Apidologie (1995) 26, 255-271
© Elsevier/INRA/DIB/AGIB

Review article

Parasites and social insects

P Schmid-Hempel

ETH Zürich, Experimental Ecology, ETH-Zentrum, NW, CH-8092 Zürich, Switzerland

(Received 23 December 1994; accepted 8 March 1995)

Summary — A short review shows that social insects have many parasites on larvae and adults but few on eggs. Social organisation simultaneously affects parasite transmission within and between colonies. Overall, the biology of social insects may be favourable to an epidemic, but such a process may quickly die out in the host population.

social insects / parasite / polyandry / social organisation / epidemiology

INTRODUCTION

Under natural conditions, organisms are exposed to a wide range of parasites that may threaten their survival and reproductive success. Research over the past 2 decades has broadened our knowledge and demonstrated that the effects of parasitism may often be quite subtle rather than obvious. For example, a number of studies have documented subtle behavioural changes of the infected hosts that often seem to favour the parasite. Many species of acantocephalan parasites seem to rely on inducing changes in host behaviour to facilitate transmission to the next host (Moore, 1984). An infected isopod which serves as an intermediate host will become positively phototactic and stay in exposed areas more frequently than their uninfected counterparts. As a consequence, the infected host is more likely to be preyed upon by a bird which is the final host of the parasite (Moore, 1983). Such changes of host behaviour which increase the chances of transmission for the parasite seem not to be uncommon and may have larger-scale consequences for population dynamics (see Dobson, 1988; for discussion).

Social insects as hosts are no different from other organisms, but the investigation of their parasites has been largely neglected, with the exceptions of commercially important species (*eg,* honey bees; Bailey and Ball, 1991), pest species (*eg,* fire ants; Jouvenaz, 1983), and studies of social parasitism and inquilines (mostly in ants and bees; *eg,* Lin, 1964; Fisher, 1988). For example, similar observations on behavioural changes have been made in the classic case of a parasite infecting a social insect. The liver fluke (*Dicrocoelium*) infects wood ants as intermediate hosts. The infected ant changes its behaviour so as to climb onto exposed parts of its habitat (*eg,* grass tips), where the ant will normally stay until eaten by the final host of the fluke, a herbivorous mammal such as a sheep (Hohorst and Graefe, 1961; Schneider and Hohorst, 1971).

Parasites can have additional effects on hosts. Snails infected by the trematode *Schistosoma* (the causative agent of human bilharzia) change their life history by increasing fecundity early in life at the expense of later reproduction. Minchella and Loverde (1981) demonstrated that such altered fecundity schedules benefit the host because parasitism leads to castration of the snail at an older age. Parasites have also been implicated in the pattern of geographical distribution of species because parasites could act as weapons of competition among their hosts (Price *et al,* 1986, 1988). In fact, some drastic cases of range reduction in birds and ungulates have been traced back to the action of parasites (Dobson and Hudson, 1986). More recent work has concentrated on the hypothesis that entire species communities may be affected by the presence of parasites (Dobson and Crawley, 1994). Finally, parasites have also been assigned a prominent role for the evolution of sexual selection and mate choice (Andersson, 1994), an area of interest which has grown explosively over the last years.

Parasites should be especially important for social species, although this aspect has often been neglected in discussions on the evolution of sociality. In social animals, parasites can be contracted by many individuals and subsequently may threaten many members of the social group. For this reason, it has been suggested that characteristics which at first sight seem quite disparate, such as group aggression towards newcomers, territory maintenance, or group size, may all have evolved to prevent novel infections from being introduced to the group (Alexander, 1974; Freeland, 1976). Indeed, the number of parasite species per host and infection intensity often show a positive correlation with group size (Davies *et al,* 1991; Keymer and Read, 1991). Negative correlations have been reported for some vector-transmitted diseases (Poulin and Fitzgerald, 1989). A possible cause for this difference may be related to the increased rate of contacts in large groups that facilitates the transfer of directly transmitted parasites, and, at the same time a dilution effect that reduces the per capita rate of vector attacks ('the selfish herd'). Besides this, the spread of an infection within a group is likely to proceed more rapidly than the spread of the infection between groups. Such suggestions have been made for human smallpox in African households (Becker and Angulo, 1981), a population that for many purposes is structured in similar ways to social insect populations. Furthermore, fitness effects of parasitism have been reported for animals living in groups, *eg,* cliff swallows that have high levels of ectoparasitism (Brown and Brown, 1986). Such evidence strongly suggests that we should be concerned about parasitism in social insects, and that in fact social insects may be highly suitable study objects for investigating the interactions between parasitism and social organisation. This paper discusses a somewhat arbitrary selection of issues on host–parasite interactions in social insects.

PARASITES OF SOCIAL INSECTS

Colonies of social insects should be a highly rewarding target for parasites, because they offer both a locally high density of potential hosts and, at the same time, an assemblage of hosts that (on a crude level) are genetically more similar to each other than the population average. In discussions of modern epidemiology and evolutionary ecology it is usual to use the category of microparasites which refers to parasites whose dynamics can be described by referring to infected, uninfected (susceptible), or resistant hosts ('SIR models', Anderson and May, 1981). Viruses, bacteria, and protozoa would all qualify for this category despite the many differences in their biology. On the other hand, macroparasites are those parasites where the dynamics can be better described by looking at individual parasites and their fate within hosts ('Sir model", Anderson and May, 1981). Helminths, such as trematodes and nematodes, fall into this category. Finally, social insects are hosts to parasitoids and social parasites. I will not discuss the case of subsocial arthropods, which may shed an extra light on the origin of the association between social insects and their parasites.

A brief survey of the literature will show that a wide variety of parasites of all categories are associated with social insects (table I). As in other organisms, parasites can attack different life cycle stages of the host (table II). In social insects, this would include eggs, larvae, pupae and adults, and we may, for practical reasons, add the nest as such, for example, its supporting structure (*eg,* wax) or debris. In termites, which have a hemimetabolous development, different nymphal stages could be the target of parasites. Furthermore, parasites may infect a particular stage, *eg,* the larva, but be transmitted to the next host or a vector by another, *eg,* from the pupa or adult. An example is the microsporidian *Burenella dimorpha* infecting the fire ant *Solenopsis.* Infection occurs in the fourth larval instar by the attendant nurse workers that provide food, but parasitic spores are released and transmitted to these workers which act as vectors in the pupal stage (Jouvenaz *et al,* 1981).

In social insects, there seem to be few cases in which the egg is attacked (table II). In particular, only those parasites that are transmitted vertically, *ie* from mother to offspring, *via* ovaria and eggs, seem to be described (*eg,* some viruses). It is not known whether this lack of egg parasites is real or reflects a lack of studies. Given the many taxa of parasitic wasps that specialise on eggs of lepidoptera (Strand, 1986), this deficiency is remarkable and is possibly the result of the widespread mode of brood care and the use of sheltered nest sites that may make eggs difficult to utilise for most parasitoids. Consequently, if present at all, the most likely targets of egg parasites must be surface nesters, a nesting habit found in many wasps and some bees.

Larval parasites, on the other hand, are quite common, but these often include infectious parasites. This may reflect the fact that infectious diseases can readily spread within a nest once infected. It is unclear, however, why eggs are not attacked at the same time, but essentially a similar absence of infectious diseases of eggs is also true for non-social insects. Possibly, it is simply more difficult to penetrate the egg and its chorion. Another reason may be the fact that infections cannot be easily transmitted by the eggs since they are immobile and will not easily get in contact with new hosts, unless the mode of brood care ensures transmission. In polydomous social insects eggs and brood are often carried from one nest to the other and thus infections may easily spread to different nests within the colony.

