

# Parasites and the superorganism

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## 8.1 Introduction

We know that parasites affect the behavior of their hosts in weird and wonderful ways. Contained within this book are surveys of parasites affecting all manner of hosts and reviews of the mechanisms by which these behaviors occur and the ecological and evolutionary significance of such strategies. The field of parasite manipulation of host behavior is maturing quickly (Chapter 1). To date studies have mainly focused on the effects of parasites on the behavior of the individual organism. This is both sensible and logical given the importance of the organism in the long history of evolutionary biology and the on-going discussion of where selection acts (Mayr 1997). But of course behavior is not expressed only by unitary organisms. Behavior is also expressed by superorganisms.

The superorganism is a term used exclusively in the context of eusocial organisms like ants, wasps, bees, and termites (Hölldobler and Wilson 1990, 2009). The eusocial insects account for a low diversity of animal life (<2% of all insects) but by virtue of having multiple individuals in a single colony their biomass is disproportionately large and in some habitats, such as the tropical rainforests, eusocial insects may account for over half of all free-living biomass, including vertebrates (Tobin 1991; Hölldobler and Wilson 2009). As such these groups are interesting to parasitologists because all these bodies moving through the environment present either a large number of hosts to be infected or avoided if social insects are not the target host (Hughes 2005). The word “superorganism” describes how the cooperative group living that we observe in eusocial insects leads to phenotypes that

are a product of multiple individuals that have become specialized to perform separate tasks such that their action can be viewed as distinct parts of the collective. The most fundamental separation of tasks is the division of labor where only a small fraction of the colony reproduces (queen and males) with the majority of individuals performing work and not reproducing directly. Beyond that the non-reproducing majority can be further specialized to perform distinct tasks, which I discuss in more detail below.

In this chapter I want to explore parasites that manipulate social insect behavior. I will ask whether such behavioral changes fit into the framework developed for parasites affecting the behavior of individual hosts. I will then examine a range of collective behaviors expressed by diverse taxa to ask if lessons from studies on superorganisms and their behavior can inform collective behavior more generally. Finally, I will look towards future work that empirically addresses the difference in environments between solitary and eusocial hosts.

## 8.2 The extended phenotype and the unitary organism

In a landmark book, *The Extended Phenotype*, Richard Dawkins (1982) advocated that the phenotype need not be attached directly to the organism but could be physically distant to the organisms whose genes are encoding it. There are three categories of extended phenotypes (EPs). The first is animal architecture which the Nobel Prize sharing ethologist, Karl Von Frisch called “frozen behavior” (1974). The work of Michael Hansell gives an

excellent insight into this little studied, but fascinating component of animal behavior (Hansell 2004, 1996). By the far the most well-known is the beaver dam, which is a physical representation of beaver behavior in wood and mud that increases the fitness of the genes encoding the building behavior. The second EP is parasite manipulation of host behavior. This topic is the focus of this edited volume and has also been extensively reviewed by others (Poulin 2011; Moore 2002; Barnard and Behnke 1990; Poulin 1994). An exemplar of this field is the suicidal behavior 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. 2002a; see also Chapters 2, 3, and 9). This behavior 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: the manipulation of host behavior by cuckoo chicks (see Chapter 6). In this case the chick is not physically associated with the host, as in the case of hairworms, but influences the expression of its behavioral 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, as in pheromone based social communication or territorial disputes (Sergio et al. 2011).

The extended phenotype view of behavior is intimately related to the view of the gene as the unit of selection. This paradigm emerged during a period of much debate between advocates of individual and group level selection and through the work of Hamilton (Hamilton 1963, 1964). Dawkins then subsequently developed it as a transparent concept with his selfish gene approach (1976) and it became the foundation for sociobiological theory (Wilson 1975). As an historical aside it was recently emphasized that Wilson's sociobiology stance leaned more towards group rather than individual selection and it is Dawkins who deserves the major credit in the current association between sociobiology and gene level/individual selection (Segerstråle 2007). In the last six years Wilson has spoken out against the current sociobiological view that relies heavily on the indirect fitness framework (Hughes 2009, 2011;

Wilson and Wilson 2007; Wilson 2005) culminating in a model with mathematical biologists (Nowak et al. 2010) which was formally critiqued in the *Brief Communications* section of *Nature* (24 March 2011 issue).

The debate on individual versus group selection is both important and valuable (Hughes 2011) but it should not obscure the fact that the gene is still the unit of selection. What this paradigm states is that genes alone 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).

Having discussed the mechanism of genetic material transfer between generations let us return to phenotype. The phenotype has principally been considered a trait of the individual organism. Examples include flower color, head size, butterfly wing spots, behavior, and chemical signals released into the air, to name just a few. But such foci reflect the convenience with which we could study those easily visible attributes of organisms (Dawkins 1990). It also reflects historical effects as modern approaches follow on from the natural history tendencies of previous generations (Burkhardt 2005). Now of course behavioral ecologists are taking advantages of advances in cellular and chemical biology to measure less obvious phenotypes of the organism such as the surface of cells, tissues, and organs. This chain of phenotypes extends down to the transcriptome that affordable next generation sequencing allows to be used for a broad array of non-model taxa (Bonasio et al. 2010).

