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Life Histories and Parasite Pressure Across the Major Groups of Social Insects

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Thus, whereas ant colonies participate in many symbioses and are sometimes largely dependent on them, honeybee colonies, which are much less permanent in place of abode, have no known symbionts but many parasites.

R. Axelrod and W.D. Hamilton, *The evolution of co-operation. Science* 211, 1390–1396 (1981)

1. Introduction

Animal societies are aggregations of cooperating individuals that are isolated from other societies by limitations of dispersal and/or hostile exclusion mechanisms. The individuals within them are more related to the members of their own society than to random individuals in the population at large and quite often this relatedness is high because societies are families or groups of families. For parasites and diseases, however, animal societies are merely patches of suitable hosts to be colonized and exploited and to ultimately produce dispersing propagules to reach other similar patches (Freeland, 1979).

Living in groups or societies has generally been thought to be associated with increased parasitism (Alexander, 1974; Freeland, 1976; Hamilton, 1987; Sherman *et al.*, 1988; Côté and Poulin, 1995; Schmid-Hempel, 1998). However, several recent studies have questioned the generality of this assertion (Watve and Jog, 1997; Lewis, 1998; Naug and Camazine, 2002; Wilson *et al.*, 2003). Others have provided data to show that social behaviour can also be associated with reduced parasite load, due to either behavioural interactions providing an effective defence (Rosengaus *et al.*, 1998; Hughes *et al.*, 2002; Traniello *et al.*, 2002), or density-dependent immune responses (Reeson *et al.*, 1998, Barnes and Siva-Jothy, 2000; Wilson *et al.*, 2003). These discrepancies may result from the

exact mode of transmission. In fact, a meta-analysis by Côté and Poulin (1995) has shown that rates of parasitism tend to be positively correlated with group size for parasites that are transmitted by direct contact, whereas these same correlations are negative for parasites that actively find their hosts. Furthermore, while a gregarious habit may increase the risk of intragroup transmission, this may be more than compensated for by a decrease in intergroup transmission (Watve and Jog, 1997), as has been recently demonstrated in a comparative study of Lepidoptera larvae (Wilson *et al.*, 2003).

Ecological epidemiology has developed general theoretical models exploring the conditions under which diseases can co-exist with their hosts. In a series of seminal studies, Anderson and May (1979, 1981, 1982) showed that essentially all diseases need a minimal threshold number of susceptible hosts to maintain themselves. The threshold depends on the rate at which a disease is able to infect new hosts by dispersal, relative to the rate of disappearance of existing infections due to disease-induced mortality and immunity after recovery. When short-range transmission is effective and virulence not too high, diseases may endemically coexist with their hosts in every patch at some expense to the number of hosts and their fitness (Anderson and May, 1979, 1982). Otherwise, extant diseases will have a dynamic metapopulation structure depending on incidental long-range dispersal between patches and epidemic outbreaks hitting different patches at different times (Anderson and May, 1982; Grenfell and Harwood, 1996).

On an evolutionary timescale, parasites often become specialized on a single host species, and coevolve with their hosts in a Red-Queen-like manner (e.g. Jaenike, 1993; Gandon *et al.*, 2002). Other parasites, however, remain generalists exploiting multiple hosts (Johnson *et al.*, 2003a). Host defences have been categorized as avoidance, resistance (before or after recovery) and tolerance, mechanisms that each have their own cost-benefit trade-offs and coevolutionary dynamics with specific pathogens (e.g. Boots and Bowers, 1999; Schmid-Hempel and Ebert, 2003; Weinig *et al.*, 2003). Finally, recent research has increasingly emphasized that virulence of a parasite is a plastic trait, subject to natural selection and sometimes conditionally expressed (Frank, 1996a,b; Herre *et al.*, 1999). Although intermediate virulence often seems to be an evolutionarily stable strategy (ESS), in fact any level of virulence can evolve depending on ecological conditions and evolutionary trade-offs (Ebert and Herre, 1996). This implies that mutualistic and parasitic symbionts are increasingly considered to be two sides of the same coin, with many gradual transitions between them (Frank, 1996a,b; Herre *et al.*, 1999; Bot *et al.*, 2001a).

This chapter concentrates on social insects which, together with our own species, represent extreme examples of group living. We investigate the extent to which non-uniform loads of parasites and diseases can be explained by differences in ecology and life history among the four major groups of social insects: the ants, termites, social bees and social wasps. We realize that comparisons at this large taxonomic scale necessitate crude assumptions and bold generalizations that may not hold for every particular parasite-host interaction. However, we believe that this approach will be helpful to establish an extended general framework for the further investigation of how parasitism

affects social species and to clarify what particular elements of coevolution between parasites and social hosts deserve to be emphasized in future studies.

The ants, social bees and social wasps belong to the haplodiploid and holometabolous order of the Hymenoptera and have independently evolved advanced social behaviour (the bees did so multiple times) (Wilson, 1971; Michener, 1974). The termites belong to the hemimetabolous order of the Isoptera, are obligatory social, and share a single common ancestor (Eggleton, 2001). Although the four groups have advanced social behaviour in common, they differ in a series of key traits that will be relevant for the analyses and arguments to be presented in this chapter (Table 6.1). Following Wilson (1971) these can be characterized as follows. Wasps and ants are mostly carnivorous, but many qualify as omnivores as they also collect nectar (wasps) and aphid honeydew (ants). Bees have almost exclusively a vegetarian diet consisting of pollen and nectar, whereas the termites are mostly decomposers of plant-derived biomass. Most bees and wasps have closely related non-social relatives and an annual, semelparous colony cycle, with honeybees, stingless bees and polybiine wasps being important, evolutionarily derived, exceptions to this rule. Ants and termites, on the other hand, are universally eusocial and perennial, with the exception of only very few derived social parasites. Bees and wasps build their nests as an arrangement of brood cells made from freshly collected or manufactured substrates (mud, paper, wax), whereas ants and termites build their nests in

Table 6.1. A comparative overview of the major ecological differences among the four main groups of insects in which eusociality has evolved independently (after Wilson, 1971).

Trait	Bees	Wasps	Ants	Termites
Life cycle	Semelparous/ annual ^a	Semelparous/ annual ^a	Iteroparous/ perennial	Iteroparous/ perennial
Diet	Pollen and nectar	Carnivorous/ omnivorous	Carnivorous/ omnivorous	Decomposer of plant material
Foraging	Flying, foraging areas of colonies typically overlap	Flying, foraging areas of colonies typically overlap	Walking, typically territorial with partly separated foraging grounds	Walking, colonies with strongly separated foraging grounds
Nest building	Constructs of paper or wax, brood arranged in cells	Constructs of paper or wax, brood arranged in cells	Galleries, loose piles of chambers	Galleries, loose piles of chambers
Nest habitat	Closed nests in soil and cavities ^b	Typically open suspended nests ^c	Closed nests, mostly in soil	Closed nests, mostly in wood and soil

^a Some Apidae and polistine wasps are iteroparous and perennial and some halictine bees are annual but bivoltine.

^b Some species with open suspended nests (Apidae).

^c Some Vespinae build nests in underground cavities.

soil or wood by excavating a system of galleries and nest chambers. Finally, there are important differences in worker morphology and foraging. Workers of bees and wasps have wings and a relatively large foraging range, whereas workers of ants and termites are wingless, and normally forage within distinct territories that they may defend against other colonies.

As outlined in Schmid-Hempel (1998), the study of parasites and disease in social insects has been plagued by a general lack of data and a high degree of data skew, with data on honeybees, for example, being much more abundant and accurate than data on other species. Although it has been suspected that social insects do not suffer as much from parasites as their high and aggregated densities would predict, the deficit of data has made it difficult to assess any differences in the prevalence and impact of parasites and diseases across the ants, social bees, social wasps, and termites. Since Schmid-Hempel's (1998) review, theoretical (Naug and Camazine, 2002) and particularly experimental research on social insect diseases has expanded: a number of new parasite–host interactions have been discovered, and experimental studies have clarified detailed mechanisms of defence against diseases (e.g. Baer and Schmid-Hempel, 1999, 2001; Brown *et al.*, 2000; Moret and Schmid-Hempel, 2000, 2001; Lord *et al.*, 2001; Doums *et al.*, 2002; Hughes *et al.*, 2002; Poulsen *et al.*, 2002a, 2003; Traniello *et al.*, 2002). It is timely, therefore, to attempt a specific comparative review of disease pressure across the four major groups of social insects, particularly in connection to the key life-history differences characterizing these groups (Table 6.1), to investigate whether disease pressures are likely to co-vary with these fundamental life-history differences in similar ways as shown for other organisms (Côté and Poulin, 1995; Wilson *et al.*, 2003).

Previous reviews on social insect diseases (Bailey, 1963; Hamilton, 1987; Bailey and Ball, 1991; Macfarlane *et al.*, 1995; Schmid-Hempel, 1995, 1998; Schmid-Hempel and Crozier, 1999) have emphasized the social Hymenoptera, their varying haplodiploidy-induced degrees of relatedness among colony members, and their differences in colony size within each of these groups. This chapter will, without implying any lower importance to relatedness factors, concentrate on differences in ecology between the obligatory perennial ants and termites on one hand and the mostly annual bees and wasps on the other. We offer an updated (compared to Schmid-Hempel, 1998) analysis of comparative data and an explicit life-history framework for comparing insect societies that differ in colony longevity (annual versus perennial), nest building (mud, paper or wax versus galleries in the soil or in wood), and the mode and range of foraging (flying versus walking, and the concomitant range overlap between colonies). Section 2 reviews the various ways in which the different categories of parasites are recruited and transmitted in the four groups of social insects and how their virulence may depend on this. Section 3 evaluates the actual defence mechanisms of individuals and colonies and the ways in which selection is likely to have shaped investment in defences for different social insect life histories. Section 4 presents novel analyses of comparative data to see whether expectations inferred from conceptual considerations in Sections 2 and 3 are supported by evidence.

