *et al.* (2004). Novel insect picorna-like virus identified in the brains of aggressive worker honeybees. *Journal of Virology*, **78**, 1093–1100.

Gardner, J., Marsack, P., Trueman, J., Calcott, B., and Heinsohn, R. (2007). Story-telling: an essential part of science. *Trends in Ecology and Evolution*, **22**, 510–510.

Garnier, S., Gautrais, J., and Theraulaz, G. (2007). The biological principles of swarm intelligence. *Swarm Intelligence*, **1**, 3–31.

Gould, S.J. and Lewontin, R.C. (1979). Spandrels of San-Marco and the Panglossian paradigm—a critique of the adaptationist program. *Proceedings of the Royal Society of London Series B: Biological Sciences*, **205**, 581–598.

Greene, M.J. and Gordon, D.M. (2003). Social insects—cuticular hydrocarbons inform task decisions. *Nature*, **423**, 32.

Hamilton, W.D. (1963). Evolution of altruistic behavior. *The American Naturalist*, **97**, 354–356.

Hamilton, W.D. (1964a). The genetical evolution of social behaviour. I. *Journal of Theoretical Biology*, **7**, 1–16.

Hamilton, W.D. (1964b). The genetical evolution of social behaviour. II. *Journal of Theoretical Biology*, **7**, 17–52.

Hansell, M. (2004). *Animal Architecture.* Oxford University Press, Oxford.

Hansell, M.H. (1996). Wasps make nests: nests make conditions. In: S. Turillazzi and M.J. West-Eberhard (eds), *Natural History and Evolution of Paper-wasps*, pp. 272–289. Oxford University Press, Oxford.

Hölldobler, B. (1979). Territories of the African weaver ant (Oecophylla longinoda (Latreille)). A field study. *Zeitschrift für Tierpsychologie—Journal of Comparative Ethology*, **51**, 201–213.

Hölldobler, B. (1981). Foraging and spatiotemporal territories in the honey ant *Myrmecocystus mimicus* Wheeler (Hymenoptera: Formicidae). *Behavioural Ecology and Sociobiology*, **9**, 301–314.

Hölldobler, B. (1995). The chemistry of social regulation: multicomponent signals in ant societies. *Proceedings of the National Academy of Sciences of the USA*, **92**, 19–22.

Hölldobler, B. and Wilson, E.O. (1990). *The Ants.* Harvard University Press, Cambridge, MA.

Hoover, J.P. and Robinson, S.K. (2007). Retaliatory mafia behavior by a parasitic cowbird favors host acceptance of parasitic eggs. *Proceedings of the National Academy of Sciences of the USA*, **104**, 4479–4483.

Hughes, D.P. (2005). Parasitic manipulation: a social context. *Behavioural Processes*, **68**, 263–266.

Hughes, D.P. and Kathirithamby, J. (2005). Cost of strepsipteran macroparasitism for immature wasps: does sociality modulate virulence? *Oikos*, **110**, 428–434.

Hughes, D.P., Moya-Raygoza, G., and Kathirithamby, J. (2003). The first record among Dolichoderinae (Formicidae) of parasitism by Strepsiptera. *Insectes Sociaux*, **50**, 148–150.

Hughes, D.P., Kathirithamby, J., and Beani, L. (2004a). Prevalence of the parasite Strepsiptera in adult *Polistes* wasps: field collections and literature overview. *Ethology, Ecology and Evolution*, **16**, 363–375.

Hughes, D.P., Kathirithamby, J., Turillazzi, S., and Beani, L. (2004b). Social wasps desert the colony and aggregate outside if parasitized: parasite manipulation? *Behavioral Ecology*, **15**, 1037–1043.

Jablonka, E. (2004). From replicators to heritably varying phenotypic traits: the extended phenotype revisited. *Biology and Philosophy*, **19**, 353–375.

Jeanne, R.L. (1979). Construction and utilization of multiple combs in *Polistes canadensis* in relation to the biology of a predaceous moth. *Behavioral Ecology and Sociobiology*, **4**, 293–310.

Kastberger, G. and Sharma, D.K. (2000). The predator-prey interaction between blue-bearded bee eaters (*Nyctyornis athertoni* Jardine and Selby 1830) and giant honeybees (*Apis dorsata* Fabricius 1798). *Apidologie*, **31**, 727–736.

Kathirithamby, J. and Hughes, D.P. (2005). Description and biological notes of the first species of *Xenos* (Strepsiptera : Stylopidae) parasitic in *Polistes carnifex* F. (Hymenoptera : Vespidae) in Mexico. *Zootaxa*, 35–45.