### 8.3 The behavior of social insects

When we think of the social insects it is the ants, termites, wasps, and bees that come to mind. The technical term is eusocial, which is defined as having overlapping generations, cooperative care of brood, and division of labor 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) and there are many other taxa besides ants, termites, wasps, and bees in which we find sociality. Examples of these are: mites, spiders, shrimp, thrips, aphids, beetles, and naked mole rats (Costa 2006; Wilson 1971; Bennett and Faulkes 2000; Crespi and Cho 1997). Even humans and pilot whales have been called social (McAuliffe and Whitehead 2005; Foster and Ratnieks 2005). In this chapter I will restrict myself to the traditionally defined social insects (ants, termites, wasps, and bees). Also, for convenience, and in line with most authors, I will use the term social insects, rather than eusocial insects.

Social insects live in family based groups where a minority of individuals reproduce (queens and kings/males) and the majority (the workers) are functionally sterile and collect resources to provision the offspring of the reproductives. In hymenoptera the male is represented as stored sperm in the female and in termites the male (termed king) is a whole individual that continually mates with the queen. The non-reproducing state of the workers, that is their functional sterility, is an example of altruism. It is considered adaptive for workers since the offspring are usually the full siblings of the workers and by helping to raise future queens and males that begin new colonies they gain indirect fitness benefits (Hamilton 1963, 1964). Social insects live in colonies that vary in size from 10 individuals in hover wasp societies (Turillazzi 1991) to more than 10 million in army ant societies (Hölldobler and Wilson 1990). They can occupy living spaces ranging in size from an acorn (*Temnothorax*) to 5 m high mounds (termites).

Living in societies requires effective communication strategies and studies of social insects have been instrumental in the development of communication theory (Hölldobler and Wilson 1990; Abe et al. 2001; Seeley 1995; Ross and Matthews 1991). Obvious examples are status communication 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 (Richardson et al. 2007; Franks and Richardson 2006). Social insects communicate with other members of the society: signaling identity (which colony they belong to), soliciting of food by larvae, and adults soliciting nutritious regurgitations from larvae; individuals signaling 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: signaling identity (nest of origin), aggressive displays signaling fighting ability and resource ownership. Collective actions involving many individuals also have communicative roles and are usually used 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, is 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 parallel in African bees whose sound was shown to deter herds of elephants (King et al. 2007).

Societies also require the evolution of elaborate architecture and social insects are rivaled only by humans in their ability to construct living spaces. No bird nest, spider web, or caddis shell can compare with the multifunctional cathedral mounds built by fungus growing termites; these 5-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 passage-ways, and, at the center, a rock hard protective chamber in which the king and the 3,000 egg per day egg-laying machine that is the queen, reside (Abe et al. 2001). 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 Australian outback (Aanen and Eggleton 2005).

## 8.4 Behavior of the superorganism

Having provided some brief background to social insects and how they live I now want to discuss the valid use of the metaphor of the colony as a superorganism. The large sizes of social insect societies, the multiple examples of collective action, and the way society members are often behaviorally or morphologically specialized for certain tasks, together with the localization of the colony in a bounded structure that is built by multiple individuals, have led to the view that the whole colony is a superorganism (Wheeler 1911). This view, though intuitively appealing, lost favor 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 (Reeve and Keller 1999; Bourke and Franks 1995, p. 64–66). 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). Colonies can split in two, giving rise to two colonies (e.g., honeybees and army ants) but this is not replication in the strict sense. I would stress that much confusion arises from an inability to parse studies of behavior into mechanistic or functional approaches (Duckworth 2009).

The second reason 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 favor a 0.75 bias towards females and the latter an equal sex ratio (Bourke and Franks 1995; Bourke 2011). There is also conflict between workers if one decides to reproduce, and here we see the evolution of policing behavior

(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. A particularly nice discussion of the superorganism view was recently given by Hamilton et al. (2009).

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 Argentinean 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 behavioral 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 labor (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 is comprised of cooperating genes that have resolved potential conflicts because of shared interests in gamete production (Dawkins, 1990), 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).

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 behavior we see is “more than the sum of its parts” (Oster and Wilson 1978, p. 10). In order to produce effective responses to collective goals (e.g., colony survival) the multiple 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. The desiderata, or interests, of the distinct members are aligned for a period of time (Dawkins 1990).

### 8.5 Parasites divide the interests of superorganism

I have gone to some lengths to stress the biology of social insects and the real unity that exists among social insect society members, because the introduction of parasites into the system leads to cryptic competition within an apparently unified group of colony members. Parasites can live either inside the host body or external to it (and inside the colony). This is shown in Fig. 8.1 for parasites of ants. In the former case which individual is infected is not obvious. 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 conflict is predicted. A parasite infecting a worker will not want its host to exit the colony on foraging trips when such activity entails an appreciable risk of mortality before the parasite is ready to transmit to a new host or complete its development. Note that timing is important since many social insect parasites are trophically transmitted so require the host to be predated upon (e.g., cestodes, trematodes, and nematodes). While we do not generally 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 it 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 the 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 behaviorally modifying parasites these chimeric individuals contain.