2. A Comparative Appraisal of the Major Groups of Social Insects as Hosts of Diseases

2.1 The categories of parasites and diseases

Insect societies have a multitude of parasites and diseases. There are microparasites (bacteria, viruses, protozoa, fungi) and macroparasites (mites, nematodes, helminths, insects, many of the latter being true parasitoids). Microparasites are small, have short generation times, and very high rates of reproduction within a host body. Macroparasites are larger, have longer generation times, no or very slow reproduction within a host body, and free-living stages outside the host (Anderson and May, 1979, 1981). Parasites are either endemic or epidemic (mostly restricted to microparasites) and may be specialist or generalist. An extensive review on many aspects of parasitism of insect societies has been provided by Schmid-Hempel (1998). The major characteristics of reproduction, transmission and virulence that can be derived from his review are summarized in Table 6.2. The categorizations of Table 6.2 are obviously generalizations with many exceptions, and only have heuristic value, but they define, together with the host life-history generalizations of Table 6.1, the conceptual framework of this chapter.

In recent years, most work on social insect diseases has been inspired by the idea (Hamilton, 1987; Sherman *et al.*, 1988; reviewed and extended in Schmid-Hempel, 1998) that the dense packing of social insects in nests should have aggravated their problems with diseases over evolutionary time. As 'nature abhors a pure stand' (because it breeds diseases; Hamilton, 1982, 1987), the pressure of rapidly evolving parasites was hypothesized to have been a major driving force behind secondary developments towards genetically less homogeneous societies via multiple queen-mating and multiple queening of colonies (e.g. Crozier and Page, 1985; Keller and Reeve, 1994; Schmid-Hempel, 1994; Boomsma and Ratnieks, 1996). The most straightforward tests of hypotheses of this kind can be done with microparasites. However, on closer inspection, genetic diversity is only one of an entire suite of possible colony-level defence mechanisms against parasites (see e.g. Naug and Camazine, 2002). Before discussing defences though, we need a systematic overview of the assaults that different insect societies may suffer. The factors that determine the frequency and potential severity of challenges by parasites and disease have been listed in Table 6.2. The subsections below evaluate the three processes that are each affected by these factors and which define the impact of parasites for hosts: exposure, intercolony transmission and intracolony transmission.

2.2 Exposure to parasites: nesting ecology, foraging and food

Of the four categories of microparasites, three (bacteria, viruses and protozoa) are usually transmitted orally (*per os*) via the sharing of regurgitated food, ingestion of excrement, etc. (see Table 6.2), whereas the spores of insect

Table 6.2. The categories of social insect diseases and their major characteristics of reproduction, transmission and virulence, the latter assuming that defences are unsuccessful (after Schmid-Hempel, 1998).

	Reproduction within host	Generation time	Transmission stage	Typical infection mode ^e	Transmission route/range	Survival of transmission stage outside host	Virulence for individual ^m	Virulence for colony ^p	Intracolony epizootic potential
Macroparasites									
Parasitoids	No ^{a,c}	Very long	Free-living	Active entry	Active dispersed	Moderate, long ^l	High, death inevitable ⁿ	Low ^q	Absent
Other insects	No ^b	Very long	Free-living	Active entry	Active dispersed	Moderate, long ^l	High, death inevitable ⁿ	Low ^q	Absent
Mites	No ^{b,c}	Very long	Free-living	Active entry	Active, local	Short, moderate ^k	Moderate	Moderate	Moderate
Helminths	No ^d	Very long	Free-living, durable eggs	<i>per os</i>	Active dispersed, local ^f	Moderate	Moderate ^o	Low	Absent
Nematodes	Yes	Intermediate	Free-living	<i>per os</i> and other openings	Local	Moderate	Low to high	Moderate	Moderate
Microparasites									
Fungi	Yes	Very short	Spores	Through cuticle	Passive dispersed ^g	Moderate, long ^l	Generally high	High	Very high
Protozoa	Yes	Short	Cells, spores	<i>per os</i>	Local, direct contact ^h	Short	Moderate	Moderate	High
Bacteria	Yes	Very short	Spores	<i>per os</i>	Local, direct contact ^h	Short to long ^l	Low to high	High	Very high
Viruses	Yes	Very short	Spores	<i>per os</i>	Local, direct contact	Very short	Low to high	High	Very high

- a Some species with sexual dimorphism and females staying inside host (e.g. Strepsiptera).
- b Most species parasitize immatures and grow in brood cells.
- c Many mites reproduce on or inside the host (e.g. tracheal mites).
- d Social insects are intermediate hosts to helminths (trematodes, cestodes). Reproduction occurs in the final vertebrate host.
- e Many exceptions to the typical infection mode are known. Indication given here only as a crude classification.
- f Range depends on dispersal by final host.
- g Large-scale dispersal by wind, more local dispersal by water or passive transport by other organisms.
- h Long-lasting transmission stages also transmitted indirectly through contact with substrates.
- i Survival outside hosts depends on life cycle of adult insect, which is typically annual.
- k Dispersal stages often do not feed and hence cannot survive for long.
- l Some fungi and bacteria are known to have durable stages of extreme longevity.
- m Effect on survival or performance of host individual.
- n Obligate death sometimes prevented by encapsulation.
- o Most helminths do not seriously harm host. Some cause changes that render social insect host more susceptible to predation by final host.
- p Effect on survival or reproductive performance of colony.
- q In exceptional cases colonies can be devastated (e.g. wax moths).

pathogenic fungi are mostly dispersed passively via wind, rain, etc. and enter hosts via the cuticle or openings such as the trachea (Andreadis, 1987). This implies that fungal spores will be spread out over relatively large areas and will often be associated with the soil, whereas propagules of the other disease categories will be deposited at sites visited by infected individuals. Ant and termite hosts usually start colonies by excavating galleries in the soil or in wood (Table 6.1). Some may erect nest mounds or paper nests when colonies mature, but as a rule the developing brood and foraging workers will remain associated with soil and wood (Brian, 1982). It thus seems obvious to expect that fungal diseases should be common in ants and termites. Most wasps build nests in the open, generally hanging freely from branches, so that they have minimal contact with soil or wood. Bees seem intermediate. Primitively eusocial bees (e.g. halictines) tend to excavate nests in the soil, whereas more advanced taxa (bumblebees, stingless bees, honeybees) mostly use existing cavities underground or in hollow trees. This implies that soil contact of nest workers in the latter category of bees is less than that which is normal for ants and termites (Brian, 1982; see also Table 6.1) although probably not quite as low as for wasps. These differences in nesting behaviour among bee taxa have earlier been hypothesized to be associated with different parasite pressure (Michener, 1985), an inference that is supported by data on solitary species (Wcislo, 1996).

Exceptions to these general rules do occur, such as arboreal ants and termites making nests of silk or carton (overviews in Wilson, 1971; Brian, 1982; Hölldobler and Wilson, 1990; Schmid-Hempel, 1998), and allodapine bees nesting in plant stems without making cells (Michener, 1974). However, it seems reasonable to infer that in the course of their social evolution ants and termites have been 'recruiting' their parasites from different habitats than bees and wasps, and that this should be particularly true for parasites and diseases that do not disperse widely. Parasites of ants and termites should thus tend to have close relatives that are soil-borne and relatively intolerant to dehydration, whereas parasites of social wasps and the advanced social bees will tend to be related to organisms that can survive in drier habitats, such as the surfaces of wood and vegetation and the interior of hollow trees. That wet or dry nesting material matters for exposure to microparasites has recently been documented for dampwood and drywood termites (Rosengaus *et al.*, 2003). Similarly, the typical habit of wasps (and some bees) to construct open nests predisposes them to attack by actively searching macroparasites (Keeping and Crewe, 1983; Schmid-Hempel, 1998), whereas the closed nests of most bees, ants, and especially termites, prevent most exposure of this kind. General exposure patterns would thus predict that ants and termites are prone to contracting fungal microparasites and macroparasitic worms (nematodes and helminths), while their underground or otherwise enclosed nesting habits would protect them from assaults by many flying macroparasites. On the other hand, wasps and, to some extent, bees with open nests away from soil may have fewer soil-borne microparasites and relatively more mobile and actively searching macroparasites (Table 6.2). However, these generalizations may not always apply to highly specialized macroparasites, as they may have evolved highly effective host-finding adaptations.