Keller, L. and Genoud, M. (1997). Extraordinary lifespans in ants: a test of evolutionary theories of ageing. *Nature*, **389**, 958–960.

Kilner, R.M. and Davies, N.B. (1999). How selfish is a cuckoo chick? *Animal Behaviour*, **58**, 797–808.

King, L.E., Douglas-Hamilton, I., and Vollrath, F. (2007). African elephants run from the sound of disturbed bees. *Current Biology*, **17**, R832–R833.

Laland, K.N. (2004). Extending the extended phenotype. *Biology and Philosophy*, **19**, 313–325.

Laland, K.N. and Sterelny, K. (2006). Seven reasons (not) to neglect niche construction. *Evolution*, **60**, 1751–1762.

McAuliffe, K. and Whitehead, H. (2005). Eusociality, menopause and information in matrilineal whales. *Trends in Ecology and Evolution*, **20**, 650–650.

Maeyama, T., Terayama, M., and Matsumoto, T. (1994). The abnormal behavior of *Colobopsis* sp. (Hymenoptera: Formicidae) parasitized by *Mermis* (Nematoda) in Papua New Guinea. *Sociobiology*, **24**, 115–119.

Martin, S.J., Beekman, M., Wossler, T.C., and Ratnieks, F.L.W. (2002). Parasitic Cape honeybee workers, *Apis mellifera capensis*, evade policing. *Nature*, **415**, 163–165.

Matsuura, M. (1999). Size and composition of swarming colonies in *Provespa anomala* (Hymenoptera, Vespidae), a nocturnal social wasp. *Insectes Sociaux*, **46**, 219–223.

Mayr, E. (1997). The objects of selection. *Proceedings of the National Academy of Sciences of the USA*, **94**, 2091–2094.

Miura, O., Kuris, A.M., Torchin, M.E., Hechinger, R.F., and Chiba, S. (2006). Parasites alter host phenotype and may create a new ecological niche for snail hosts. *Proceedings of the Royal Society B: Biological Sciences*, **273**, 1323–1328.

Mock, D.W. and Parker, G.A. (1997). *The Evolution of Sibling Rivalry.* Oxford University Press, Oxford.

Monnin, T., Ratnieks, F.L.W., Jones, G.R., and Beard, R. (2002). Pretender punishment induced by chemical signalling in a queenless ant. *Nature*, **419**, 61–65.

Moore, J. (2002). *Parasites and the Behavior of Animals.* Oxford University Press, Oxford.

Moore, J., Adamo, S., and Thomas, F. (2005). Manipulation: expansion of the paradigm. *Behavioural Processes*, **68**, 283–287.

Muller, C.B. and Schmid-Hempel, P. (1993). Exploitation of cold temperature as defense against parasitoids in bumblebees. *Nature*, **363**, 65–67.

Odling-Smee, F.J., Laland, K.N., and Feldman, M.W. (2003). *Niche Construction: the Neglected Process in Evolution.* Princeton University Press, Princeton, NJ.

Oster, G. (1976). Modelling social insect populations I. Ergonomics of foraging and population growth in Bumblebees. *The American Naturalist*, **110**, 215–245.

Oster, G.F. and Wilson, E.O. (1978) *Caste and Ecology in the Social Insects.* Princeton University Press, Princeton, NJ.

Pardi, L. (1948). Dominance order in *Polistes w*asps. *Physiological Zoology*, **21**, 1–13.

Pierce, N.E. (1995). Predatory and parasitic Lepidoptera: carnivores living on plants. *Journal of the Lepidopterists Society*, **49**, 412–453.

Pierce, N.E., Braby, M.F., Heath, A. *et al.* (2002). The ecology and evolution of ant association in the Lycaenidae (Lepidoptera). *Annual Review of Entomology*, **47**, 733–771.

Pigliucci, M. and Kaplan, J. (2000). The fall and rise of Dr Pangloss: adaptationism and the Spandrels paper 20 years later. *Trends in Ecology and Evolution*, **15**, 66–70.

Ponton, F., Biron, D.G., Moore, J., Moller, A.P., and Thomas, F. (2006). Facultative virulence: a strategy to manipulate host behaviour? *Behavioural Processes*, **72**, 1–5.

Poulin, R. (1994). The evolution of parasite manipulation of host behavior: a theoretical analysis. *Parasitology*, **109**, S109–S118.

Poulin, R. (1998) *The Evolutionary Ecology of Parasites.* Chapman & Hall, London.

Poulin, R. (2000). Manipulation of host behaviour by parasites: a weakening paradigm? *Proceedings of the Royal Society Series B: Biological Sciences*, **267**, 787–792.