### 8.6 Behaviorally modifying parasites of social insects

The keystone concept of social insect biology is the reproductive division of labor. Understanding this is central to all studies on the evolutionary biology of social insects and this is equally true for parasites that infect social insects. The reproductive division of labor means that parasites that infect and kill workers need not necessarily affect the fitness of the worker. This paradoxical statement is resolved when we realize that worker fitness is realized via indirect fitness via helping behavior towards relatives (Hamilton 1964). This is fundamentally different to infection in solitary organisms (Hughes 2005; Hughes et al. 2008). Natural selection might not act on individual defense (e.g., innate immunity for workers) if the cost of that worker’s loss from the colony via behavioral manipulation is less than the cost of defense. But if sufficient numbers of workers are lost to infection then we could expect that the colony defends itself against infection. Colonies are well known to be highly adaptable units that rapidly respond to changes: producing more or fewer workers of a certain size for example (Wilson 1983a, 1983b).

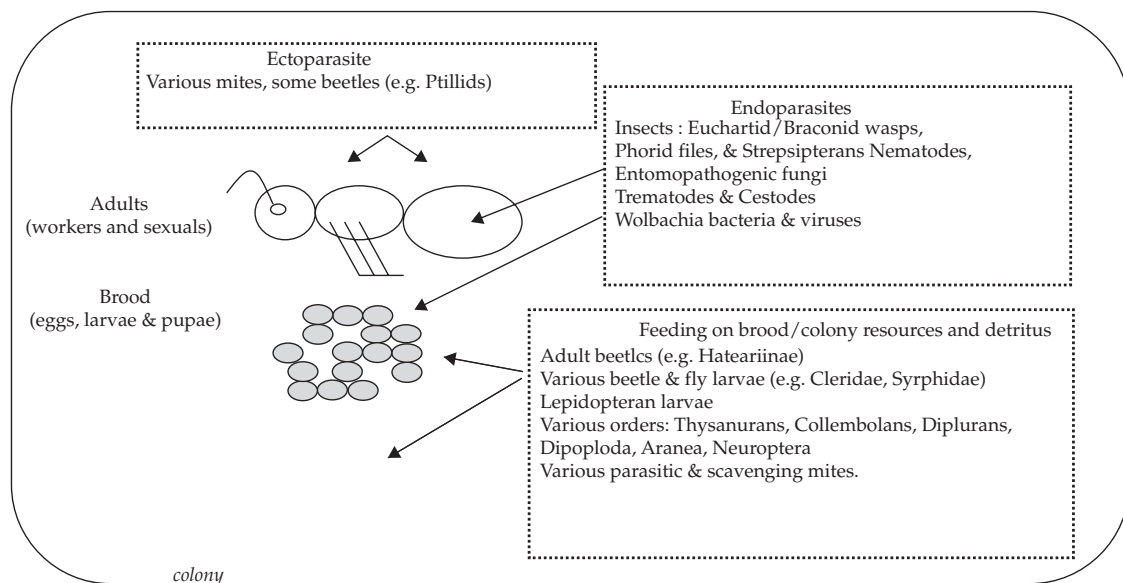
Because of the potential for a colony-level response it is correct to view a parasite of a social insect as having two hosts: the individuals in whose body it lives and the colony that the individual belongs to. This means that parasites infecting social insects always infect two hosts at once (Sherman et al. 1988, p. 263; Schmid-Hempel 1998; Hughes et al. 2008). The two-host view of social insects is valid and fully accepted and with this in mind let us progress to examine which parasites infect social insects, and importantly, which manipulate them.

Parasites of social insects have provided prominent and compelling examples of parasite EPs where host behavior is manipulated. The best known example is the “brain-worm” which is a

trematode inducing its intermediate ant host to leave the colony and climb blades of grass and bite hard (Carney 1969). The final host is a grazing animal such as a sheep that is presumed to ingest ants along with the grass it is eating (Manga-Gonzalez et al. 2001). So emblematic is this example that it “made the cover” of Janice Moore’s excellent review entitled *Parasites and the Behavior of Animals* (2002). Another manipulating parasite that I work on, the fungus *Cordyceps*, which also causes ants to bite onto vegetation, similarly adorned the cover of Paul Schmid-Hempel’s book, *Parasites in Social Insects* (1998). There are many parasites in social insect societies (Kistner 1979, 1982; Schmid-Hempel 1998). A sense of this diversity can be had by examining Fig. 8.1 which only shows those infecting ants (called myrmecophiles).