Social insect workers that forage on the wing mostly encounter relatively sterile medium, except when they land on flowers, insect prey or carrion, where disease propagules may be dense, particularly on the latter two. In contrast, social insects whose workers forage on foot will almost never encounter fully sterile habitat, and will thus be likely to have a lower variance in exposure. Also the typical food items collected and ingested differ among the four groups of social insects (Table 6.1) and may incur different risks. Bees almost always forage only on nectar and pollen, which will represent a relatively hygienic food source with very little potential to act as a transmission route for entomopathogens. On the other hand, wasps and, to some extent, ants are largely predatory, and their prey normally consists of other insects. This therefore exposes them frequently to diseases that they will risk contracting via the *per os* route from the animals they eat. Wasps and ants are also predators and scavengers of dead or dying insects infected by disease (Smirnoff, 1959; Tanada and Fuxa, 1987; Baur *et al.*, 1998) and wasp nests and larval faeces commonly contain a very wide range of entomopathogenic microorganisms that they have probably contracted from their food (Morel and Fouillaud, 1992; Rose *et al.*, 1999). Indeed, the life cycles of certain nematode and helminth worms are based upon the infection of their ant or wasp host when it feeds upon another infected arthropod (Kaya, 1987; Molloy *et al.*, 1999), while those of certain protozoan parasites rely upon workers cannibalizing infected pupae and feeding meat from them to larvae (Jouvenaz, 1986; Buschinger and Kleespies, 1999). Finally, a number of wasps and ants are specialized predators on other social insects, which may expose them to diseases that are already adapted to social insect hosts. Overall, therefore, a 'vegetarian' diet (bees and termites) may thus incur a lower risk for general insect diseases than an omnivorous diet (ants and wasps).

2.3 Intercolony interactions, infections and the maintenance of diseases

Although social insects are exposed to diseases via their food, nesting habitat and foraging behaviour as outlined above, a potentially more significant risk of exposure stems from contact with conspecifics, as this transmission route would facilitate the evolution of specialized parasites. A disease can only be maintained if its basic ratio of infection (R_0) remains >1 (Anderson and May, 1979; Grenfell and Harwood, 1996). A detailed treatment of models on transmission between and within social insect colonies is given by Schmid-Hempel (1998), so that here, a verbal summary of the key factors that affect transmission will suffice. For any disease to spread, its growth rate R_0 needs to be >1 , i.e. every newly created infection needs to create on average at least one further infection before it disappears with a specific natural death rate (b), a specific disease-induced death rate (α) and a host recovery rate (γ). This requires a minimum threshold number of susceptible hosts N_T , which equals $(\alpha + b + \gamma) / \beta$ (see Anderson and May, 1979, 1982, for the basic theory and Schmid-Hempel, 1998, for more specific elaborations). A key question, therefore, is whether differences in nesting ecology and foraging are likely to

affect the intercolony transmission rate (β). Efficient transmission (high β) implies that a disease can maintain itself at relatively low densities of susceptible hosts, whereas inefficient transmission will cause a disease to go extinct, unless the number of susceptible hosts is large. The model sketched out here only applies to microparasites. Macroparasites have free-living stages independent of the host, which complicates their transmission dynamics and implies that the growth rates of populations of macroparasites cannot be simply derived from the rates of gain and loss of infections (Anderson and May, 1979; Schmid-Hempel, 1998). We will restrict our discussion here to horizontal transmission (between individuals within a colony and between individuals from different colonies), as vertical transmission (from a parent colony to a daughter colony via the reproductives) will be dealt with in the next subsection on intracolony transmission.

The intercolony transmission rate is a direct function of the encounter rate of infected and uninfected individuals from different colonies, where encounters are defined as either direct physical contact or indirect contact with an object or patch that contains viable disease propagules. The likelihood of intercolony disease transmission in the four groups of social insects depends to a large degree on how the foraging areas are used. Bees and wasps may cover up to several kilometres on the wing (Spradbery, 1973; Roubik, 1989; Beekman and Ratnieks, 2000; Goulson and Stout, 2001; Dramsted *et al.*, 2003) and typically exploit food sources that are accessible to all colonies in the area. Bees from many different colonies are thus likely to visit the same flowers for nectar and pollen, and wasps from many different colonies may scrape fibres for nest building from the same pieces of dry wood, forage for insect prey in the same patches, or cut pieces of meat from the same carrion. As a consequence, direct or indirect contact between workers from different colonies is frequent, the latter when visits are separated in time but with such short intervals that short-lived transmission propagules survive and can be transmitted between colonies (Durrer and Schmid-Hempel, 1994). The situation in ants and termites is quite different. In both groups, workers forage on foot, cover shorter distances by comparison, and often maintain foraging territories that secure privileged access to food sources (see Brian, 1982; Hölldobler and Wilson, 1990). Termites carry this principle to the extreme. In particular, the 'single site nesters' (Abe, 1987) live 'within their food' and do not forage outside the protected boundaries of their colony in the way that most ants do. As a consequence, contact between neighbouring colonies of termites during the foraging process is extremely limited (Table 6.1). In addition, many bee and wasp species nest in cavities. The availability of such nest sites is limited and the consequent reuse of the same nest sites carries with it the risk of exposure to parasite propagules that may have been left from the previous colony (Ratnieks and Nowakoski, 1989; Roubik, 1989; Greene, 1991; Reeve, 1991; Hansell, 1996). The rates at which colonies are challenged by novel infections may therefore differ considerably across groups of social insects and, once more, the ants and termites seem to be better off than the bees and wasps.

This conclusion is equivalent to one that was reached in a general model showing that clustering of individuals increased within-cluster transmission of

diseases, but could also disproportionately decrease between-cluster transmission, making clustering a potentially effective strategy to minimize the overall risk of infection (Watve and Jog, 1997; Wilson *et al.*, 2003). Following Anderson and May (1979, 1981), we would thus expect that the density of susceptible hosts of ants and termites will often be (and has often been over evolutionary time) too low for pathogens to maintain themselves, whereas this constraint would have been much less for pathogens of bees and wasps. In other words, the frequency of extant parasites per average species of ant or termite should be significantly lower than the disease load per average species of bee or wasp. In fact, for ants and termites with large colonies (and thus few colonies per square kilometre of habitat) it seems hard to imagine how selection could maintain any virulence in specialized diseases that would depend on direct or indirect contact with non-nestmates across territory borders. The product βN_T would be low and would still be required to exceed $\alpha + b + \gamma$, which would only be possible with very low values of the disease-induced mortality rate α .

A final corollary would be that the few more virulent specialized diseases of ants and termites that do exist would be expected to be epidemic rather than endemic, because the threshold density condition of susceptible hosts is only occasionally met in some host patches. This implies that such diseases will appear in a metapopulation pattern of relatively transient outbreaks (Grenfell and Harwood, 1996; Schmid-Hempel, 1998). Routine searches for infections are unlikely to register such epidemic diseases, in contrast to endemic diseases. Also sexually transmitted diseases will be selected against in social insect hosts, because they require high rates of promiscuous mating (see Hurst *et al.*, Chapter 8, this volume), which does not occur in any social insect (Baer and Boomsma, 2004; Boomsma *et al.*, 2005).

2.4 Intracolony interactions and virulence

The horizontal infectiveness of a diseased colony will depend on the proportion of workers that disperse propagules either while performing their normal foraging activities in spite of being infected, or by dying in places that allow spores to be transmitted. In addition, there is the possibility that a disease is passed on horizontally from workers to the reproductives that they raise, thus resulting in vertical transmission at the colony level (for a model incorporating both, see Schmid-Hempel, 1998). Roughly speaking, there are the following scenarios of intracolony transmission:

- *No transmission*: a diseased individual is recognized as such and 'treated', isolated, or expelled, so that no further nestmates are infected.
- *Only horizontal transmission*: an infection spreads and slows down colony growth and reproductive effort to a degree proportional to the rate of spread; infected workers transmit the disease to other nestmates but not to the reproductives, or infected reproductives are prevented by the disease from founding colonies.

- *Horizontal and vertical transmission*: a disease spreads through the colony and also affects part or all of the colony's reproductives, resulting in direct transmission to the next generation.

Standard epidemiological theory holds that vertical transmission enhances the possibility of a parasite maintaining itself within a fluctuating host population (Anderson and May, 1979, 1981), dynamics that are likely to be typical for many social insect hosts. This is because vertical transmission helps the parasite to survive periods when the minimum threshold density of susceptible hosts is not available. In fact, there is no such threshold for purely vertically transmitted diseases (see Wilson, Chapter 10, this volume). However, vertical transmission may be impossible to maintain in many social insects, when colonies are founded by a single inseminated female (many ants, bees, wasps) or a single mating pair (termites). The demands of raising the first worker brood are likely to be so great that colony foundation is unlikely to succeed when performance is reduced by even mildly negative effects of a disease. Brown *et al.* (2003) have found that the otherwise mild parasite *Crithidia bombi* is apparently vertically transmitted to bumblebee queens and has a severe negative effect on colony founding. In general, therefore, it would seem that vertical transmission can only be maintained when parasites are rather avirulent or in social systems that have multiple queens per colony.

A further general factor that will tend to select against virulence of social insect diseases is the fact that essentially all colonies go through an ergonomic phase of colony growth (a period in which they exclusively produce sterile workers; Oster and Wilson, 1978) before reproducing. For infections that are expressed during this ergonomic phase, there will thus be evolutionary trade-offs between virulence and other fitness components of a disease. For example, an increase in virulence is selected against when the effectiveness of the transmission vehicles is more than proportionally reduced (for a review, see Ebert and Herre, 1996). Selection against virulence should be particularly strong in the perennial ants and termites, where most transmission events will be within the colony. Their ergonomic phase of somatic colony growth normally takes several years and involves numerous subsequent worker cohorts, so that even minor expressions of virulence are likely to terminate the colony in its normal competition with more healthy neighbouring colonies.