A large number of parasites attack workers. These include viruses, bacteria, fungi, protozoa, helminths, and parasitoids (table II). Workers, together with larvae, are thus the major target of parasitic infections. On the other hand, few cases seem to exist where only the sexuals, particularly the queen but not the workers, are attacked. The case of the nematode *Sphaerularia bombi,* which infects hibernating queens of *Bombus* spp while they are staying in the ground (Lundberg and Svensson, 1975), is special because it relies on the solitary phase of the species. Such parasitism must be expected in similar cases of primitively eusocial species where the queens (or males) pass some time as solitary animals. Although little is known about such taxa, the general pattern appears to be that parasites will be able to attack all castes in the social phase of the species, as is the case for *Bombus* (Schmid-Hempel *et al,* 1990).

GENETIC ASPECTS

Variability in the susceptibility of hosts to infection and in the ability of parasites to infect and establish in the host is based on host–genotype *vs* parasite–genotype inter-

Table I. Examples of different parasite types in social insects.

Type	*Parasite*	*Host*	*Remarks*	*Reference*
Microparasites	*Nosema apis* (Microsporidia)	*Apis mellifera*	High prevalence in spring	1
	Apicystis (Mattesia) geminata (Gregarina)	*Solenopsis invicta*	Parasite has different cycles of merogony	2
	Viruses	*Apis mellifera*	Including bee paralysis virus	3
	Entomophtora sp (fungus)	*Formica pratensis*	Causes behavioural changes in host	4
	Beauveria bassiana (fungus)	*Solenopsis richteri*	Infection in the laboratory is possible	5
	Spiroplasma sp (bacteria)	*Apis mellifera*	Stays infectious after many passages through host	6
Macroparasites	Cestoda sp	*Leptothorax curvispinosus*	Primary hosts are probably birds	7
Parasitoids	*Schizaspidia polyrhachidida*	*Polyrhachis dives*	Rich fauna described for the Philippines	8
	Volucella inanis	*Paravespula vulgaris*	Closely associated with its host species	9
	Strepsisptera spp	*Pheidole radoschkowski*	Many hosts and parasite species known in this complex	10

1) Doull and Cellier, 1961; 2) Jouvenaz and Ellis, 1986; 3) Bailey and Ball, 1991; Bailey *et al,* 1981; 4) Loos-Frank, 1978; Loos-Frank and Zimmermann, 1976; 5) Broome *et al,* 1976; 6) Clark, 1977; 7) Stuart and Alloway, 1988; 8) Wheeler and Wheeler, 1924; 9) Rupp, 1987; 10) Ogloblin, 1939.

actions in almost all cases analysed so far (*eg,* Wakelin, 1985). In a narrow sense, such interactions are based on gene-for-gene interactions (with host resistance genes exactly matched by parasite virulence genes; see Thompson and Burdon, 1992, for discussion). However, more commonly inheritance is polygenic and resistance or infectibility is a quantitative trait (*eg,* Thompson and Burdon, 1992; Schmid-Hempel and Koella, 1994). Although less well investigated than other groups, this is also the case for social insects. Breeders of honey bees have long taken advantage of this fact.

Table II. Examples of parasites that attack different stages of the host.

Attacked stage	*Parasite*	*Host*	*Remarks*	*Reference*
Larva	*Caenocholax fenyesi* (Strepisptera)	*Solenopsis invicta*	Parasites reside in hemocoel and leave host at end of larval stage	1
	Sacbrood virus	*Apis mellifera*	Rarely devastating for colony	2
Pupa	*Obeza floridana* (parasitoid)	*Camponotus abdominalis floridanus*	Likely to attack pupae only	3
Worker	*Pseudaceton curvatus* (parasitoid)	*Solenopsis saevissima*	Parasites gather around nest during mating flights of the host	4
	Mermis sp (nematode)	*Lasius flavus*	Nematodes can survive outside host in soil	5
	Acarapis woodi (mite)	*Apis mellifera*	Colony mortality high when infection intensities high. Devastation depends on environment and host genotype	6
Queen	*Crithidia bombi* (protozoa)	*Bombus terrestris*	Also infects workers	7
	Cestoda sp (helminth)	*Leptothorax curvispinosus*	Infects all castes	8
	Sphaerularia bombi (nematode)	Bombus spp	Exclusively infecting overwintering queens	9

1) Kathirithamby and Johnston, 1992; 2) Anderson and Giacon, 1992; 3) Davis and Jouvenaz, 1990; 4) Pesquero *et al,* 1993; 5) Crawley and Baylis, 1921; 6) Otis and Scott-Dupree, 1992; 7) Skou *et al,* 1963; Shykoff and Schmid-Hempel, 1991a; 8) Stuart and Alloway, 1988; 9) Bedding, 1985; Lundberg and Svensson, 1975.

Selection for increased resistance is, for instance, possible against the microsporidian *Nosema* (Rinderer *et al,* 1983), acarine disease, hairless-black syndrome, American foulbrood (Rothenbuhler, 1964b) and various other diseases (Kulincevic, 1986; Tanada and Kaya, 1993). Moreover, honey bees show natural variation in resistance (which is of course a prerequisite for selective breeding) against the mite *Acarapis woodi*, foulbrood and microsporidia (Bailey and Ball, 1991).

Genotypic variation as a determinant of host–parasite interactions has ramifications for the discussion of the genetic make-up of colonies. Consider the widely accepted hypothesis that the unusually close genetic relatedness of female offspring in social hymenoptera, as generated by the haplodiploid sex determination system, facilitates the evolution of social behaviour and altruism (Hamilton, 1964). Hence, it is expected that extant colonies of social insects are characterised by high degrees of average relatedness among workers. A large number of studies, however, have demonstrated that this is not universally the case and that colonies are genetically quite variable (*eg,* Pamilo, 1981; Ward, 1983; Schwarz, 1986; Queller and Strassmann, 1988). The major reason for this observation is that queens often mate multiply with a number of males ('polyandry') as in the honey bee (Laidlaw and Page, 1984), or that several functional queens are contributing to the worker force of the colony ('polygyny'), as in many ants (Keller, 1993). In either case, the genetic variability within colonies is high by comparison to the total available variation in the population and the average relatedness drops below the theoretically possible value of 3/4 for full-sibs of female hymenoptera. There are alternative views on the relevance of genetic relatedness and kin selection for the evolution of sociality. In fact, the need for cooperative construction of nests (West-Eberhard, 1975), for nest defence by a powerful sting (Starr, 1985), or for life cycles that favour biased sex ratios (Seger 1983) have all been identified as important factors.