In reviewing here the range of parasites causing behavioral changes among the social insects it will be useful to introduce categories (Table 8.1). There are five categories of behavioral modification in social insects. (1) The first is adaptive manipulation of individual host behavior that favors 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 rhabditid Nematodes, Entomophthoralean 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 multi-step 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), walking in an exposed location so as to be eaten by vertebrates (cestodes, trematodes, nematodes), inactivity in a prominent place to facilitate parasite mating (Strepsiptera), and moving around the environment to disperse parasite propagules from the parent parasite in the social insect. In each of these cases the biology of the



**Figure 8.1** A schematic diagram of an ant colony showing a worker and some brood. The relative positions occupied by various parasites are shown. The list of myrmecophiles is not exhaustive.

parasite and its mode of reproduction is such that nest desertion is 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 transferred to a final host).

(2) The second category is adaptive manipulation of more than one individual (i.e., the colony) that favors 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 (discussed below). Because the parasite is not internal to the individual host (i.e., worker) then we may view this as the action at a distance extended phenotype like the familiar example of cuckoo chicks manipulating their hosts to feed them (Chapter 6). Indeed, the social parasites are often 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).

(3) The third category switches the benefits of the parasite associated behavioral change from the parasite to the host and into defensive behaviors. Individual social insects have a very large repertoire of defensive behavioral reactions against parasites. Most mundane, but evidently important for colony level defense, is self-grooming, allo-grooming and

in the case of crop rearing ants, grooming, or “weeding,” their mutualistic fungus (Cremer et al. 2007). More dramatic is cold seeking behavior by conopid-fly infected bees to retard parasite development; every night they move outside of the high temperature nest (Müller 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 behavior against parasites but here it requires the coordinated action of multiple individuals to succeed. The “dancing behavior” of paper wasps in response to the presence of an ovipositing Ichneumonidae wasp is a good example (West-Eberhard 1969). Another example is construction behavior 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, that of construction, is an EP of ants and wasps as a defense against parasites and has nice parallels with avian construction such as oven and weaver bird nests as a defense against predators like snakes (Hansell 2004).

(5) The fifth category does not interpret the behavioral 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; Poulin 1994,

**Table 8.1** The five categories of altered behavior in social insects and examples (discussed and referenced in the text).

	Parasite adapted	Host adapted	Byproduct
1	Manipulating the individual e.g., <i>cordyceps</i> , <i>strepsipterans</i>	-	-
2	Manipulating the colony (Multiple individuals) e.g., ant warfare by parasitoid	-	-
3	-	Individual defense e.g., <i>Bombus</i> workers seeking cold temperature against Conopid infection	-
4	-	Multiple individuals defending e.g., Wasp dance against ovipositing parasitoids	-
5	-		At individual and colony level e.g., Generalist fungi like <i>Metarizhium</i>

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 (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).

These are the five categories of behavioral changes among social insects due to the presence of parasites. I will now consider three ways parasites manipulate superorganism behavior.

## 8.7 Manipulating the whole colony

### 8.7.1 Parasitizing social resources

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 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 parasites that manipulate the care giving behavior of social insects (Hölldobler et al. 1981; Hölldobler 1971; Als et al. 2001). These are called social parasites and they are exclusively large organisms similar in size to the hosts (e.g., beetles, caterpillars). Social parasitism is also the term applied to 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 (= behavioral manipulation) is the explanation.

There are many examples of social parasites. A common feature is that the parasite is not internal inside the body of an individual ant, wasp, bee, or termite but only internal in the host colony. In societies of ants, for example, it is possible to find beetles, flies, caterpillars, mites, molluscs, and other macroparasites parasitizing the nest. In some cases these parasites are very well camouflaged to avoid detection or use appeasement substances from specialized glands to avoid being evicted (Fiedler et al.

1996; Pierce 1995). In yet other systems the parasites rely on physical protection to avoid the aggressive overtures of ants, such as protective plates in the fly *Microdon* or a protective parasite-constructed case as in Chrysomelid beetles (Kistner 1982). Social parasites also include other wasps, bees, and ants that ancestrally were social but have lost the ability to build their own nests (Hölldobler and Wilson 1990; Wilson 1971).

Traditionally non-hymenopteran social parasites have been investigated because their biology is unique with respect to close relatives that have not adopted parasitism as a life history trait (Pierce 1995). For hymenopteran social parasites a large focus has been on the phylogenetic relationship between host and parasite (Als et al. 2002). The perspective of the parasite and the effect of behavioral manipulation on the whole colony has not been explicitly considered. There is a great deal of evidence (mainly from studies on beetles, lepidopterans, and hymenopterans in ant societies) of control of individual host behavior (Hölldobler and Wilson 1990). These parasites do affect the behavior of multiple individuals at once. What I feel is interesting here is that such a superorganism effect would not simply be a summation of multiple smaller effects but may, possibly, be some qualitative change we have not yet appreciated. We do not of course know but the point made by Oster and Wilson (1978, p. 9–11) that social insects do not have novel behavior but rather a novel collective phenotype resulting from parallel operating, remains true despite being largely ignored by researchers. How behaviorally manipulating parasites affects the efficiency of an evolved parallel operating modular unit like the superorganism remains to be seen.