Independent of their virulence, social insect diseases gain their short-term fitness by the extent of within-colony transmission that they achieve. Long-term fitness is likewise dependent on within-colony transmission, as the proportion of infected workers ultimately determines the probability that workers or reproductives will carry the parasite to another colony (horizontal transmission) or directly into the next generation (vertical transmission). It is here that social interactions, and in particular liquid food exchange (trophallaxis) between nestmates, are likely to play a key role (Schmid-Hempel, 1998; Naug and Camazine, 2002). Trophallaxis may considerably increase the intracolony transmission rates, thus lowering the threshold density of susceptible hosts needed for the disease to be maintained in the population. Most non-fungal microparasites are transmitted orally and may thus spread through a colony

rapidly, because both their arrival in the colony and their subsequent spread via trophallaxis remain unnoticed. High degrees of trophallaxis normally characterize advanced social insects with large colonies. In bees, trophallaxis seems mainly restricted to taxa with progressive provisioning. It is most advanced in honeybees (Wilson, 1971; Seeley, 1985), but also occurs in the allodapine bees (Melna and Schwarz, 1994). Trophallaxis has been shown to occur in stingless bees, but is infrequent and mostly linked to the mass provisioning of brood cells with stored pollen and honey (Sommeijer and De Bruijn, 1994; Hart and Ratnieks, 2002a), in contrast to the honeybee, where it is an almost continuous process. The more primitive bumblebees rarely, if ever, engage in direct food exchange (Michener, 1974) and there is only a single record in carpenter bees (Velthuis and Gerling, 1983). This implies that advanced, long-lived societies could probably only evolve after considerable selection pressure to effectively counter the disease-related negative side-effects of liquid food exchange, i.e. after evolving a series of first-line defences that prevented infections from gaining even a foothold in the colony. Interestingly, the lower termite taxa universally have both oral and anal trophallaxis, partly in connection with the transmission of mutualistic gut flagellates, whereas the higher termites, which have different mutualistic symbionts, no longer have anal trophallaxis (Schmid-Hempel, 1998). It is also interesting to note in this regard, that whereas orally transmitted microsporidian protozoa are the principal parasites of *Solenopsis* fire ants (Jouvenaz, 1983, 1986), which engage in extensive trophallaxis, the non-trophallactic leaf-cutting ant *Acromyrmex octospinosus*, which belongs to the same subfamily (Myrmicinae) but which only rarely engages in trophallaxis, appears to completely lack such parasites (Van Borm *et al.*, 2002).

2.5 Differences in typical disease pressure across the four groups of social insects

In conclusion, we should expect the following pattern in the disease spectra of the four groups of social insects.

- Orally transmitted diseases should be relatively rare, avirulent or transiently epidemic in ants and termites, and more common, up to moderately virulent and often endemic in bees and wasps.
- The soil nesting habit of ants and termites should make them particularly exposed to fungi, nematodes and helminths.
- The occurrence of macroparasites, and especially parasitoids, should be greatest in the wasps, less in the bees, and should be particularly rare in the termites with their cryptic lifestyle.
- Vertical transmission of all but the most avirulent parasites should be absent in ants and termites and rare in bees and wasps, although exceptions may be found in species that always have multiple queen colonies.

Deviations from these overall trends across the four groups of social insects can be expected because wasps and ants have less hygienic food, and thus potentially

more parasites than bees and termites, and because perennial societies may have more specialist macroparasites than annual societies. Within each group, comparable species with trophallaxis should have more *per os* transmitted parasites than species without trophallaxis.

3. Defences Against Disease

3.1 The major mechanisms of defence against parasites

A flow diagram of all relevant aspects of the infection process of social insects is shown in Fig. 6.1. The previous section dealt with exposure, infection and transmission, i.e. with the ecological and evolutionary dynamics of disease reproduction, while largely assuming that the individual hosts and their colonies are mostly passive vehicles of disease transmission. This section focuses on the various individual and collective defences that social insects possess and on differences in sophistication and effectiveness of these defences across the major groups of social insects. The part of Fig. 6.1 that addresses defences is marked by the grey frame in the centre of the figure. Essentially there are defences at two different levels: the individual level and the collective level. Each of these in turn also has two components: avoidance (by recognition or expulsion) and the minimization of damage. Successful avoidance at the individual level implies that an exposed individual avoids infection, whereas avoidance at the colony level implies that an individual infection will not spread within the colony. The latter distinction is probably most crucial, because it will determine whether a colony is resistant to a disease, in the sense of not suffering any negative effect on its fitness (i.e. loss of workers, perhaps with the exception of the occasional infected workers that are not admitted back into the colony), or whether a colony can at best be tolerant of a disease (in other words 'accepting' the loss of some significant part of its workforce or brood).

3.2 Individual defences

Individual recognition and avoidance of infection has been documented for pathogenic fungi in ants and termites (Kermarrec *et al.*, 1986; Oi and Pereira, 1993; Rosengaus *et al.*, 1998, 1999a; Jaccoud *et al.*, 1999). Workers are able to recognize spores and are thus often able to prevent them from sticking to their cuticle. As already mentioned, the equivalent recognition of infection sources of *per os* transmitted diseases seems more problematic but has been demonstrated (Drum and Rothenbuhler, 1985). Also in avoidance possibilities, there seems to be a difference between the social insects that forage on the wing and those that forage on foot. Flying workers usually ingest at least part of their food on the spot, bees by drinking nectar (although they collect pollen in external pollen baskets) and wasps by masticating prey or carrion (although they also carry complete prey to the nest). This implies that workers guarding the nest entrance will frequently encounter situations in which it is difficult to

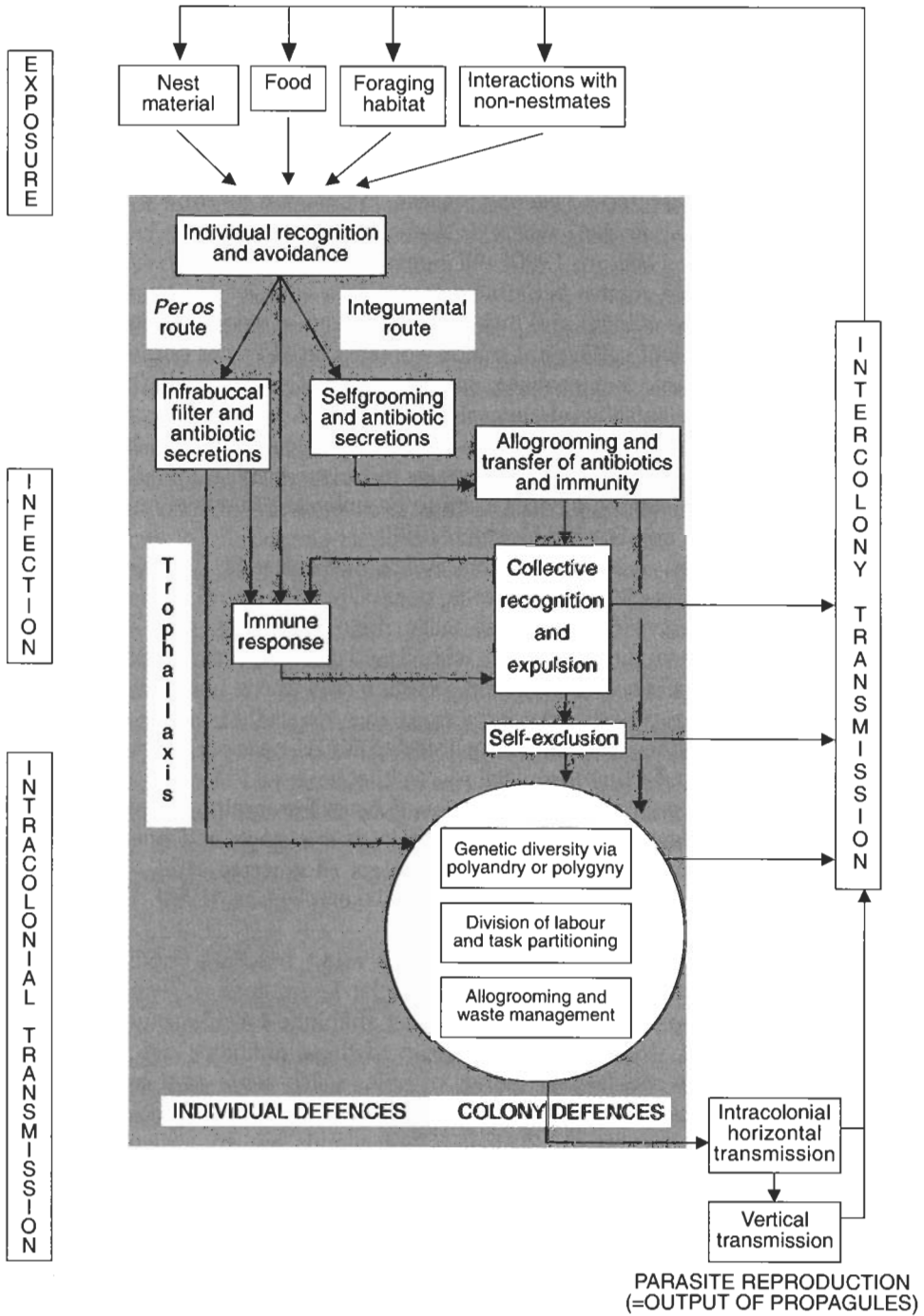


Fig. 6.1. Flow diagram summarizing the dynamics of exposure to, infection by, transmission of, and defence against diseases of individuals and colonies of social insects. See text for details.

detect orally transmitted infections in workers that return to the nest. Recognition of sources of infection thus relies completely on the skills of individual foragers to detect disease propagules before ingesting them. Ants, on the other hand, seem less vulnerable to *per os* transmitted diseases, as they normally carry their prey items wholesale to the nest and only ingest aphid honeydew outside the nest. If recognition at exposure fails, *per os* infections can still be prevented by filtering devices. In ants, this function is carried out by the infrabuccal pocket, which is located at the entrance to the pharynx (Hölldobler and Wilson, 1990). All ingested food is passed through this pocket, with particulate matter being compacted into a pellet for later regurgitation (away from the colony) and thus prevented from entering the digestive system. For example, leaf-cutting ant minor workers can filter out particles at least as small as 10 μm , and probably much smaller (Quinlan and Cherrett, 1978), whereas in fire ants the infrabuccal pocket catches particles as small as 0.88 μm (Glancey *et al.*, 1981). In bees, the proventriculus serves as the filtering mechanism (Seeley, 1985), but appears to be less effective than the mechanism used by ants. Filtering devices seem to be unknown in wasps and termites (for further details, see Schmid-Hempel, 1998).