Because of the apparent violation of predictions from kin selection theory, a number of hypotheses have been suggested to explain the adaptive significance of polyandry and polygyny. For example, Crozier and Page (1985) hypothesised that increased genetic variability within the colony may allow the expression of a better colony phenotype. Genetic variability for task attendance of workers has indeed been demonstrated (*eg,* Robinson and Page, 1988). Polyandry would thus allow workers to respond to a wider and more variable set of task-specific stimuli (Robinson, 1992). Polyandry could also reduce the amount of genetic load that is associated with the production of less viable or sterile diploid males (Page, 1980; Page and Metcalf, 1982). It may also have evolved as a response to sperm limitation in the males (Cole, 1983), although it remains unclear why under such circumstances males do not evolve larger sperm loads, as, for instance, in *Apis* where single males are capable of filling the spermatheca of a queen (Koeniger, 1991). Polyandry may also reduce the conflict over sex ratio of offspring between the queen (that prefers an even sex ratio) and the workers (preferring a female bias) (Boomsma and Grafen, 1991; Queller, 1993). Polygyny has also been explained by a number of adaptive hypotheses. These include an unspecified advantageous degree of genotypic variation at the colony level (Crozier and Consul, 1976), low probability of independent colony foundation (Pamilo, 1991), or queens being comparatively short-lived with respect to the colony, such that supernumerary queens can act as replacements (Nonacs, 1988).

On the other hand, and more generally, parasites have been repeatedly invoked as selective agents that can maintain genetic variability. In particular, the production of genetically diverse offspring would allow the host to evade the constantly coevolving parasites (Hamilton, 1980; Hamilton *et al,* 1990; Ladle, 1992). These scenarios are associated with genotype–genotype interactions and negative frequency-dependent selection. In this case, rare host genotypes are favoured because the parasites have not yet been able to adapt to them. Common host genotypes, on the other hand, are at a disadvantage, since they are rapidly targeted by the more rapidly evolving and more numerous parasites. It is obvious that such a selection regime is likely to apply in the interaction with parasites such as protozoa that have short generation times and occur in large numbers. It should be less relevant for other groups, *eg,* parasitoids, that have similar generation times and population sizes to their hosts.

These hypotheses mainly addressed the problem of sexual reproduction whose crucial element, genetic recombination, generates a large variety of genotypes among offspring. They have nevertheless important implications for social insect biology. Consider a case where offspring dispersal is high. Not only could hosts in such a situation escape from their parasites in time, but also in space, by occupying new sites. In contrast, when dispersal of offspring is limited, the generation of variability among offspring is much more important. This should be particularly relevant for social insects, where, by definition, most offspring do not disperse but stay at home to help (*ie* barring the sexuals leaving their natal colony). Consequently, several authors have suggested that the maintenance of increased degrees of within-colony genotypic variation, as a result of polyandry and polygyny, could be selected for by parasites (Tooby, 1982; Hamilton, 1987; Sherman *et al,* 1988). Although of far-reaching importance, this hypothesis, unfortunately, has not been widely tested.

Here, I briefly address the problem of multiple mating or polyandry in social hymenoptera. In the bumble bee *Bombus terrestris* L, Shykoff and Schmid-Hempel (1991b) have found that the transmission of the trypanosome *Crithidia bombi* is easier between relatives, *ie* full-sibs, than between unrelated individuals (fig 1). Further studies have shown that this variation is likely to be due to the match between parasite strain and host genotype (Shykoff, 1991). This finding is a necessary precondition that genetic diversity within colonies would reduce the probability of transmission and to render polyandry an adaptive mating strategy in the face of parasite pressure. Opposite results have recently been reported for the honey bee (Woyciechowski *et al,* 1994) where the spread of a disease in experimentally multiply mated colonies was

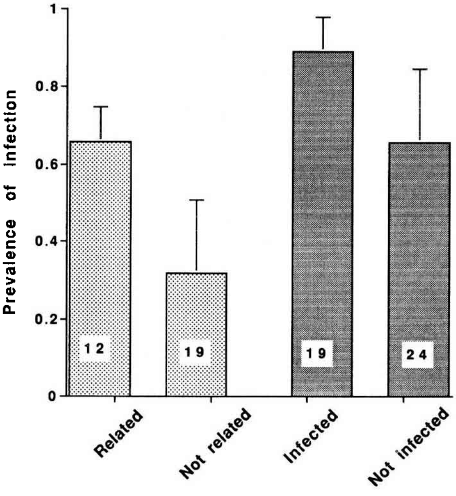

Fig 1. Prevalence in worker groups that have been subject to infection of *C bombi* by either a related or unrelated workers (left-hand columns), or coming for colonies that have already have or have not been naturally infested (right-hand columns). In both cases, workers were not infected at the beginning of the experiments. The figure shows that transmission is easier among relatives and that certain colonies are more susceptible than others (after Shykoff and Schmid-Hempel, 1991b).

not reduced as compared with those mated with fewer males.

It could be argued that polyandry would not only increase the possibility for a queen to garner good resistance alleles to transmit to offspring, but may also increase her risk of mating with 'bad' males, *ie* those that do not provide useful alleles, or increase the risk of becoming infected during mating (a cost of mating which seems relevant mainly for sexually transmitted parasites). This situation is analysed in more detail elsewhere (Schmid-Hempel, 1994), where a simple system of gene-by-gene interactions is assumed, together with multiply mated queens, sufficient degrees of horizontal transmission (*ie* among colonies), and the potential for multiple infections. The calculations show that polyandry is favoured in some regions of the parameter space (fig 2). At present, however, it is not clear whether parasites could act as selective factors for the maintenance of high degrees of within-colony genetic variability and thus for different mating systems.

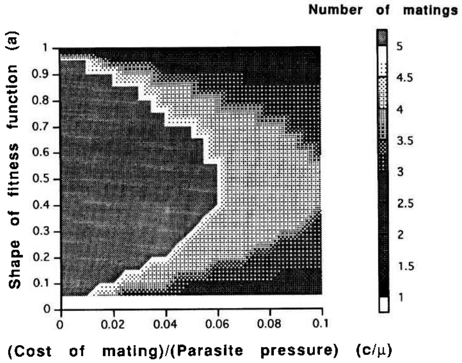

Fig 2. Number of matings (see scale of grey values) that yield maximum fitness (defined by the number of sexuals produced and their mating chances). The selection coefficient, *s*, describes the loss in the contribution that infected workers make towards colony growth and where, by definition, not infected or immune workers have $s = 1$; *k* is the number of alleles that are available and which code for host susceptibility and parasite infectivity, respectively, in a gene-for-gene interaction. The distribution of the number of independent infections among colonies in the population is assumed to be Poisson with mean μ. Extra matings are assumed to be costly with a proportional reduction in fitness, *c*. Colonies grow according to the contributions made by the uninfected or immune (with weight 1) and infected workers ($1 - s$). Colony size, *X*, at reproduction is then converted into fitness, *W*, according to a generic function of the form $W \infty X^{a}$. The coefficient *a* is affected by forces outside parasitism, for example, by the available size of the nesting sites, intra-colony conflict and so forth. The figure is based on the following parameter values: $s = 0.9$, $k = 4$, $\mu = 2$. The values of *c* (reflected in the *x*-axis) and *a* (*y*-axis) have been varied, and for each combination of *c and a* the number of matings that yields maximum fitness is determined (from Schmid-Hempel 1994, reproduced with permission).

SOCIAL ORGANISATION

Parasites have to infect and establish themselves in a host. In addition, parasites have to be transmitted to new susceptible hosts. Such should be an easy task in social insects, because many similar individuals are found in dense aggregations of the nests. The chances of a parasite being transmitted to new hosts is additionally increased in cases where it is able to manipulate its host's behaviour in its own favour. Such a situation is found in the liver fluke that infects wood ants as intermediate hosts, which was mentioned above. Interestingly, a parallel case has been reported for ants infected by the fungus *Entomophtora* (Loos-Frank and Zimmermann, 1976) which also causes the ant to climb onto grass tips from where the fungal spores can be spread by wind over larger areas. A further situation is demonstrated by the example of the brown or yellowish colouration of worker ants infected by a cestode (*eg,* Crosland, 1988). Their normal colour is black and hence parasitisation should make workers more visible to the final host, which is assumed to be a bird.