### 8.7.2 Cheating the mutualism

For many the leaf-cutting ants surely represent one of the most powerful and dramatic examples of social insect society (Hölldobler and Wilson 2010). Their attraction holds for social insect biologists also and these marvelous insects have received an enormous amount of attention over the years (Hölldobler and Wilson 1990, Ch 17; Schultz et al. 2005). One of the most impressive features of leaf-



cutters is their coevolved mutualism with a fungus that they eat. They collect leaves, the fungus eats the leaves, and the ants eat the fungus. It is an ancient association extending back 50 million years (Currie et al. 2006; Schultz et al. 2005) and one which is paralleled in the Old World by termites who similarly raise a fungus which they consume (Aanen and Boomsma 2005; Aanen and Eggleton 2005).

In both cases a colony only raises one strain of fungus (Aanen et al. 2009; Poulsen and Boomsma 2005). Since the fungus is liable to infection from specialized or generalist myco-parasites (Currie et al. 1999) then ant societies would be better served by having diverse strains that would reduce the chance of failure if one crop fails. The extent to which greater diversity is desired is a balancing act as too much diversity would select for competitive traits among domesticated fungi which would reduce the food yield (Aanen 2010). As it stands the reliance on one monoculture has selected for expensive chemical (Bot and Boomsma 1996; Bot et al. 2001; Poulsen et al. 2002) and behavioral (Little et al. 2005) defense as well as architectural behavior by the hosts (Aanen et al. 2009; Schultz et al. 2005). It has also selected for the incorporation of other mutualists into the association, and some ants have evolved a relationship with an antibiotic producing bacteria which is then itself infected by a black yeast fungus (Little and Currie 2008). It is reasonable to ask if more diversity would have changed this. Simply having more strains of fungi to feed from would be a better solution. So why don't colonies of fungal growing ants have more strains?

The answer may be because the fungus is manipulating the physiology of the ants, preventing them taking on board new strains. We tend to think that ants (or termites) as having domesticated fungi, but it could also have been the other way around. In the ant system the rounded tips of the hyphae are called Bromatia and in the termites the "bulbous structure developed by fungi cultivated by termites" are Gongylidia (although gongylidia is incorrectly used by ant people (Kirk et al. 2008)). In the ant mutualism the fungus produces a suite of enzymes that pass through the ant's body to act as plant degrading compounds (Schiøtt et al. 2010).

In this system ants defecate on freshly collected leaves and the enzymes from the bromatia have many enzymes like those found in phytopathogenic fungi that degrade plant tissue. The implication that the fungus is manipulating the ant is from a particularly nice study where ants were removed from their symbiont and forced to eat another (Poulsen and Boomsma 2005). They could not, and it required nine days of force feeding before ants could switch cultivar strains; a barrier unlikely to be overcome in the wild. Definitive proof is lacking but given the ability of these fungi to evolve enzymes that can pass through ants to affect plant tissue it is not a stretch to also imagine they affect ant digestion preventing the easy acquisition of other strains, which after all is in the colony's interest. If this is true then fungi could manipulate whole colony behavior just as *Ophicordyceps* (= *Cordyceps*) manipulates individual behavior (Andersen et al. 2009).

### 8.7.3 Panicking the crowd

Social parasites need to get into and remain inside the colony. E.O. Wilson, with his usual metaphoric flair, described the colony as a "factory within a fortress" (Wilson 1968) and Schmid-Hempel picked this up leading to the evocative language of parasites "breaking into the fortress" (1998). Many of the entry routes involve chemical signals that affect host behavior. In one example a parasitoid wasp *Ichneumon eumerus* has evolved the ability to induce ant warfare (Thomas et al. 2002b). The parasitoid does not attack ants but rather lays eggs inside a socially parasitic caterpillar *Maculinea rebeli* that infects ant nests (genus *Myrmica*). The caterpillar uses chemicals to trick ants into bringing it home and continues to use chemicals to obtain food inside the nest (Als et al. 2004). As a consequence, caterpillars are always surrounded by ants. The challenge for the parasitoid wasps is laying an egg in a caterpillar surrounded by formidable bodyguards. What the parasitoid wasp female does, and this is very special, is produce semiochemicals that induce ferocious fighting among ants leaving the caterpillar unattended (Thomas et al. 2002b).

There is a similar example whereby parasitoid flies (Phoridae) cause excessive panicking behavior among trails of ants. Here flies hover above trails and dart down to lay eggs in the heads of workers (Feener et al. 1996). The infection progresses and the head eventually falls off and the fly pupates inside. The loss of the worker for the colony is slight and given that infection levels are very low one cannot imagine the loss at the colony level is high. Yet, the presence of a single fly is enough to cause hundreds of ants to hide under leaves or simply stop foraging (Orr et al. 1995; Feener and Brown 1992). In one study the daily foraging rate decreased by 50% (Mehdiabadi and Gilbert 2002). It is possible that this is just a maladapted trait: the ants just overreact. But what is also possible is that panicking the crowd increases the egg laying ability of parasitoid flies in the same way it does for parasitoid wasps of *Maculinea* discussed above. We don't know, but considering the behavior of the superorganism helps us design research questions to test this.