Closed nests with one or relatively few nest entrances (relative to the size of the worker population) give better possibilities for guard workers to inspect incoming foragers for infections while they are in any case checking their identity as nestmates. In species with closed nests, kin-recognition (e.g. Breed and Bennett, 1987) and disease recognition may thus go hand in hand. On the other hand, open nests have large exposed surfaces that can be accessed from all sides, so that protection from infected kin is necessarily less. This would most strongly affect *per os* infections, as integumental (cuticular) infections with fungal spores will probably be removed by self-grooming behaviour, another individual defence mechanism coming in at this stage and one at which the ants and termites appear particularly adept (Kermarrec *et al.*, 1986; Oi and Pereira, 1993; Rosengaus *et al.*, 1998; Jaccoud *et al.*, 1999; Hughes *et al.*, 2002).

In addition to self-grooming and filtering practices, both *per os* and cuticular infections can be prevented by gland secretions with antibiotic and/or antifungal properties and possibly also by antibiotic cuticular exudates (Boucias and Pendland, 1998). The best-known of these antibiotic defences in social insects are the metapleural glands of ants, which serve as a broad-spectrum defence against unwanted microorganisms (Beattie *et al.*, 1985, 1986; Bot *et al.*, 2002; Poulsen *et al.*, 2002a). These glands are an ancient and unique synapomorphy for the ants and have been retained in almost all genera (Hölldobler and Wilson, 1990) in spite of being metabolically costly (Poulsen *et al.*, 2002a). It thus seems reasonable to infer that disease defence based on the metapleural glands has been of crucial importance for the early evolution and subsequent radiation of the exclusively eusocial ants (Hölldobler and Wilson, 1990). The glands have been secondarily lost on at least two occasions, once in the Oecophyllinae (*Oecophylla*) and once or more in the Camponotini (*Camponotus*, *Dendromyrmex* and *Polyrhachis*) (Johnson *et al.*, 2003b). It is interesting to note that the absence of the glands in these genera appears to be

significantly associated with arboreality and the development of nest-weaving, both characters that may reduce exposure to disease (Hölldobler and Engel-Siegel, 1984; Johnson *et al.*, 2003b). Antiseptic glandular compounds, body exudates and faeces have been shown to occur in termites (Rosengaus *et al.*, 1998, 2000), but a convergent equivalent of the metapleural glands is lacking. The salivary glands of wasps and bees have antiseptic properties, which are primarily used to protect the stored honey and nest material (Cane *et al.*, 1983; Gambino, 1993; Schmid-Hempel, 1998). However, these defences seem comparable to defences that ants possess in addition to metapleural gland secretions, for example the ability of *Acromyrmex* leaf-cutting ants to inhibit microbial growth in their infrabuccal pocket by labial gland compounds (Febvay *et al.*, 1984). Overall, it seems therefore that ants have the most sophisticated antibiotic defences, whereas similar defences in the bees and wasps are far more restricted. The termites may well be intermediate.

The final individual defence is the insect immune system (see Rolff and Siva-Jothy, 2003, for a recent review). Studies have clarified functional details of insect immune systems compared with vertebrate ones (reviewed in Schmid-Hempel, 2003; Schmid-Hempel and Ebert, 2003) and experimental work on bumblebees has shown that immune responses are costly and conditionally expressed (König and Schmid-Hempel, 1995; Moret and Schmid-Hempel, 2000, 2001; Lord *et al.*, 2001; Doums *et al.*, 2002). Recent work on termites has revealed individual humoral immune responses to pathogenic fungi (Rosengaus *et al.*, 1999b). Unfortunately, it is at present impossible to evaluate the relative efficiency of individual immune systems across the four groups of social insects, because the studies on bees and termites used different pathogens and comparable data on wasps and ants are lacking. In the absence of such data, one could assume that individual immune defence capacities across the four groups of social insects are similar, and that the major differences are likely to result from variation in collective organization (see below). On the other hand, it cannot be excluded that there may be trade-offs between individual defence and collective defence, and that ants may have reduced humoral defences because they possess metapleural glands. Furthermore, workers in large-sized and thus typically more advanced insect societies tend to be shorter-lived than workers in primitive societies (Schmid-Hempel, 1998), which may imply that investment in individual immune systems has been under selection to be diminished once collective defences improved.

3.3 Colony defences

The various elements of collective (colony-level) defence are summarized at the right-hand side of the defences frame in Fig. 6.1. These second-line defences (after the first-line individual defences) consist of mechanisms such as collective recognition and expulsion of infected individuals, curing of infected individuals by allogrooming or allotransfer of antibiotics before allowing them into the colony or brood chambers, and preventive measures such as the transfer of

antibiotic compounds and the induction of faster immune responses in nestmates when re-exposed to the same infection (Rosengaus *et al.*, 1998; Traniello *et al.*, 2002). When successful, alone or in combination, these defence mechanisms effectively prevent a single infected individual from spreading its infection among nestmates and would thus make the colony as a whole resistant to the disease. However, this collective resistance has a price in terms of joint investments in vigilance and allogrooming and in the loss of expelled individuals, expenses that should be added to the individual costs of self-grooming, antibiotics production and the maintenance of immune responses. Finally, infected and expelled individuals may become a source of intercolony transmission if they drift to neighbouring colonies (Fig. 6.1). Defences by collective recognition of sources of infection would probably be most effective if aimed at *per os* infected foragers that return to the colony. However, similar collective screening procedures may also reduce the infection risk from prey items. For example, the wholesale prey items that ants transport to their nest may be processed and screened by a number of other ants before being fed to the larvae, which implies that any other worker would potentially be able to recognize and remove an infected item that the forager and other nestmates might have missed. Social wasps often do not have this option as foragers tend to feed larvae directly (Wilson, 1971).

If individual avoidance, individual defence and collective recognition all fail, a disease brought in by one or several workers will have the possibility of spreading through the colony. When this happens, colonies will suffer more severely and may fail to survive or reproduce because of the infection, unless measures are in place to significantly reduce the impact of the disease. These measures roughly fall into three categories (Fig. 6.1), reducing the rate of spread by:

- Division of labour and/or task partitioning;
- Increasing the genetic diversity of nestmates through polyandry and/or polygyny;
- Hygienic behaviour and waste management.

All three topics have been prominent in disease-related research on social insects during the last decade, and the effects of some of them have recently been modelled (Naug and Camazine, 2002). These studies have significantly improved our understanding of disease tolerance and are briefly summarized below.

Division of labour and task partitioning compartmentalize insect societies in two fundamentally different ways. Division of labour implies that different worker castes specialize on different tasks (Wilson, 1971), whereas task partitioning implies that workers of the same caste split up a complex task into subtasks on which they specialize (Jeanne, 1986; Anderson and Ratnieks, 1999; Ratnieks and Anderson, 1999). Castes can either be permanent, differing in body size (size polymorphism) or genetic inclination to express specific behaviours (genetic polyethism) or temporary, changing with age through the lifetime of a worker (age polyethism). In general, divisions of this kind increase in frequency in the more advanced forms of social organization,

i.e. in species with large and long-lived colonies. Although they evolved for reasons of ergonomic efficiency (Oster and Wilson, 1978; Jeanne, 1986), their joint additional effect is a general reduction in interactions between individuals in a society and thus a reduction in intracolony transmission of diseases (Schmid-Hempel and Schmid-Hempel, 1993; Anderson and Ratnieks, 2000; Hart and Ratnieks, 2001; Naug and Camazine, 2002).