Poulin, R. (2007). *Evolutionary Ecology of Parasites*, 2nd edn. Chapman & Hall, London.

Pratt, S.C., Mallon, E.B., Sumpter, D.J.T., and Franks, N.R. (2002). Quorum sensing, recruitment, and collective decision-making during colony emigration by the ant *Leptothorax albipennis. Behavioral Ecology and Sociobiology*, **52**, 117–127.

Queller, D.C. and Strassmann, J.E. (2002). The many selves of social insects. *Science*, **296**, 311–313.

Ratnieks, F.L.W. (1988). Reproductive harmony via mutual policing by workers in eusocial Hymenoptera. *The American Naturalist*, **132**, 217–236.

Rau, P. (1933). *Jungle Bees and Wasps of Barro Colorado Island*. Published by the author.

Read, A.F. (1994). The evolution of virulence. *Trends in Microbiology*, **2**, 73–76.

Reeve, H.K. and Keller, L. (1999). Burying the units-of-selection debate and unearthing the crucial new issues. In: L. Keller (ed.), *Levels of Selection in Evolution*. Princeton University Press, Princeton, NJ.

Reeve, H.K., Peters, J.M., Nonacs, P., and Starks, P.T. (1998). Dispersal of first 'workers' in social wasps: causes and implications of an alternative reproductive strategy. *Proceedings of the National Academy of Sciences of the USA*, **95**, 13737–13742.

Richardson, T.O., Houston, A.I., and Franks, N.R. (2007). Teaching with evaluation in ants. *Current Biology*, **17**, 1520–1526.

Ross, K.G. and Matthews, R.W. (1991). *The Social Biology of Wasps.* Cornell University Press, Ithaca, NY.

Salt, G. (1927). The effects of stylopization on aculeate Hymenoptera. *Journal of Experimental Zoology*, **48**, 223–331.

Salt, G. (1931). A further study on effects of stylopization. *Journal of Experimental Zoology*, **59**, 133–166.

Schmid-Hempel, P. (1998). *Parasites in Social Insects.* Princeton University Press, Princeton, NJ.

Schmid-Hempel, P. and Schmid-Hempel, R. (1984). Life duration and turnover of foragers in the ant *Cataglyphis bicolor* (Hymenoptera, Formicidae). *Insectes Sociaux*, **31**, 345–360.

Schmid-Hempel, P. and Schmid-Hempel, R. (1990). Endoparasitic larvae of conopid flies alter pollination behavior of bumblebees. *Naturwissenschaften*, **77**, 450–452.

Schmid-Hempel, P. and Stauffer, H.P. (1998). Parasites and flower choice of bumblebees. *Animal Behaviour*, **55**, 819–825.

Schmid-Hempel, R. and Muller, C.B. (1991). Do parasitized bumblebees forage for their colony. *Animal Behaviour*, **41**, 910–912.

Schultz, T.R., Mueller, U.G., Currie, C.R., and Rehner, S.A. (2005). Reciprocal illumination: a comparison of agriculture in humans and in fungus-growing ants. In: F.E. Vega and M. Blackwell (eds), *Insect–Fungal Associations*, pp. 149–190. Oxford University Press, New York.

Seeley, T.D. (1995). *The Wisdom of the Hive.* Harvard University Press, Cambridge, MA.

Seeley, T.D. and Buhrman, S.C. (1999). Group decision making in swarms of honey bees. *Behavioral Ecology and Sociobiology*, **45**, 19–31.

Seeley, T.D., Visscher, P.K., and Passino, K.M. (2006). Group decision making in honey bee swarms. *American Scientist*, **94**, 220–229.

Segerstråle, U. (2007). An eye on the core: Dawkins and sociobiology. In: A. Grafen and M. Ridley (eds), *Richard Dawkins: How a Scientist Changed the Way we Think*. Oxford University Press, Oxford.

Sherman, P.W., Seeley, T.D., and Reeve, H.K. (1988). Parasites, pathogens, and polyandry in social Hymenoptera. *The American Naturalist*, **131**, 602–610.

Shykoff, J.A. and Schmid-Hempel, P. (1991). Incidences and effects of four parasites in populations of bumble bees in Switzerland. *Apidologie*, **22**, 117–125.

Strambi, C., Strambi, A., and Augier, A. (1982). Protein levels in the haemolymph of the wasp *Polistes gallicus* L. at the beginning of imaginal life and during overwintering. Action of the strepsipteran parasite *Xenos vesparum* Rossi. *Experentia*, **38**, 1189–1191.