When considering parasite transmission, it is necessary to distinguish vertical (*ie* from parent to offspring) from horizontal transmission. For social insects, it is also necessary to distinguish within- from between-colony transmission.

Within-colony transmission is vertical when the parasite transfers from queens or males to their worker offspring and to the sexuals. To the extent that within-colony transmission between workers keeps the parasite within the same breeding unit, this may be considered 'vertical' in an extended sense. It therefore seems rather obvious how vertical transmission can be achieved, namely through the spread of an infection within the colony and then onto the sexuals that will carry the parasite to the next generation and to own offspring. Between-colony transmission is horizontal to the extent that different colonies are not necessarily offspring of each other. Parasitoids or social parasites, where the parasitic females actively seek out their hosts, have no difficulty in affecting different colonies in the population and they may thereby act as horizontal vectors for other parasites. The available evidence does not yet allow judgment of whether vector-transmitted disease is common in social insects. Of course, insects in general are vectors for disease of vertebrates rather than hosts to vector-transmitted parasites, perhaps because no blood-sucking vectors prey on insects in similar ways as they do on vertebrates. However, social insects could qualify as a target for a vectoring species, because they form large and long-lived host 'bodies' (*ie* the colonies) which remain available as a rich source for potential vectors to utilise. In this light, it is possible that some inquilines may act as vectors of parasites, *eg,* for viruses, bacteria, fungal infections or protozoa (Jouvenaz, 1983). Vectoring by social parasites may be important, because social parasitism has arisen in all major groups of social insects, including the termites. Alternatively, mites may assume this role and they have indeed been identified as carriers of entomopathogenic fungi (Schabel, 1982). Particularly those mites that live on haemolymph, such as tracheal mites in the honey bee (Bailey and Ball, 1991), should be able to vector protozoa, viruses, bacteria and other parasites residing in the haemocoel. The best evidence comes from the mite *Varroa jacobsoni* infecting brood of honey bees. Mites prefer nurse bees over other classes of workers (Kraus *et al,* 1986) and are thereby transported to the larvae of the colony. Several studies have shown that infection by different viruses (acute bee paralysis viruses APV, Egypt bee virus EBV, sacbrood virus SBV, black queen cell virus BQCV) is associated with infection by *Varroa* . From experiments (Koch and Ritter, 1989) and from such correlations it is clear that the mites act as vectors for viral diseases (Ball, 1985, 1989; Allen *et al,* 1986; Ball and Allen, 1988; Chastel *et al,* 1990). Actual infection seems to occur *via* trophallaxis, faeces and transovarially, by nectar and pollen, and by contacts among mites and between bees and mites. Certainly, exciting bee-mite associations with the implication of parasite transmission remain to be discovered (Eickwort, 1994).

The workers themselves may act as vectors if they enter foreign nests. This seems relevant for kleptoparasitic, honey- or nest-material robbing species of bees, for instance in the eusocial meliponine genera *Lestrimelitta* in the Americas and *Cleptotrigona* in Africa (Roubik, 1989). One can easily imagine that such habitual robbery would facilitate the spread of spores or other infective forms to and from the robbed colonies. The occasional drifting and entry of foreign workers or drones into a nest (Free, 1958) could also lead to between-colony transmission. Given the well-documented phenomenon of parasite-induced manipulations of host behaviour mentioned above, such drifting among colonies may perhaps be in the genuine interest of the parasite and not reflect an 'erroneous' behaviour on the part of the host. Indeed, in an experiment the workers from honey bee colonies infected by *V jacobsoni* were more likely to drift to other colonies than those from uninfested nests (Sakofski, 1990). This transfer occurs mainly in late summer. However, horizontal transmission among colonies in a population could be achieved in still other ways. In a recent study, Durrer and Schmid-Hempel (1994) demonstrated that the trypanosome *C bombi* can be transmitted between workers within and between different species of bumble bees through the shared use of flowers. Hence, infected workers seem to deposit infective cells that are later picked up by uninfected workers which happen to visit the same flower. Similar inferences might be drawn from the case of the bacterium *Spiroplasma* picked up by honey bee foragers in the spring (Clark, 1977), although it is not known precisely where the parasite is contracted in this case. This transmission pathway has several ramifications for the relationship between plants and their pollinators. In the present context, the fact that between-colony transmission is established by foraging activity and the common use of food resources, also has implications for the kind of parasites that food specialists among social insects might be able to sustain.

The problem of within- and between-colony transmission has some bearing on social organisation and the division of labour in social insect societies. Imagine a species with a strict division of labor such that only certain morphological and/or temporal castes attend a set of tasks with little overlap. This extreme system is found in no social insect, but cases like the leaf-cutting ants, *Atta,* with their impressive array of different worker morphologies, or *Pheidole* and *Apis* with pronounced age-dependent polyethisms may come close (Wilson, 1971; Hölldobler and Wilson, 1990). In these societies, not only will work be rather strictly partitioned, but also the frequency of contacts among individuals of different castes is likely to be more structured than in a society where division of labour is more diffuse. Moreover, the highly sophisticated systems of division of labour are often accompanied by a corresponding spatial separation of the tasks (*eg,* Seeley, 1982) which adds to the within-colony structure of possible contacts among individuals. To the extent that contacts also determine parasite transfer (as in directly transmitted pathogens such as microsporidia or fungi; Wang and Moeller, 1970; Kramm *et al,* 1982), or when certain groups of colony members must be infected (*eg,* last instar larvae; Jouvenaz *et al,* 1981), the routes of parasite transmission depend on colony organisation in important ways.

Using the bumble bee, *B terrestris* and its intestinal parasite *C bombi,* Schmid-Hempel and Schmid-Hempel (1993) tested the hypothesis that transmission routes may depend on the age-dependent polyethism typical for social insects. In particular, horizontal transmission of this parasite to other colonies may be accomplished by the foragers (the older workers), for example, *via* flowers (Durrer and Schmid-Hempel, 1994), while within-colony transmission is possible by those workers that stay inside the nest, *ie* by the younger workers. The results suggested variation among colonies in their propensity to transmit the parasite either by young or old workers but could not directly confirm the hypothesis (Schmid-Hempel and Schmid-Hempel, 1993). Nevertheless, these findings lend at least some credibility to the idea that the social organisation may affect parasite transmission.