The immune resistance of even a fraction of a colony's members may prevent the spread of a disease through the colony, because it makes the local number of susceptible hosts drop below the critical threshold needed for a disease to spread (herd immunity; Anderson and May, 1985). Genetic variation for resistance is well known in many animals and has been demonstrated in several social insect species (Baer and Schmid-Hempel, 2003; Palmer and Oldroyd, 2003; Hughes and Boomsma, 2004). Correlative evidence indicates that genetically more diverse ant colonies have fewer diseases (Schmid-Hempel and Crozier, 1999) and experimental work has shown that genetically diverse colonies of bumblebees (Baer and Schmid-Hempel, 1999, 2001), honeybees (Tarpy, 2002) and leaf-cutting ants (Hughes and Boomsma, 2004) are better able to cope with infections than genetically homogeneous colonies. Recent experimental studies on worker caste allocation and disease resistance in *Acromyrmex* leaf-cutting ants have shown that advantages of genetic diversity may derive from a more flexible allocation to different worker castes (Hughes *et al.*, 2003) or heightened resistance to disease (Hughes and Boomsma, 2004). As the worker castes differ in their exposure to diseases and their effectiveness in defending against them (Hughes *et al.*, 2002; Poulsen *et al.*, 2002b), the two benefits of polyandry will be intertwined. Although patriline-level variation in the chemical mixture of the metapleural gland secretion of *Acromyrmex* workers has not been found (Ortius-Lechner *et al.*, 2003), a better representation of the full spectrum of individual variation in metapleural gland sizes does occur in more genetically diverse colonies (J.J. Boomsma and A.N.M. Bot, unpublished; see also Bot and Boomsma, 1996), suggesting a possible mechanism by which an improvement in disease resistance may occur. The cumulative evidence for social bees and ants (there are no data for social wasps) indicates that genetic diversity for herd immunity is important for disease dynamics, although polyandry may not necessarily have evolved to its present frequencies because of this, with there being a number of other possible benefits that may also apply (Boomsma and Ratnieks, 1996; Crozier and Fjerdingstad, 2001). A direct or indirect causal link between parasite load and relatedness is unlikely if not impossible in termites, because of the almost invariably monogamous colony structure of these social insects (Thorne, 1985).

The most active and flexible forms of behavioural defences can be captured under the category of allogrooming and waste management (Fig. 6.1). Not only do social insects allogroom incoming foragers as discussed above, this behaviour is often routine throughout the colony. However, there are differences in how elaborate and effective this behaviour is across the four groups of social insects. Allogrooming is known to be highly efficient in ants

and termites (Kermarrec *et al.*, 1986; Oi and Pereira, 1993; Rosengaus *et al.*, 1998; Hughes *et al.*, 2002), whereas this type of mutual cleaning by nestmates seems to be unknown in the social wasps and bees, except for occasional observations in the honeybee (Naug and Camazine, 2002). A factor connected to this difference may be the extent of hairiness of workers and queens. Bees, in particular, are very hairy so that pollen can be easily collected and transported back to the nest, but this makes grooming for spores of pathogenic fungi difficult. The same applies (but to a lesser extent) to wasps, but the body surfaces of ants and termites are normally smooth enough to make allogrooming effective. A further factor that makes colony-level behavioural defences more effective in ants and termites is that they have the possibility to abandon sections of the nest (without having to abandon the entire nest) that have an infection that cannot be controlled. This can be done because nests normally consist of a complex network of galleries and brood chambers (Table 6.1). Bees and wasps, however, have single nest units organized as an arrangements of cells in comb-like structures, which makes it much harder if not impossible to abandon sections. Abandoning nest fragments is likely to be costly, but will be far less so than being forced to abandon the entire nest as is otherwise often necessary (Roubik, 1989; Knutson and Murphy, 1990; Williams, 1990; Gadagkar, 1991).

Hygienic behaviours are individually based in social bees and hardly coordinated at the colony level (Trump *et al.*, 1967). The partly genetic determination of this behaviour implies that honeybee colonies may differ considerably in the expression of hygienic behaviour, resulting in different tolerances to disease across colonies (Rothenbuhler, 1964a,b). *Vespula* wasps are surprisingly poor in hygienic behaviour (Greene, 1991; Glare *et al.*, 1996; Harris *et al.*, 2000). In leaf-cutting ants, however, hygienic behaviour and waste management have become a highly integrated colony activity, employing a significant proportion of the worker force (Bot *et al.*, 2001b; Hart and Ratnieks, 2001, 2002b). It has probably been the particular challenges from large amounts of waste due to the fungus agriculture of these ants that have selected for this advanced waste management behaviour that seems to be unmatched in other ants. However, it is also clear that the social characteristics of ants in general (Table 6.1) have predisposed them to evolving elaborate waste management behaviour. They possibly share this predisposition with termites, but not with the social bees and wasps. Again, the honeybee may be an exception, as extreme task specialization of cleaning workers has been observed (Arathi *et al.*, 2000).

3.4 The differences in defence against parasites across the four groups of social insects

Overviewing the above considerations on defences, we conclude that many of them fit and reinforce the conclusions drawn at the end of Section 2. The fundamental differences in our expectations of disease pressure across the four groups of social insects that appeared from analysing differences in exposure

and transmission (Section 2) are normally not compensated by opposite differences in individual or collective defence (this section). The annual social bees and wasps face higher risks of introducing infections in their colonies when returning from foraging trips because they are more likely to ingest contaminated food away from the colony and have less effective filtering devices to prevent *per os* infections. Their individual antibiotic defences seem less general and elaborate, and their allogrooming, hygienic behaviour and waste management practices are generally less well developed or less frequent. Although task partitioning probably occurs in all major groups of social insects, physical worker castes that would help in defence against disease are restricted to the perennial ants and termites. In fact, the only factor that is not unambiguously pointing towards a significant advantage in disease defence for the long-lived, perennial societies of ants and termites is intracolony genetic diversity. Ants are clearly champions in the number of independent transitions to genetically diverse colonies, either because of polygyny or polyandry (Keller and Reeve, 1994; Boomsma and Ratnieks, 1996). They are followed by the social wasps, where polygyny is frequent in the Polistinae (Reeve, 1991) and multiple queen mating occurs in the Vespinae (Foster and Ratnieks, 2001). Next in line are the social bees, where polyandry is almost completely restricted to the honeybees (Palmer and Oldroyd, 2001; Tapy, 2002) and where polygyny seems less frequent than in the social wasps (Michener, 1974). The termites clearly have the least genetically diverse colonies. The entire group is essentially monogamous, as most documented cases of multiple breeders have been shown to concern offspring reproductives that are on their way to replace parent breeders or to head bud-nests (Thorne, 1985). The only parameter that seems to be correlated with this sequence is the diet: carnivory/omnivory in ants and wasps, followed by a pollen and nectar diet in bees and a decomposer diet in termites (Table 6.1).

We thus expect a number of trends to be apparent in the comparative data. As hosts, we expect ants and termites to be more similar to each other than to the bees and wasps, which should be mutually similar as well. We expect these respective groups of social insect hosts to suffer predominantly from types of parasites and diseases that match their typical nesting and foraging habitats, and we expect these differences to be expressed particularly when grouping parasites and diseases in categories such as the ones proposed in section 2.5.

The next section analyses available comparative data to investigate the extent to which these expectations are supported.

4. An Update and Reappraisal of the Comparative Data

The database of Schmid-Hempel (1998), which was closed in 1996, has been updated with any new host–parasite interactions involving social insect hosts that were not already included in the Schmid-Hempel (1998) database. For the most part, updating was limited to literature that has appeared post-1996. Sampling effort varies dramatically between the social insect groups, with termites and wasps having received considerably less attention than have the ants and bees.

More importantly, the distribution of the effort varies, most notably with a single bee species (*Apis mellifera*) having been studied with very great intensity whereas, for example, a very large number of ant species have been studied, but each relatively little. We used two methods to eliminate the confounding effects of sampling effort. The first method is the same as that applied by Schmid-Hempel (1998) and used the number of studies published on particular host species as an approximation of study effort. Residuals from a regression on these numbers were then analysed. Our second method counted the number of host–parasite interactions for host groups (ants, bees, termites, wasps) as a whole. This means that a large number of parasite species recorded from a single host species counts the same as an identical number of host species recorded for a single parasite species. The method of interaction numbers also allowed the large number of ambiguous records to be included in an estimated, but realistic, fashion. The distribution of such records is not uniform due to the variation in the difficulty of identifying parasites between the different parasite groups. Inclusion of ambiguous records, even in an imprecise manner, helps to reduce the taxonomic bias in the dataset. Although the numbers used for ambiguous records were estimates, the results were reproduced using both the estimated maximum and the absolute minimum number of interactions. In neither case did the patterns observed change significantly.

For the interaction method, data were listed as a column of parasite species and a column of host species, such that each unique parasite–host interaction was represented as an individual row. Where the number of species involved in an interaction was uncertain, due to ambiguous references (for example '*Formica* spp.', '*Camponotus*', 'other ant genera', 'unidentified strepsipteran'), they were estimated by us. Interactions that most probably involved single species, but where the identity of the species was unknown, were counted as being single-species interactions. Interactions that most probably involved multiple species were counted as representing three species (with a minimum of one and an assumed maximum of five), unless the details of the studies allowed a more precise estimate to be made. In as far as it was possible to be certain, only species that had been demonstrated to be parasitic were included and only interactions that were natural, as opposed to those recorded only from laboratory experiments.