#### 8.7.4 Shifting foraging ecology

Dipteran and hymenopteran parasitoids are large insects that generally fly and so are visible to foraging social insects. As such, behavioral defenses against ovipositing females, such as ant workers reducing foraging (above) or the coordinated dance behavior among paper wasps in the presence of an ovipositing Ichneumonidae wasp (West-Eberhard 1969) are beneficial. But most parasites of social insect are not surgically delivered into new hosts by ovipositing mothers. Rather, propagules are dispersed in the environment where foraging workers encounter them and bring them back into the colony (e.g., nematodes, cestodes, trematodes, strepsipterans, fungi (including microsporidians), gregarines, coleopterans, and lepidopterans). Therefore, the presence of parasites in the environment could lead to shifts in where social insects forage if avoiding parasites is adaptive to the colony (avoidance may not be adaptive, see Hughes et al. 2008).

There are three ways that parasite-induced shifts in social insect foraging can happen and all three are, not surprisingly, examples of where social

insect behavior is changed to reduce infection (category 4 from Table 8.1). When paper wasps nests (*Polistes canadensis*) are infected by a predaceous moth caterpillar (Tineidae) the workers construct satellite nests to reduce the loss to parasites (Jeanne 1979). In this case the moth burrows through the lower walls of the nest, eating brood as it goes. Once the moth is in it is impossible to stop so satellite nest construction evolved to limit damage. Wasps will have to alter flying patterns in response to two nests. This may not appear to be a big deal but since we know wasps can, and do, accidentally shift between colonies (Sumner et al. 2007) the presence of a parasite may increase the incidence of such shifting. In wood ants, *Formica*, from temperate forests workers collect a resin from pine trees, which has been shown to have antibiotic properties and reduce the microbial load inside the colony (Christe et al. 2003). In this case defending against microbial pathogens (i.e., not specialized parasites) will lead to changes in foraging routes as resin is collected. Finally, a group of microbial parasites that are highly specialized are *Cordyceps* fungi (now called *Ophiocordyceps*) (Sung et al. 2007). Here social insects (wasps and ants) are infected when foraging as a spore attaches to and penetrates through the cuticle. Infection takes hours and so the worker has returned to the nest by the time the spore has entered the cuticle. Once through, the parasite proliferates inside the host over days and then instructs the worker to leave the nest since the fungus needs to produce a large stalk from the host's body after it kills it. Since killing the host inside the nest would just result in the dead worker being dumped on the trash pile (midden), selection has led to a range of manipulative strategies where workers desert the nest to die either on the ground outside the nest or attached to leaves and branches of plants. From these platforms spores are released to infect new workers. Anecdotal evidence from one of our field sites in Thailand showed that the principal host, *Camponotus leonardi*, was rarely encountered on the forest floor where spore were released (Pontoppidan et al. 2009). At one site where the fungus was completely absent, the target host was very common on the forest floor. While anecdotal this does suggest parasites can structure where foraging trails can

go. Besides these examples there are nematodes (Poinar 2003), strepsipterans (Hughes et al. 2004), and microsporidians (Schmid-Hempel and Loosli 1998) that all distribute propagules in places where social insects forage for food thereby placing selection on colonies to avoid patches of high parasite density. In conclusion, shifting trails is likely not an extended phenotype of the parasite on the collective phenotype of the superorganism. Rather we are likely to discover that changes in the collective phenotype we observe in groups foraging occur when parasite pressure is highly selecting for behavioral defense.

## 8.8 Future directions and tests

Thinking in terms of superorganisms is not helpful unless by doing so we can be pushed into experimental approaches that a unitary organism view cannot provide. I hope that I have made two essential points obvious in this chapter. The first is that social insects, through group behavior, are sufficiently distinct from solitary organisms in ways that require a different mindset when examining adaptation by natural selection. This is well established and social insect biology rests upon 400 years of natural history and experimental approaches (Hölldobler and Wilson 2009). The second essential point is obviously less well known but is, I feel, relevant nonetheless. Parasites of social insects experience environments wholly different from those parasites infecting solitary organisms. The great evolutionary transition from solitary living to advanced sociality was also a transition for the parasites that hitchhiked from the solitary ancestor to highly integrated group member (Hughes et al. 2008). Just as we discuss sociobiology so we might also discuss socioparasitology. By socioparasitology I do not mean the ability of parasites to recognize kin and evolve group behaviors as we know parasites can do (Hechinger et al. 2010; Reece et al. 2008). Rather, the name should encourage us to think of what happens to parasites whose hosts are social. How should socioparasitology proceed?

Historically biology has progressed rapidly from its natural history beginnings by using the compara-

tive method. The tools twenty-first century biology offer unparalleled scope to compare manipulative parasites between the social and non-social. First among these tools is comparative genomics, where whole genomes of closely related species manipulating social insect and non-social insect behavior are arrayed and compared. This has proved very popular in identifying gene regions involved in infection. The recent move to sequence hundreds of insect genomes in the next five years (Robinson et al. 2011) would be a great opportunity to test this, as many insect parasites of social insects also infect non-social ones (e.g., strepsiptera, diptera). The comparative genomic approach could be combined with comparative transcriptomics using RNA-seq experimental approaches. These two approaches will identify in gene presence our behavior differences between hosts. To this one can add standard physiological assays such as metabolomics.