In addition to the effects of multiple matings discussed above, social organisation may be affected by parasitism. Some knowledge comes from scattered findings of how parasite transmission within colony occurs. For example, worker honey bees not only spread American foulbrood (a larval disease) among each other but also get it from the queen when attending her (Bitner *et al,* 1972). Acute bee paralysis virus (ABPV) is presumably transmitted *via* trophallaxis (Bailey and Gibbs, 1964), and many viruses perhaps in additional ways (Chastel *et al*, 1990). Grooming is involved in the transmission of a fungal parasite in termites (Kramm *et al*, 1982). Queen and brood attendance, and allogrooming, therefore gain additional significance in the light of infection risks. In particular, workers may infect their (single) queen and thus doom the entire colony. Therefore, if novel infections are primarily brought into the colony by the foraging or guarding workers, then the pattern observed in social insects, namely that the young workers attend the queen, would be advantageous, as the probability that a worker carries an infection should generally increase with age (Schmid-Hempel and Schmid-Hempel, 1993). Whether age-dependent polyethism has evolved mainly for such reasons or because of its ergonomic advantages given the high forager mortality rates (Jeanne, 1986) could be investigated further. On the other hand, direct effects of parasitic infection on division of labour have been found. For instance, infection by *Nosema apis* in the honey bee is associated with an earlier start of the foraging career of the affected workers (Wang and Moeller, 1970) which thus shifts the entire work profile of the colony. Moreover, certain parasites are more specific in preferentially attacking certain age groups of hosts (Kraus *et al*, 1986). This should give the ergonomics of colony demography (*cf*, Oster and Wilson, 1978) an additional dimension. For the time being, a lot of this discussion must remain speculative but it is certainly an aspect worthy of further attention.

EPIDEMIOLOGY

Instead of focusing on single colonies in all detail, one could adopt a macroscopic view of host–parasite interactions in the sense that colonies assume the role of 'individuals' in epidemiological theory. Colonies, of course, are not biological individuals but a colony of individuals. Consequently, the macroscopic properties of colonies vary considerably among species, as there are different colony sizes, structures, degrees of polyandry, polygyny and so forth. Furthermore, we find semelparous annual species such as in bumble bees and iteroparous, perennial species such as in ants. In general, within-host processes are important for the dynamics of host and parasite (*eg*, Antia *et al*, 1994), and so the actual colony structure and the fact that colonies consist of individuals will have to be accounted for in any comprehensive framework. However, for the time being these complications will be put aside and the colony as a whole is assumed to have the model's properties.

As an example, the case of infectious diseases and the well-known SIR-type of model is used (*eg*, Anderson and May, 1979). In this theory hosts are assumed to be susceptible (*ie* not yet infected but available to the parasite), infected, or recovered and immune. The dynamics of the parasite are then considered against this background in a large host population that is assumed not to be regulated in numbers by the parasites. Hence, for this purpose parasites are assumed to have small effects on host mortality, *ie* on the mortality rate of colonies as a whole. The fitness of the parasite is then given by its net reproductive rate, R_0, which describes the number of secondary infections generated per infected host (colony). The parasite spreads if $R_0 > 1$. A characteristic result of epidemiological dynamics is that

$$R_0 = \frac{\beta . N}{a + b + v} \qquad [1]$$

where N = the number of hosts in the population, β = the transmission rate to new hosts, a = the parasite-induced mortality rate of hosts, b = the background host mortality rate, and v = the recovery rate from parasitic infection (Anderson and May, 1991). This equation describes the reproductive rate of parasites in a non-equilibrium situation, *ie* during the build up of an epidemic (epizootic) infection.

How does this equation apply to social insects? With the macroscopic view the unit of interest is the colony as a whole, N refers to the number of colonies in a population, while β is the rate of parasite transmission between colonies (*ie* the horizontal transmission component). The background mortality rate, b, of established colonies is typically small (this is of course not true for incipient colonies). But also the values of a and v should typically be small for social insect colonies. The latter quantity, *ie* the rate of recovery from infection, is closely related to immunity and clearance of infection in individual hosts. Insects are capable of mounting immune defences and recovering (Gupta, 1986). In colonies of social insects, which in this view count as the 'individual', infections can probably persist for extended periods of time, as workers could constantly become either reinfected or the newly emerging workers contract the disease which is thus sustained within the nest. On the other hand, hygienic behaviour, such as removal of dead individuals (Robinson and Page, 1988) or removing brood, as documented for honey bees infected by *Bacillus larvae* (Rothenbuhler, 1964a), would help to eliminate the infection and lead to recovery of the colony. Swarming also could lead to the elimination of a parasite, as implicated for tracheal mites in honey bees (Royce *et al*, 1991).

Barring these uncertainties about the frequency and effectiveness of infection elimination in entire colonies, evaluating equation [1] with values for the parameters as discussed above would result in a high value for R_0, depending of course on N and β. This means that at the beginning of an epidemic, where parasites can realise their full potential of R_0, the disease should rapidly spread. Therefore, in principle, social insects should be quite prone to such invasions. However, if rates of recovery and recruitment of new colonies into the population are low (colonies being long-lived), which seems likely for social insects, then the epidemic will soon die out, leaving a proportion of colonies infected. In this equilibrium state, following the epidemic build-up, each infected colony will produce on average one secondary infection, therefore standard theory predicts that $R_0 \bullet x^* \approx 1$, where x^* the equilibrium proportion of susceptible (uninfected) colonies in the population. Since R_0 is large, x^* must be small, hence, virtually all colonies are left infected once the epidemic has ground to a halt due to the lack of newly available host colonies.

It is hardly known whether such epidemics occur often, with the exception of economically interesting cases, such as *Varroa* mites in honey bees which have rapidly spread throughout Europe. The lack of more reports, which after all would describe quite spectacular cases of infestation of colonies, suggests that epidemics are perhaps not often observed. Perhaps this relates to low values of β or low values of N in many cases. As already stated, the assumptions of the standard epidemiological models may not be met in many cases. In particular, within-colony dynamics could be very important and lead to different outcomes. Nevertheless, the considerations of epidemiology should lead to new insights about the evolution and maintenance of parasites in populations of social insects. These and other questions about parasitism in social insects have only just begun to be addressed.

ACKNOWLEDGMENTS

I thank R Schmid-Hempel for discussions of these issues and for help during many experiments and field work. Comments by an anonymous reviewer improved many pages of an earlier version of the manuscript. Financial support came from grants of the Swiss National Science Foundation (No 31-32193 91) and the Swiss Priority Programme 'Environment' (No 5001- 035217).

Résumé — Parasites et insectes sociaux. Bien que les parasites soient omniprésents, ils ont été jusqu'à présent peu étudiés chez les insectes sociaux, à l'exception du parasitisme social et de quelques espèces hôtes ayant une importance commerciale. Tous les grands groupes de parasites utilisent les insectes sociaux comme hôte : virus, bactéries, champignons, protozoaires, helminthes ainsi que des parasitoïdes. Bien que tous les stades soient attaqués, il semble qu'il y ait peu de parasites d'œufs (par exemple quelques virus), il y a en revanche une multitude de parasites des stades larvaires et adulte. Diverses caractéristiques des insectes sociaux peuvent être en relation avec le parasitisme. Par exemple, les accouplements multiples (polyandrie) accroissent comparativement la variabilité génétique des ouvrières au sein d'une colonie et sont ainsi susceptibles de diminuer la transmission des parasites infectieux entre les ouvrières. L'organisation sociale et la division du travail déterminent les interactions entre les membres de la colonie et devraient donc influencer les voies de transmission des parasites dans et entre les colonies. Par exemple, la transmission horizontale entre colonies pourrait être liée à l'activité des butineuses qui disséminent les parasites ou en rapportent de nouveaux dans la colonie. Finalement la théorie de l'épidémiologie moyenne prédit que la biologie des insectes sociaux peut être favorable à une épidémie, bien que celle-ci puisse rapidement disparaître. Des études plus détaillées sur le parasitisme social sont nécessaires et semblent prometteuses pour expliquer des faits de la biologie des insectes sociaux qui jusqu'à présent semblent sans rapport les uns avec les autres.