Figures 6.2–6.4 show the make-up of the parasites recorded for each of the four social insect groups. In each case, the figures consist of versions produced using each of the two methods described above. The two methods consistently produced extremely similar results, demonstrating that the broad patterns are robust to methodology. The four social insect groups differed significantly in the degree to which they are afflicted by micro- or macroparasites (Fig. 6.2) (Fig. 6.2A: $G_{\text{Het}} = 392.5$, d.f. = 3, $P < 0.001$; Fig. 6.2B: $F_{3, 514} = 76.9$, $P < 0.001$). Wasps are mostly recorded as suffering from macroparasites, while termites suffer predominantly from microparasites. The ants and bees are intermediate. The average ranking of the relative share of microparasites was: 1, termites; 2, ants; 3, bees; 4, wasps, in concordance with the expectations outlined in Sections 2 and 3. Figure 6.3 shows further details of the relative representation of interactions between hosts and ten different categories of parasites and diseases. It shows that wasps are mostly afflicted by parasitoids (particularly

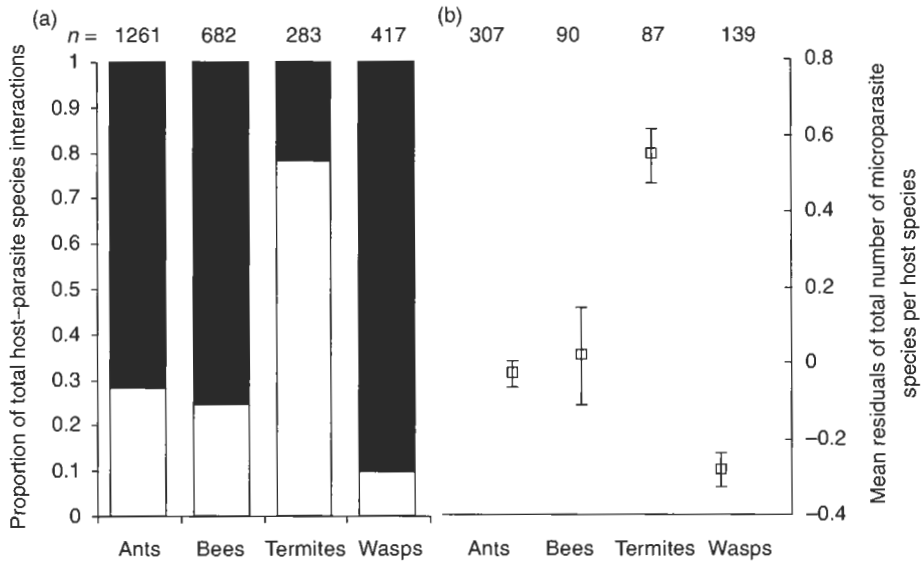


Fig. 6.2. Representation of microparasites (viruses, bacteria, protozoa, fungi) and macroparasites (nematodes, helminths, mites, dipteran and hymenopteran parasitoids and other arthropods) for each social insect group. The graph on the left (a) shows the representation as proportions of the total host–parasite interactions recorded for each social insect group (white: microparasites; black: macroparasites). Interactions were defined as each filled cell in a cross tabulation of parasite species against host species. Sample sizes for each host group are listed above the bars. The graph on the right (b) is based on the method used in Schmid-Hempel (1998) and shows the mean standardized residuals for the arcsine-transformed proportion of parasites (\pm SE) recorded for individual host species in each social insect group that were microparasites. Sample sizes are given above the means. See text for further details.

Hymenoptera) and other arthropods (which for wasps were mostly Strepsiptera). This is as expected given the highly accessible nests of wasps, which usually hang in free air. Termites are mostly afflicted by fungi and have very few macroparasites. This fits the predictions based on the difficulty for *per os* transmitted microparasites to maintain themselves with termite hosts, the difficulty for mobile macroparasites to find and penetrate their concealed nests, and the hemimetabolous nature of termites, which implies that their immature individuals are not as defenceless as the brood of social Hymenoptera. Bees are afflicted by many mites, while helminths are almost entirely restricted to ants. Finally, Fig. 6.4 tests the expectation that *per os* transmitted diseases should be more common in the bees and wasps, compared with the ants and termites. The results confirm this prediction to a large extent, with the four social insect groups again differing in the make-up of their microparasites (Fig. 6.3A: $G_{\text{Het}}=183.4$, d.f. = 3, $P < 0.001$; Fig. 6.3B: $F_{3, 151} = 70.0$, $P < 0.001$). Within the microparasites, bees suffer predominantly from *per os* transmitted parasites, whereas ants and termites suffer mostly from fungi.

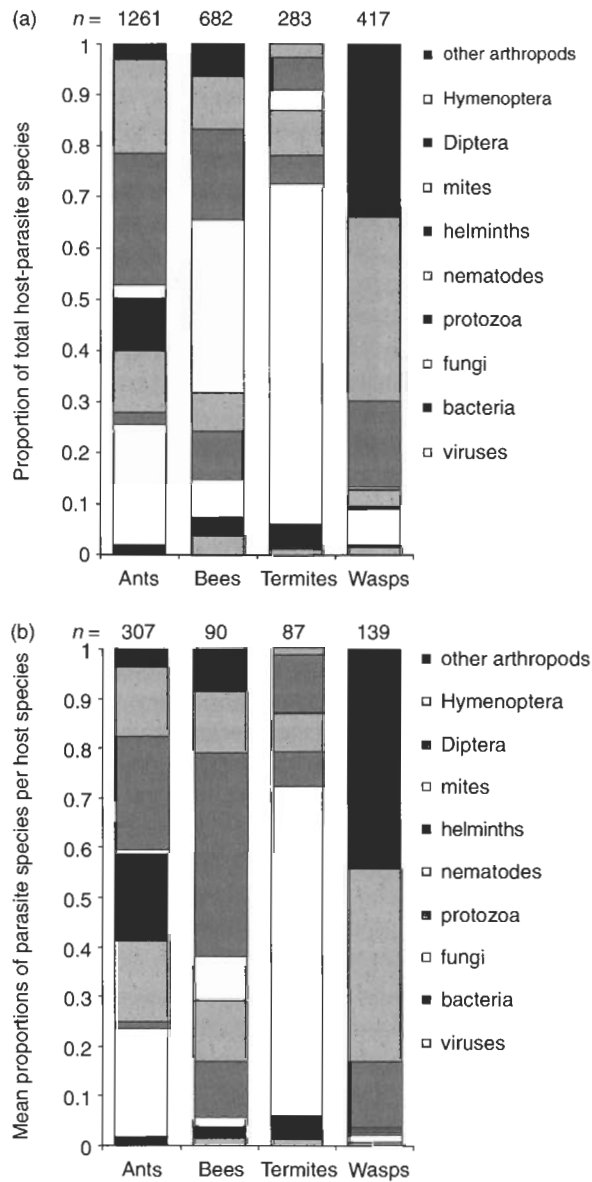


Fig. 6.3. Relative proportions of different parasites among all parasites reported for each social insect group. The top graph (a) shows the proportions of the total host–parasite interactions recorded for each social insect group (parasite groups represented by black, light shading, dark shading and white in a set sequence). Interactions were defined as each filled cell in a cross tabulation of parasite species against host species. Sample sizes for each host group are listed above the bars. The bottom graph (b) is based on the method used in Schmid-Hempel (1998) and shows the mean standardized residuals for the arcsine-transformed proportions of parasites (\pm SE) recorded for individual host species in each social insect group. Sample sizes are given above the means. See text for further details.

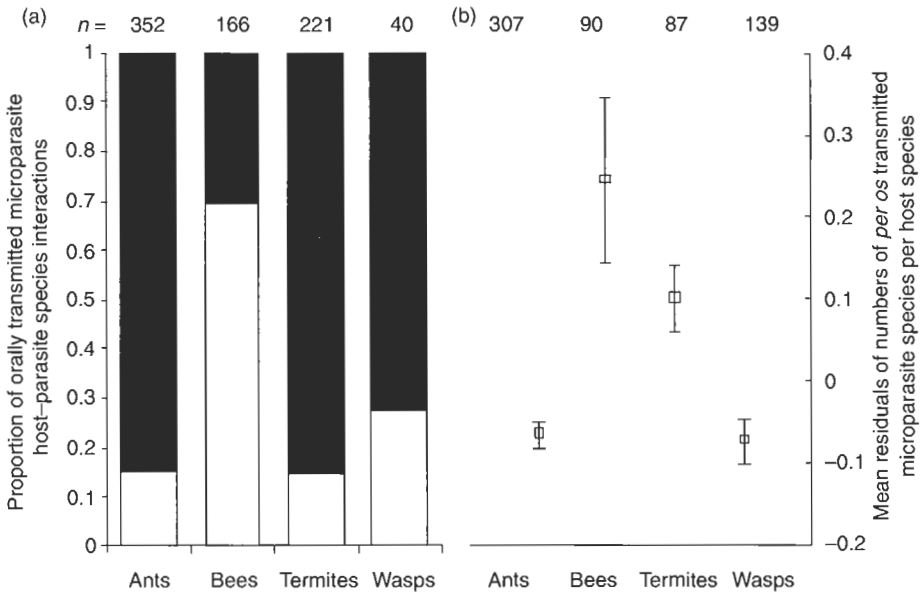


Fig. 6.4. Relative proportions of microparasites that were orally transmitted (viruses, bacteria and protozoa) or fungi. The graph on the left (a) shows the representations of host–microparasite interactions for orally transmitted microparasites (white) and fungal microparasites (black) as proportions of total microparasite interactions recorded for each social insect group. Interactions were defined as each filled cell in a cross tabulation of parasite species against host species. Sample sizes for each host group are listed above the bars. The graph on the right (b) is based on the method used in Schmid-Hempel (1998) and shows the mean standardized residuals for the arcsine-transformed proportion of microparasites ($\pm SE$) recorded for individual host species in each social insect group that were orally transmitted. Sample sizes are given above the means. See text for further details.

5. Discussion

5.1 Important issues for future work

In the previous sections we have shown that there are many reasons to expect major differences in disease pressure across the four major groups of social insects. These were expected to be visible as differences in the total number and predominant type of parasites, in the degree of specificity of these parasites, and in their respective virulence. The comparative data largely confirmed the expectations for the overall number and type of parasites, but our large-scale approach does not allow more precise conclusions. Coordinated screening surveys across the major taxa of social insects will be needed to redress the sampling bias of the presently available comparative data and in-depth population-level and experimental studies will have to provide more detailed specific tests. We hope that our analysis will stimulate such work.