The above approaches are of course extensions of the natural phase and are not directed towards an *a priori* experimental approach. For this a very useful approach to adopt would be testing the cumulative effect of manipulator parasites on colony performance. At which stage does the loss of individuals due to manipulation lead to a feedback to the colony resulting in defense? Also, which defense comes first: behavioral, structural or immunological (see also Hughes and Cremer 2007)? Exploring empirically or mathematically the feedback between fitness loss and defense and how this differs between solitary and social insects would be productive. Likewise, since sociality is a gradient from the primitively eusocial with small societies to highly advanced ones with millions of workers, comparisons can also be made within social insects. The long history of social insect research has provided an enormous wealth of knowledge on the “beauty and elegance” of superorganisms (Hölldobler and Wilson 2009). This provides a fabulous opportunity for biologists interested in parasites that change host behavior.

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# Afterword

**Bert Hölldobler**

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A superorganism is a colony of individuals self-organized by division of labor and united by a closed system of communication. The eusocial insect society possesses features of organization analogous to the properties of a single organism. The colony is divided into reproductive castes (analogous to gonads) and sterile worker castes (analogous to somatic tissues). Its members may exchange nutrients and pheromones by trophallaxis (analogous to the circulatory systems and signaling with hormones in organisms). Nevertheless, among the thousands of known social insect species, we can find almost every conceivable grade in the division of labor, from hierarchical organizations with competition among nest mates for reproductive status and poorly developed division of labor, to highly complex cooperative networks with specialized worker subcastes. The level of this gradient at which the colony can be called superorganism is perhaps subjective. It may be at the origin of eusociality, or at a higher level, in which within colony competition for reproductive status is greatly reduced or absent (Hölldobler and Wilson 2009).

In my view, insect societies with considerable reproductive competition among nest mates, and as a consequence, poorly developed division of labor among workers, may have some incipient superorganismic traits, but do not deserve to be called fully functional superorganisms. Thus, from this perspective many of the poneromorph ant societies should not be considered true superorganisms, because there is little or no morphological skew between reproductive and non-reproductive individuals, and intra-colony reproductive competition is indeed conspicuously common (see Hölldobler and Wilson 2009). In contrast, in true superorgan-

isms the size dimorphism (morphological skew) between reproductive individuals (queens) and sterile individuals (workers) is large and reproductive division of labor is deep and not plastic. Although workers receive all their genes from the queen and her mates, they exhibit very different phenotypes, because during their larval development due to social environmental influences, different genes are turned on and expressed in workers than in queens and males. This phenotypic plasticity continues during adult ontogeny. From the behavioral interactions of hundreds, thousands, or even millions of workers colony specific traits emerge which are part of a collective colony phenotype, the phenotype of the superorganism.

The chapter on "Parasitism and Superorganism" in this book makes a strong and convincing case for the concept of "superorganism" when we consider the evolution of social parasitism in ants. Although no ant species appears to be totally free of parasites, social parasites in poneromorph ant societies are rare or absent. This contrasts sharply with the rich fauna of social parasites in ant species, the colony of which can be considered true superorganisms. I name as examples colonies of species belonging to the genera *Formica*, *Lasius*, *Camponotus*, *Oecophylla*, *Myrmica*, or fungus growing attine species, or species of the army and driver ants (Ecitoninae and Dorylinae) (Hölldobler and Wilson 1990). These superorganisms, like any normal organism, are subdivided into functional units or sites that provide special niches for parasites. In a normal organism such niches might be the stomach, intestinal tract, liver, or any other organ or tissue. In the ant superorganism we may identify the nest chambers where eggs, larvae, or pupae are housed, or the queen



chamber, the peripheral nest chambers, the kitchen-middens, or the foraging routes as special sites for social parasites specifically adapted to make their living inside these niches.

Most insect superorganisms, like normal organisms, are characterized by precise recognition of "self" and rejection of "non-self" or "foreign." And as is the case for any parasite of normal organisms that have to overcome the organism's immune barriers, social parasites have to conquer social barriers of the superorganism. In other words, they have to break the chemical code by which each colony member is identified as nest mate. In addition social parasites have to evolve behavioral key stimuli that enable them to manipulate the innate behavioral releasing mechanisms that underlie the social life within each niche of the superorganism.