insectes sociaux / parasite / polyandrie / division du travail / épidémiologie

Zusammenfassung — Parasiten und soziale Insekten. Parasiten sind allgegenwärtig und haben oft subtile Wirkungen auf ihre Wirte. Parasiten sozialer Insekten sind bis heute nicht gut untersucht worden, mit der Ausnahme der Sozialparasiten, und derjenigen kommerziell wichtiger oder schädlicher Arten. Parasiten sind in allen wichtigen Gruppen zu finden und umfassen Viren, Bakterien, Pilze, Protozoen, verschiedene Helminthen und Parasitoiden. Sie attackieren alle Stadien des Wirtes, doch sind bemerkenswert wenige Eiparasiten (zB einige Viren) bekannt. Dagegen gibt es eine Vielzahl von Parasiten der Larven und Adulten. Verschiedene Charakteristika von sozialen Insekten könnten im Zusammenhang mit Parasitismus stehen. Mehrfachpaarung durch die Königin (Polyandrie), zum Beispiel, erhöht vergleichsweise die genetische Variabilität unter den Arbeiterinnen einer Kolonie und würde dadurch eine reduzierte Transmission von Parasiten innerhalb der Kolonie zur Folge haben. Auch die Sozialorganisation und Arbeitsteilung kann durch Parasiten beeinflusst sein. So wird zum Beispiel die horizontale Transmission zu anderen Kolonien in der Population durch die Sammeltätigkeit der Arbeiterinnen beeinflußt, welche Parasiten verbreiten oder neu in die Kolonie eintragen. Schließlich legt die Standardtheorie der Epidemiologie den Schluss nahe, daß soziale Insekten im Prinzip günstige Bedingungen für das Entstehen einer Epidemie bieten, diese aber wahrscheinlich nicht lange aufrechterhalten werden kann. Mehr und detaillierte Studien von Parasiten sozialer Insekten sind nötig. Sie bergen die Hoffnung, daß vorher schein-

bar zusammenhanglose Aspekte neu verstanden werden können.

Soziale Insekten / Parasite / Polyandrie / Arbeitsteilung / Epidemiologie

REFERENCES

Alexander RD (1974) The evolution of social behaviour. *Annu Rev Ecol Syst* 5, 325-383

Allen MF, Ball BV, White, RF, Antoniw JF (1986) The detection of Acute Paralysis Virus in *Varroa jacobsoni* by the use of a simple indirect ELISA. *J Apic Res* 25, 100-105

Anderson D, Giacon H (1992) Reduced pollen collection by honey bee (Hymenoptera: Apidae) colonies infected with *Nosema apis* and sacbrood virus. *J Econ Entomol* 85, 47-51

Anderson RM, May RM (1979) Population biology of infectious diseases. I. *Nature (Lond)* 280, 361-367

Anderson RM, May RM (1981) The population dynamics of microparasites and their invertebrate hosts. *Philos Trans R Soc London, B* 291, 451-524

Anderson RM, May RM (1991) *Infectious Diseases of Humans.* Oxford University Press, Oxford, UK

Andersson M (1994) *Sexual Selection.* Princeton Univesity Press, Princeton, NJ, USA

Antia R, Levin BR, May RM (1994) Within-host population dynamics and the evolution and maintenance of microparasite virulence. *Am Nat* 144, 457-472

Bailey L, Ball BV (1991) *Honey Bee Pathology* (2nd ed). Academic Press, London, UK

Bailey L, Ball BV, Perry JN (1981) The prevalence of viruses of honey bees in Britain. *Ann Appl Biol* 97, 109-118

Bailey L, Gibbs AJ (1964) Acute infection of bees with paralysis virus. *J Insect Pathol* 6, 395-407

Ball BV (1985) Acute Paralysis Virus isolates from honeybee colonies infested with *Varroa jacobsoni. J Apic Res* 24, 115-119

Ball BV (1989) *Varroa jacobsoni* as a virus vector. *In: Proceedings of a Meeting of the EC-Experts' Group, Udine* (R Cavalloro, ed), Commission of the European Communities, Brussels, Belgium, 241-244

Ball BV, Allen MF (1988) The prevalence of pathogens in honeybee (*Apis mellifera*) colonies infested by with the mite *Varroa jacobsoni. Ann Appl Biol* 113, 237-244

Becker N, Angulo J (1981) On estimating contagiousness of a disease transmitted from person to person. *Math Biosci* 54, 137-154

Bedding RA (1985) Nematode parasites of Hymenoptera. *In: Plant and Insect Nematodes* (WR Nickle, ed), Marcel Dekker, New York, USA, 755-795

Bitner RA, Wilson WT, Hitchcock JD (1972) Passage of *Bacillus* larvae spores from adult honeybees to attendant workers (*Apis mellifera*). *Ann Entomol Soc Am* 65, 899-901

Boomsma JJ, Grafen A (1991) Colony-level sex ratio selection in the eusocial Hymenoptera. *J Evol Biol* 3, 383-407

Broome JR, Sikorowski PP, Norment BR (1976) A mechanism of pathenogenicity of *Beauveria bassiana* on larvae of the red imported fire ant, *Solenopsis richteri. J Invertebr Pathol* 28, 87-91

Brown CR, Brown MB (1986) Ectoparasitism as a cost of coloniality in cliff swallows. *Ecology* 67, 1206-1218

Chastel C, Robaux P, Le Goff F (1990) New virus from honey bee colonies. Is *Varroa* a vector or does it amplify viruses? *In: Proceedings of the International Symposium on Recent Research on Bee Pathology* (W Ritter, ed), International Federation of Beekepers Association, Gent, Belgium, 150-154

Clark TB (1977) *Spiroplasma* as a new pathogen in the honeybees. *J Invertebr Pathol* 29, 112-113

Cole BJ (1983) Multiple mating and the evolution of social behavior in the Hymenoptera. *Behav Ecol Sociobiol* 12, 191-291

Crawley WC, Baylis HA (1921) *Mermis* parasitic on ants of the genus *Lasius. J R Microsc Soc,* 353-364

Crosland MWJ (1988) Effect of a gregarine parasite on the color of Myrmecia pilulosa (Hymenoptera: Formicidae). *Ann Entomol Soc Am* 81, 481-484

Crozier RH, Consul PC (1976) Conditions for genetic polymorphism in social hymenoptera under selection at the colony level. *Theor Popul Biol* 10, 1-9

Crozier RH, Page RE (1985) On being the right size: male contributions and multiple mating in social Hymenoptera. *Behav Ecol Sociobiol* 18, 105-116

Davies CR, Ayres JM, Dye C, Deane LM (1991) Malaria infection rate of Amazonian primates increases with body weight and group size. *Funct Ecol* 5, 655-662

Davis LR Jr, Jouvenaz DP (1990) *Obeza floridana,* a parasitoid of *Camponotus abdominalis floridanus* from Florida (Hymenoptera: Ecuharitidae, Formicidae). *Fl Entomol* 73, 335-337

Dobson A, Crawley M (1994) Pathogens and the structure of plant communities. *Trends Ecol Evol* 9, 393-398

Dobson AP (1988) The population dynamics of parasite-induced changes in host behavior. *Q Rev Biol* 63, 139-165