Established single-species model systems will remain essential for further experimental studies. However, broader comparative studies will be valuable for uncovering general principles of social evolution and the ways in which parasitism affects social evolution (Schmid-Hempel, 1998; Schmid-Hempel and Crozier, 1999). Further insight into the overall patterns of disease pressure should probably also come from studying paired genera or higher taxonomic units that have much in common but differ in one or two of the key aspects affecting either the infection processes or defences (Fig. 6.1). An obvious case would be to compare disease diversity, prevalence, specificity and virulence in *Apis* honeybees and *Melipona* stingless bees. An advantage of this 'twin' model system would be that virtually all honeybee diseases are known and have been studied (Bailey and Ball, 1991), so that the organization of comparable studies in stingless bees will be straightforward. A difficulty will be to disentangle the effects of genetic diversity (*Apis* always has multiply-mated queens (Palmer and Oldroyd, 2001), whereas *Melipona* queens tend to be singly-mated (Peeters *et al.*, 1999)) and trophallaxis (which occurs at a higher level in *Apis* than in *Melipona*; Sommeijer and De Bruijn, 1994; Hart and Ratnieks, 2002a) on the probability of different diseases to maintain themselves and express virulence. Another promising approach would be to compare the vespid wasp genera *Dolichovespula* and *Vespula* (Foster and Ratnieks, 2001). The former build nests that are freely suspended in the air, whereas the latter use and expand underground cavities (Brian, 1982; Greene, 1991). Multiple queen mating occurs in both genera, obligatory throughout *Vespula* and facultative in *Dolichovespula* (Foster and Ratnieks, 2001), so that this factor can probably be controlled by instrumental insemination (Baer and Schmid-Hempel, 2000). Other good cases would be comparing ants and termites that build nests in trees with sister groups that have remained associated with the soil (see e.g. Johnson *et al.*, 2003b), and comparing ant genera with trophallaxis with sister taxa without.

Studies of virulence and specificity will be particularly rewarding in comparative experimental studies of the type suggested above. Specificity studies are difficult but badly needed, because it is mostly unclear whether what is known as a species of microparasite is indeed a largely panmictic gene pool or in reality a mixture of genetically differentiated lineages (Tibayrenc, 1999). More detailed knowledge about specificity will be crucial for making educated inferences about the extant population size of susceptible hosts and the coevolutionary potential of the interaction between the social host and parasite. The expression of virulence is related to these variables, but will also depend on whether a pathogen is actively or passively dispersed. Selection for or against virulence will generally depend on whether transmission is best served by fit and active foragers who can deposit many propagules at foraging sites, or by dead foragers producing fruiting bodies with passively dispersed (wind, rain, etc.) spores. The microsporidian parasite *Crithidia bombi* infecting bumblebees (Schmid-Hempel, 2001) and the fungus *Metarhizium anisopliae* infecting, for example, leaf-cutting ants (Kermarrec *et al.*, 1986; Jaccoud *et al.*, 1999; Hughes *et al.*, 2002; Poulsen *et al.*, 2002a) illustrate this contrast and underline the fact that any virulence can evolve depending on the ecological conditions that affect transmission and recovery (Anderson and May, 1982;

May and Anderson, 1983; Ebert and Herre, 1996). The trypanosome *Crithidia* is a chronic infection that is iteroparous and relatively mild for both the infected workers (Brown *et al.*, 2000) and established colonies (Shykoff and Schmid-Hempel, 1991), but which severely impedes colony foundation by the queen (Brown *et al.*, 2003). *Metarhizium*, on the other hand, is an 'obligate killer' that reproduces semelparously and has to kill its host in order to do so (Boucias and Pendland, 1998).

A general implication of our findings is that the overall costs of cumulative defences against parasites and diseases are expected to be significantly higher in ants and termites than in bees and wasps. These costs are generally very hard to measure and thus remain largely unknown. However, hints about their magnitude have recently been obtained in *Acromyrmex* leaf-cutting ants. These ants, with their agricultural fungus-rearing societies, have the additional need to control diseases of their fungal crop, so that selection is likely to have promoted consistently high investments in resistance against and tolerance of diseases. The two major components of defence are the metapleural gland secretions, which are generally effective against soil-borne microparasites (Bot *et al.*, 2002; Hughes *et al.*, 2002; Poulsen *et al.*, 2002a), and a cuticular cover of actinomycete bacteria that specifically control a fungal parasite of the mutualistic fungus garden (Currie *et al.*, 1999). Each of these defences has recently been estimated as being equivalent to 10–20% of the basic metabolic rate of *Acromyrmex* workers (Poulsen *et al.*, 2002a, 2003).

5.2 Towards a synthetic life-history theory of disease pressure in social insects

The question as to why ants and termites are obligatory iteroparous, whereas the social bees and social wasps (excepting a few derived lineages that originated and mostly remained in the tropics) have retained the ancestral semelparous life cycle is likely to be directly linked to the type of diseases that affect them and to the prevalence and virulence that these diseases achieve. Iteroparity is generally selected for when adult survival rates are high relative to juvenile survival rates (Stearns, 1977), whereas being parasitized selects for earlier reproduction (Forbes, 1993) and semelparity. Defences favouring colony resistance against, rather than colony tolerance of, parasites may have played a crucial role in this transition that took place early in the social evolution of both ants and termites. In organisms other than social insects, a high life expectancy after the first reproductive effort is generally associated with costly but efficient defences against natural enemies and with elaborate somatic repair mechanisms (Kirkwood, 1981) so that, all else being equal, growth has to be slower. In contrast, life histories characterized by rapid growth and a single early reproduction event are normally characterized by minimal levels of defence and degrees of repair that are only just sufficient to secure survival until the completion of reproduction. Brian (1982) estimated that the typical growth rate of social insect colonies follows the ranking order: wasps > bees > ants > termites, which fits with these expectations.

We therefore submit the hypothesis that, overall, most bee and wasp species have been selected for relatively cheap methods of disease tolerance, whereas the ants and termites have primarily evolved costly mechanisms of colony resistance. The annual bees and wasps may be able to tolerate a fairly high number of diseases of up to moderate virulence, by relying on defences such as individual immune systems, which can be facultatively adjusted according to need, and which are mostly meant to delay the impact of parasites and diseases until the reproductive cycle has been completed. On the other hand, the long-lived fortresses built by ants and termites most probably cannot afford to take such risks once they have grown beyond the colony-founding stage and have thus evolved multiple costly defences to prevent colony infections or to eliminate such infections at an early stage.

The evolution of iterparity in the ants and termites will have been facilitated by the restrictive intercolony transmission dynamics for their parasites (see Section 2). The fact that these taxa made this transition early in their evolution and without reversals in derived clades implies that most of the virulent diseases from which they still suffer are probably general diseases that also use other insect hosts, whereas most of their specialized diseases are likely to be more or less avirulent. Epidemics should thus be rare. Survey data for ants seem to confirm these expectations (Bequaert, 1921; Evans, 1974, 1982, 1989). For example, Evans (1982) argues that diseased army ants and leaf-cutting ants are rarely encountered in the field, suggesting effective defences. The same study reports that the overall number of ants killed by fungal diseases varies little among years, which is compatible with enzootic rather than epizootic prevalences (see also Oi and Pereira, 1993). This implies that the comparative data on a number of diseases may in fact overestimate the disease pressure in ants and termites, as many of the specific pathogens reported may in fact be rather close to being neutral symbionts. Also, vertically transmitted *Wolbachia* symbionts in ants seem to be more neutral in their effects on host reproduction than they often are in non-social insects (Wenseleers *et al.*, 1998; Van Borm *et al.*, 2001, 2003), which might be linked to the long ergonomic phase of colony growth, as argued in Section 3. A recent study documenting that *Wolbachia* infections reduce worker lifespan in ants (Wenseleers *et al.*, 2002) does not necessarily contradict this inference, as the host in question, *Formica truncorum*, starts colonies as a temporary social parasite.

The supposedly moderate effects of diseases in ants are in sharp contrast with the iteroparous honeybees, in which effects of diseases tend to be highly visible, although domestication has undoubtedly aggravated disease problems in this species. The quote at the start of this chapter suggests that Axelrod and Hamilton were aware of this contrast and of a possible explanation along the lines presented here more than 20 years ago. The same quote also suggests that some disease symbionts which were forced into non-virulence by the patterns of clustering and transmission typical for ants or termites, may secondarily have become mutualists.

The arguments and results presented here seem to challenge some established evolutionary concepts about disease pressure as a function of lifespan. To summarize this in a nutshell: Seger and Hamilton (1988) argued

that perennials are generally more troubled by parasites than annuals, because they are easier to find (a corollary of the ecological apparency concept; Feeny, 1976) and because they have longer generation times and thus a slower coevolutionary response to parasitic innovations. It is important to realize, however, that this argument implicitly assumes that parasites have unconstrained access to hosts, which is more realistic for plants and other non-social hosts than for insect societies, where social defences are based on active recognition and function as an additional, collective immune system. The coevolutionary part of the argument thus needs a qualifier to be fully transparent. It only says that perennials face more profound challenges because of their longer generation times, but not that they have given up being perennials because of that. The evolution of sophisticated defence systems has, in addition to maintaining sexual reproduction and recombination, allowed perennial organisms to meet these challenges successfully (see Hamilton, 2001, for a review). Social insects, in particular the perennial ones, have also been highly successful in doing exactly that.

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