As we have learned from the chapters in this book, parasites often manipulate their host's behavior to their advantage. One of the most striking and first examples was discovered by W. Hohorst in the 1960s. He was a biologist working in the department for pest control of the gigantic chemical company HOECHST in Frankfurt a.M. (Germany), where he investigated the life cycle of the liver fluke (*Dicrocoelium dendriticum*, an important parasite of grazing mammals). Hohorst and his collaborators discovered that *Formica* ants serve as intermediate hosts. The ants inadvertently take up cercaria of this trematode and subsequently some of the cercaria penetrate the pharynx and the gut walls, and develop into metacercaria inside the ants. One of them invades the ant's brain where it settles in the suboesophageal ganglion. Apparently this "brain worm" induces its *Formica* host to leave the nest and climb onto grass stalks where it attaches itself with a firm grip of its mandibles. This exposes the infected ant to be eaten by the grazing animals, the main host of the liver fluke (Hohorst and Graefe 1961; Schneider and Hohorst 1971).

The manipulations by social parasites that exploit the social life of ants are different. These parasites had to acquire the capacity to provide the correct signals to their hosts. During their evolution they have "broken the code" and are thereby able to take advantage of the benefits of social life of their hosts. Among the most simple, but nevertheless striking examples is

that of the phorid fly *Metopina formicomendicula*. This fly is riding on its host ant, the tiny thief ants (*Diplorhoptum fugax*) and rapidly strokes the ant's mouth parts with its forelegs to elicit regurgitation of food. The tactile stimulation is a crude imitation of the host ant's food exchange behavior, but the imitation is good enough to work (Hölldobler 1948).

However, in order to be able to live inside the ant colony's brood chambers and to prey unimpeded on the ant brood, and entice the nurse ants to groom and feed the parasites and raise the parasites' brood, the parasitic species have to decode a rich repertoire of chemical and behavioral communication signals employed by the host ants inside the brood chambers. At first glance it appears almost impossible to imagine how such complex parasitic adaptations could have evolved by gradual natural selection.

About 35–40 years ago I devoted much of my research efforts to trace the evolution of such social parasitic adaptations. The focus of my research was myrmecophilous beetles of the staphylinid subfamily Aleocharinae. I undertook a comparative experimental analysis of aleocharine species adapted to different niches in their host superorganism, and I hoped to discover different evolutionary grades of myrmecophilic adaptations which would allow me to at least reconstruct an evolutionary pathway from relatively simple to highly complex social parasitism. Indeed, different species of these aleocharine myrmecophiles occupy different sites within an ant colony. Some live along the trails of the ants, some at the garbage dumps outside the nest, others within the outermost nest chambers, while still others are found within the brood chambers (Hölldobler 1967, 1970, 1971, 1977; Hölldobler et al 1981). In each case the requirements of interspecific communication are different, and with each evolutionary advance towards the center of the superorganism, the brood chambers, the parasite added new features to its "tool box," such as new exocrine glands that produced either appeasement secretion or adoption signals (most likely imitations of ant brood pheromones) and behavioral patterns, such as tactile signals that elicit regurgitation behavior in host ants. In fact, in some of the most accomplished social parasites among the aleocharine staphylinids, the beetles and their larvae produce

“super-normal releasers” with which they elicit much stronger response in the host ants than the ants’ nest mates do. Let me illustrate this with a few examples.

The aleocharine beetles that live in the kitchen middens and along the ants’ trails are scavengers and predators. They evolved the chemical tools to repel or appease the ants. For example, *Pella laticollis* lives near trails of *Lasius fuliginosus* and hunts ants. When attacked by the ants, it quickly provides the appeasement secretions from a gland at the tip of its abdomen. However, it uses the moment’s pause to jump on the back of the ant and kill her by biting between the head and the thorax. The beetle then drags the ant away from the trail and devours it.

The aleocharine beetle of the genus *Dinarda* is usually found in more peripheral nest chambers of *Formica* species, where food exchange occurs between foragers and nest workers. It is here that *Dinarda* is able to participate in the social food flow. Occasionally they insert themselves between two workers exchanging food and literally snatch the food droplet from the donor’s mouth, or they use a simple begging behavior in order to obtain food from returning food-laden foragers. The ant, however, after having regurgitated liquid from its social stomach often recognizes the beetle as alien and commences to attack it. At the first sign of hostility the beetle raises its abdomen and offers the ant a tiny droplet of appeasement secretion, a proteinaceous substance, which is quickly licked up by the ant, and almost immediately the attack ceases. During this brief interval the beetle makes its escape.

Some of the most advanced myrmecophilic relationships are found in the aleocharine beetles genera *Lomechusa* and *Atemeles* which live inside the brood chambers of their *Formica* and *Myrmica* hosts. They, too, have the appeasement and repellent glands, but in addition they are equipped with dorsolateral adoption glands, the secretion of which entices the host ants to carry the beetles into the brood chambers of the nests. These myrmecophiles also have a rich behavioral repertoire which enables them to elicit regurgitation from their host ants and

quantitative measurements of the social food flow inside the nest reveal that these beetles and their larvae employ supernormal releasers that entice the nurse ants to pay more attention to them than to the ants’ sister brood.

All these remarkable social parasitic adaptations only exist in true ant superorganisms, and the chapter by David Hughes on “Parasites and the Superorganism” presents an excellently reasoned argument supporting the superorganism concept in the context of parasitism in social insects.

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