Dobson AP, Hudson PJ (1986) Parasites, diseases and the structure of ecological communities. *Trends Ecol Evol* 1, 11-14

Doull KM, Cellier KM (1961) A survey of the incidence of *Nosema* disease (*Nosema apis* Zander) in honey bees in South Australia. *J Insect Pathol* 3, 280-288

Durrer S, Schmid-Hempel P (1994) Shared use of flowers leads to horizontal pathogen transmission. *Proc R Soc London, B* 258, 299-302

Eickwort GC (1994) Evolution and life-history patterns of mites associated with bees. *In: Mites* (MA Houck, ed), Chapman and Hall, New York, USA, 218-251

Fisher RM (1988) Observations on the behaviours of three Euopean cuckoo bumble bee species (*Psithyrus*). *Insectes Soc* 35, 341-354

Free JB (1958) The drifting of honey bees. *J Agric Sci* 51, 294-306

Freeland WJ (1976) Pathogens and the evolution of primate sociality. *Biotropica* 8, 12-24

Gupta AP (ed) (1986) *Hemocytic and Humoral Immunity in Arthropods.* John Wiley & Sons, New York, USA

Hamilton WD (1964) The genetical evolution of social behavior. *J Theor Biol* 7, 1-52

Hamilton WD (1980) Sex *vs* non-sex *vs* parasite. *Oikos* 35, 282-290

Hamilton WD (1987) Kinship, recognition, disease, and intelligence: constraints of social evolution. *In: Animal Societies: Theory and Facts* (Y Ito, JL Brown, J Kikkawa, eds), Japanese Scientific Society Press, Tokyo, Japan, 81-102

Hamilton WD, Axelrod A, Tanese R (1990) Sexual reproduction as an adaptation to resist parasites (a review). *Proc Natl Acad Sci USA* 87, 3566-3573

Hohorst W, Graefe G (1961) Ameisen - obligate Zwischenwirte des Lanzettegels *(Dicrocoelium dendriticum).* *Naturwissenschaften* 48, 229-230

Hölldobler B, Wilson EO (1990) *The Ants.* Springer, Berlin, Germany

Jeanne RL (1986) The evolution of the organization of work in social insects. *Monitore Zool Ital (NS)* 20, 119-133

Jouvenaz DP (1983) Natural enemies of fire ants. *Fl Entomol* 66, 111-121

Jouvenaz DP, Ellis EA (1986) *Vairimorpha invictae* nsp (Microspora: Microsporida), a parasite of the red imported fire ant, *Solenopsis invicta* Buren (Hymenoptera: Formicidae). *J Protozool* 33, 457-461

Jouvenaz DP, Lofgren CS, Allen GE (1981) Transmission and infectivity of spores of *Burenella dimorpha* (Microsporidae, Burenellidae). *J Invertebr Pathol* 37, 265-268

Kathirithamby J, Johnston JS (1992) Stylopization of *Solenopsis invicta* (Hymenoptera: Formicidae) by *Caenochloax fenyesi* (Strepsiptera: Myrmecolacidae) in Texas. *Ann Entomol Soc Am* 85, 293-297

Keller L (ed) (1993) *Queen Number and Sociality in Insects.* Oxford University Press, Oxford, UK

Keymer AE, Read AF (1991) Behavioural ecology: the impact of parasitism. *In: Parasite–Host Associations: Coexistence or Conflict?* (CA Toft, A Aeschlimann, L Bolis, eds), Oxford University Press, Oxford, UK, 37-61

Koch W, Ritter W (1989) Examination of artificially infested brood with *Varroa* mites for secondary infections. *In: Proceedings of a Meeting of the EC-Experts' Group, Udine* (R Cavalloro, ed), Commission of the European Communities, Brussels, Belgium, 245-251

Koeniger G (1991) Diversity in *Apis* mating systems. *In: Diversity in the Genus Apis* (DR Smith, ed), Westview Press, Boulder CO, USA, 265

Kramm KR, West DF, Rockenbach PG (1982) Termite pathogens: transfer of the entomophagous *Metarhizium anisoplia* between *Reticulitermes* sp termites. *J Invertebr Pathol* 40, 1-6

Kraus B, Koeniger N, Fuchs S (1986) Unterscheidung zwischen Bienen verschiedenen Alters durch *Varroa jacobsoni* Oud und Bevorzugung von Ammenbienen im Sommervolk. *Apidologie* 17, 257-266

Kulincevic JM (1986) Breeding accomplishments with honey bees. *In: Bee Genetics and Breeding* (TE Rinderer, ed), Academic Press, Orlando, FL, USA, 391-414

Ladle RJ (1992) Parasites and sex: catching the red queen. *Trends Ecol Evol* 7, 405-408

Laidlaw HHJ, Page RE (1984) Polyandry in honeybees (*Apis mellifera*): sperm utilization and intracolony genetic relationships. *Genetics* 108, 985-997

Lin N (1964) Increased parasite pressure as a major factor in the evolution of social behavior in halictine bees. *Insectes Soc* 11, 187-192

Loos-Frank B (1978) Zum Verhalten von Ameisen der Gattung *Formica* (Hymenoptera; Formicidae) gegenüber Schleimballen des Kleinen Leberegels *Dicrocoelium dendriticum* (Digenea: Dicrocoeliidae) und über infektionsbedingte Veränderungen ihrer Hämolymphe. *Entomol Germ* 4, 12-23

Loos-Frank B, Zimmermann G (1976) Über eine dem *Dicrocoelium*-Befall analoge Verhaltensänderung bei Ameisen der Gattung *Formica* durch einen Pilz der Gattung *Entomophthora. Z Parasitenkd* 49, 281-289

Lundberg H, Svensson BG (1975) Studies on the behaviour of *Bombus* Latr species (Hymenoptera: Apidae) parasitized by *Sphaerularia bombi* Dufour (Nematoda) in an alpine area. *Norw J Entomol* 22, 129-134

Minchella DJ, Loverde PT (1981) A cost of increased early reproductive effort in the snail *Biomphalaria glabrata. Am Nat* 118, 876-881

Moore J (1983) Responses of an avian predator and its isopod prey to an acanthocephalan parasite. *Ecology* 64, 1000-1015

Moore J (1984) Altered behavioral responses in intermediate hosts – an acantocephalan parasite strategy. *Am Nat* 123, 572-577

Nonacs P (1988) Queen number in colonies of social Hymenoptera. *Evolution* 42, 566-580

Ogloblin AA (1939) The Strepsiptera parasites of ants. *Verhandlungen des VII. Internationalen Kongresses für Entomologie* 2, 1277-1285

Oster GF, Wilson EO (1978) *Caste and Ecology in the Social Insects*. Princeton University Press, Princeton, NJ, USA

Otis GW, Scott-Dupree CD (1992) Effects of *Acarapis woodi* on overwintered colonies of honey bees (Hymenoptera: Apidae) in New York. *J Econ Entomol* 85, 40-46

Page RE (1980) The evolution of multiple mating behavior by honey bee queens (*Apis mellifera* L). *Genetics* 96, 263-273

Page RE, Metcalf RA (1982) Multiple mating, sperm utilization, and social evolution. *Am Nat* 119, 263-281

Pamilo P (1981) Genetic organization of *Formica sanguinea* populations. *Behav Ecol Sociobiol* 9, 45-50

Pamilo P (1991) Evolution of colony characteristics in social insects. 2. Number of reproductive individuals. *Am Nat* 137, 83-107