Strassmann, J.E., Zhu, Y., and Queller, D.C. (2000). Altruism and social cheating in the social amoeba *Dictyostelium discoideum. Nature*, **408**, 965–967.

Sumpter, D.J.T. (2006). The principles of collective animal behaviour. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **361**, 5–22.

Thomas, F., Schmidt-Rhaesa, A., Martin, G., Manu, C., Durand, P., and Renaud, F. (2002). Do hairworms (Nematomorpha) manipulate the water seeking behaviour of their terrestrial hosts? *Journal of Evolutionary Biology*, **15**, 356–361.

Thomas, F., Adamo, S., and Moore, J. (2005). Parasitic manipulation: where are we and where should we go? *Behavioural Processes*, **68**, 185–199.

Tibbetts, E.A. (2002). Visual signals of individual identity in the wasp *Polistes fuscatus. Proceedings of the Royal Society Series B: Biological Sciences*, **269**, 1423–1428.

Trabalon, M., Plateaux, L., Peru, L., Bagneres, A.G., and Hartmann, N. (2000). Modification of morphological characters and cuticular compounds in worker ants *Leptothorax nylanderi* induced by endoparasites *Anomotaenia brevis. Journal of Insect Physiology*, **46**, 169–178.

Turillazzi, S. (1991). The Stenogastrinae. In: K.G. Ross and R.W. Matthews (eds), *The Social Biology of the Wasps*. Cornell University Press, Ithaca, NY.

Turillazzi, S. and West-Eberhard, M.J. (eds) (1996). *Natural History and Evolution of Paper-wasps.* Oxford University Press, Oxford.

Visscher, P.K. (2007). Group decision making in nest-site selection among social insects. *Annual Review of Entomology*, **52**, 255–275.

Von Frisch, K. (1968). Role of dances in recruiting bees to familiar sites. *Animal Behaviour*, **16**, 531–533.

Von Frisch, K. (1974). *Animal Architecture.* Harcourt Brace Jovanovich, New York.

Wcislo, W.T. (1999). Transvestism hypothesis: a cross-sex source of morphological variation for the evolution of parasitism among sweat bees (Hymenoptera: Halictidae)? *Annals of the Entomological Society of America*, **92**, 239–242.

Wenseleers, T. and Ratnieks, F.L.W. (2006). Enforced altruism in insect societies. *Nature*, **444**, 50.

West-Eberhard, M.J. (1969). The social biology of Polistine wasps. *Miscellaneous Publications of the Museum of Zoology, University of Michigan*, **140**, 1–101.

West-Eberhard, M.J. (2003). *Developmental Plasticity and Evolution.* Oxford University Press, New York.

Wheeler, W.M. (1911). The ant-colony as an organism. *Journal of Morphology*, **22**, 307–325.

Wilson, E.O. (1959). Source and possible nature of the odor trail of fire ants. *Science*, **129**, 643–644.

Wilson, E.O. (1971). *The Insect Societies.* Harvard University Press, Cambridge, MA.

Wilson, E.O. (1975). *Sociobiology. The New Synthesis* Belknap Press, Cambridge, MA.

Wilson, E.O. (1983). Caste and division of labor in leaf-cutter ants (Hymenoptera, Formicidae, Atta).3. Ergonomic resiliency in foraging by Atta-Cephalotes. *Behavioral Ecology and Sociobiology*, **14**, 47–54.

Wilson, E.O. (1985). The sociogenesis of insect colonies. *Science*, **228**, 1489–1495.

Wilson, E.O. (2000). *Sociobiology. The New Synthesis 25th Anniversary Edition.* Belknap Press, Cambridge, MA.

Wilson, E.O. (2005). Kin selection as the key to altruism: its rise and fall. *Social Research*, **72**, 159–166.

Wilson, E.O. and Hölldobler, B. (2005). Eusociality: origin and consequences. *Proceedings of the National Academy of Sciences of the USA*, **102**, 13367–13371.

Winfree, R. (1999). Cuckoos, cowbirds and the persistence of broad parasitism. *Trends in Ecology and Evolution*, **14**, 338–343.

Witte, V., Janssen, R., Eppenstein, A., and Maschwitz, U. (2002). *Allopeas myrmekophilos* (Gastropoda, Pulmonata), the first myrmecophilous mollusc living in colonies of the ponerine army ant *Leptogenys distinguenda* (Formicidae, Ponerinae). *Insectes Sociaux*, **49**, 301–305.

Zahavi, A. (1979). Parasitism and nest predation in parasitic cuckoos. *The American Naturalist*, **113**, 157–159.