Pesquero MA, Campiolo S, Fowler HG (1993) Phorids (Diptera: Phoridae) associated with mating swarms of *Solenopsis saevissima* (Hymenoptera, Formicidae). *Fl Entomol* 76, 179-181

Poulin R, Fitzgerald GJ (1989) Shoaling as an anti-ectoparasite mechanism in sticklebacks. *Behav Ecol Sociobiol* 24, 251-255

Price PW, Westoby M, Rice B *et al* (1986) Parasite mediation in ecological interactions. *Annu Rev Ecol Syst* 17, 487-505

Price PW, Westoby M, Rice B (1988) Parasite-mediated competition: some predictions and tests. *Am Nat* 13, 544-555

Queller DC (1993) Worker control of sex ratios and selection for extreme multiple mating by queens. *Am Nat* 142, 346-351

Queller DC, Strassmann JE (1988) Reproductive success and group nesting in the paper wasp, *Polistes annularis*. *In: Reproductive Success* (TH Clutton-Brock, ed), The University of Chicago Press, Chicago, USA, 76-98

Rinderer TE, Collins AM, Brown MA (1983) Heritabilities and correlations of the honey bee: response to *Nosema apis*, longevity, and alarm response to isopentyl acetate. *Apidologie* 14, 79-85

Robinson GE (1992) Regulation of division of labor in insect societies. *Annu Rev Entomol* 37, 637-665

Robinson GE, Page RE (1988) Genetic determination of guarding and undertaking in honey-bee colonies. *Nature (Lond)* 333, 356-358

Rothenbuhler WC (1964a) Behavior genetics of nest cleaning honeybees. IV. Responses of F1 and back-cross generations to disease killed brood. *Am Zool* 4, 111-123

Rothenbuhler WC (1964b) Behavior genetics of nest cleaning in honey bees. I. Response of four inbred lines to disease-killed brood. *Anim Behav* 112, 578-583

Roubik DW (1989) *Ecology and Natural History of Tropical Bees*. Cambridge University Press, Cambridge, UK

Royce LA, Rossignol PA, Burgett DM, Stringer BA (1991) Reduction of tracheal mite parasitism of honey bees by swarming. *Philos Trans R Soc London, Ser B* 331, 123-129

Rupp L (1987) The genus *Volucella* (Diptera: Syrphidae) as commensals and parasites in bumblebee and wasp nests. *In: Chemistry and Biology of Social Insects* (J Ederand, DH Rembold, eds), Peperny Verlag, Munich, Germany, 642-643

Sakofski F (1990) Quantitative investigations on transfer of *Varroa jacobsoni*. *In: Proceedings of the International Symposium on Recent Research on Bee Pathology* (W Ritter, ed), International Federation of Beekepers Association, Gent, Belgium, 70-72

Schabel HG (1982) Phoretic mites as carriers of entomopathogenic fungi. *J Invertebr Pathol* 39, 410-412

Schmid-Hempel P (1994) Infection and colony variability in social insects. *Philos Trans R Soc London, Ser B* 346, 313-321

Schmid-Hempel P, Koella JC (1994) Variability and its implications for host–parasite interactions. *Parasitol Today* 10, 98-102

Schmid-Hempel P, Müller C, Schmid-Hempel R, Shykoff JA (1990) Frequency and ecological correlates of parasitism by conopid flies (Conopidae, Diptera) in populations of bumblebees. *Insectes Soc* 37, 14-30

Schmid-Hempel P, Schmid-Hempel R (1993) Transmission of a pathogen in *Bombus terrestris*, with a note on division of labour in social insects. *Behav Ecol Sociobiol* 33, 319-327

Schneider G, Hohorst W (1971) Wanderungen der Metacercarien des Lanzett-Egels in Ameisen. *Naturwissenschaften* 58, 327-328

Schwarz MP (1986) Persistent multi-female nests in an Australian allodapine bee, *Exoneura bicolor* (Hymenoptera: Anthophoridae). *Insectes Soc* 33, 258-277

Seeley TD (1982) Adaptive significance of the age polyethism schedule in honeybee colonies. *Behav Ecol Sociobiol* 11, 287-293

Seger J (1983) Partial bivoltinism may cause alternating sex-ratio biases that favour eusociality. *Nature (Lond)* 301, 59-62

Sherman PW, Seeley TD, Reeve HK (1988) Parasites, pathogens, and polyandry in social Hymenoptera. *Am Nat* 131, 602-610

Shykoff JA (1991) On genetic diversity and parasite transmission in socially structured populations. PhD Thesis Phil-Naturw Fakultät, University of Basel, Basel, Switzerland

Shykoff JA, Schmid-Hempel P (1991a) Genetic relatedness and eusociality: parasite-mediated selection on the genetic composition of groups. *Behav Ecol Sociobiol* 28, 371-376

Shykoff JA, Schmid-Hempel P (1991b) Parasites and the advantage of genetic variability within social insect colonies. *Proc R Soc London, Ser B* 243, 55-58

Skou JP, Holm SN, Haas H (1963) Preliminary investigations on diseases in bumble bees (*Bombus* Latr). *Kgl Vet-og Lanbohojsk Aarsskr*, 27-41

Starr CK (1985) Enabling mechanisms in the origin of sociality in the Hymenoptera – the sting is the thing. *Ann Entomol Soc Am* 78, 836-840

Strand MR (1986) The physiological interactions of parasitoids with their hosts and their influence on reproductive strategies. *In: Insect Parasitoids* (J Waage, D Greathead, eds), Academic Press, London, UK, 97-136

Stuart RJ, Alloway TM (1988) Aberrant yellow ants: North American *Leptothorax* species as intermediate hosts of cestodes. *In: Advances in Myrmecology* (JC Trager, ed), EJ Brill, Leiden, The Netherlands, 537-545

Tanada Y, Kaya HK (1993) *Insect Pathology.* Academic Press, San Diego, CA, USA

Thompson JN, Burdon JJ (1992) Gene-for-gene coevolution between plants and parasites. *Nature (Lond)* 360, 121-125

Tooby J (1982) Pathogens, polymorphism, and the evolution of sex. *J Theor Biol* 97, 557-576

Wakelin D (1985) Genetic control of immunity to helminth infections. *Parasitol Today* 1, 17-23

Wang DI, Moeller FE (1970) The division of labor and queen attendance behavior of *Nosema*-infected worker honey bees. *J Econ Entomol* 63, 1539-1541

Ward PS (1983) Genetic relatedness and colony organization in a species complex of Ponerine ants. 1. Phenotypic and genotypic composition of colonies. *Behav Ecol Sociobiol* 12, 285-299

West-Eberhard MJ (1975) The evolution of social behavior by kin selection. *Q Rev Biol* 50, 1-33

Wheeler GC, Wheeler EW (1924) A new species of *Schizaspidia (Eucharidae)*, with notes on a eulophid ant parasite. *Psyche* 31, 49-56

Wilson EO (1971) *The Insect Societies.* Harvard University Press, Cambridge, MA, USA

Woyciechowski M, Krol E, Figurny E, Stachowicz M, Tracz M (1994) Genetic diversity of workers and infection by the parasite *Nosema apis* in honey bee colonies (*Apis mellifera*). *In: 12th Congress of the International Union for the Study of Social Insects* (A Lenoir, G Arnold, M Lepage, eds), Université Paris-Nord, Paris, France, 347