How parasites can promote the expression of social behaviour in their hosts

SEAN O'DONNELL

Department of Psychology, Box 351525, University of Washington, Seattle, WA 98195, USA

SUMMARY

Recent theory on the role of parasites in the evolution of social behaviour has emphasized the costs of social behaviour to hosts. However, parasites whose primary effect on host fitness is to reduce fecundity can favour the evolutionary origin or maintenance of social behaviour, including eusociality, under certain conditions. If the parasites are not readily transmitted among members of social groups, then other group members will not be selected to reject infected individuals as social partners, nor will adaptive suicide or avoidance of grouping be selectively favoured for infected individuals. Rather, total or partial parasitic castration may promote the expression of helping behaviour by infected individuals. Some parasites may therefore act to increase variance in direct reproductive value within populations or societies, and to promote reproductive division of labour. The necessary conditions of reduced host fecundity and low within-group transmission are met in some insect–parasite systems, and could occur in other host–parasite systems as well.

1. INTRODUCTION

Social behaviour is often assumed to entail costs associated with increased parasite loads (Alexander 1974; Möller *et al.* 1993; Schmid-Hempel & Schmid-Hempel 1993). Many types of parasites are easily transmitted within social groups of hosts, and host groups may be more attractive to some types of volant parasites (Davies *et al.* 1991). Therefore, literature reviews and theoretical models addressing the role of parasites in social evolution have focused on how parasites can disrupt social systems over evolutionary time, or on how social systems can be modified by selection to counteract the negative effects of parasite infections (Freeland 1976; Hamilton 1987; Sherman *et al.* 1988; Shykoff & Schmid-Hempel 1991*a*; but see Mooring & Hart 1992). Here I argue that parasites can favour the expression of social behaviour in their hosts under certain conditions, and that parasites may play roles in the origin and maintenance of eusociality.

Parasites can be defined as symbiotic organisms that have a negative effect on the fitness of their hosts. Host fitness comprises both survival and fecundity, and the effects of parasites on the latter component of fitness are receiving increasing attention from evolutionary biologists (Herre 1993; Hurd 1993). Many parasites are known to either fully or partially reduce the fecundity of their hosts, a pattern referred to as parasitic castration (Baudoin 1975). Given a parasite that induces sterility or reduced fecundity (but not severely reduced longevity) in infected hosts, parasite infections of some individuals could increase variance in reproductive success among potential social partners or within extant social groups (e.g. colonies) of hosts. Reduced fecundity favours the expression of helping behaviour in infected group members. Similar effects

would be seen in potentially solitary individuals (e.g. reproductive females ready to initiate new colonies) that are deciding whether to found nests of their own or to join previously founded nests as subordinate helpers (Röseler 1991).

Should parasitized individuals seek or avoid grouping with conspecifics, and with close relatives in particular? How should other group members—or potential social partners—respond to parasitized individuals? The answers to these questions depend, in part, on the risks of transmission of the parasitic infection within groups of hosts (Herre 1993). In the context of social evolution it is especially interesting to consider parasites that are not transmitted well within groups. For example, certain parasites attack host individuals when they are away from their nests (e.g. during foraging trips: Alford 1975; Durrer & Schmid-Hempel 1994). If the risk of parasite transmission within groups that include infected members is not higher than the risk to the population as a whole, then grouping is not disfavoured either by infected or by uninfected individuals (Shapiro 1975; McAllister *et al.* 1990).

If grouping is not disfavoured, then parasites can act as a mechanism of reproductive caste determination by reducing host fecundity. Parasitically castrated individuals that join or remain in groups effectively become sterile workers. Furthermore, once a subset of interacting individuals becomes infected, reproductive division of labour is automatically favoured within the group; the infected individuals should specialize on worker-like (helping) behaviour, and uninfected individuals should focus on queen-like (reproductive) behaviour (West-Eberhard 1981).

Parasitic castration can play several roles in the process of social evolution. In presocial species,

castrators may shape the size of social groups by increasing the frequency of joining among foundresses of new nests. Increased rates of group formation provide greater opportunity for selection to modify the expression of social behaviour. In primitively eusocial species, conflicts of interest over reproduction may be reduced by parasitic castrators that infect workers. Reduced conflict may, in turn, enhance colony efficiency and productivity (Shykoff & Schmid-Hempel 1991*b*).

2. REPRODUCTIVE VALUE AND DIVISION OF LABOUR

Reproductive division of labour in a social system requires that group members (often females) can assess their reproductive capacity relative to group mates, and pursue different reproductive strategies appropriate to their relative abilities (West-Eberhard 1981; Jeanne 1991). Parasites alter host behaviour by a diversity of mechanisms (Thompson & Kavaliers 1994), and the physiological pathways by which parasitic castration is translated into changes in host behaviour are poorly known (Hurd 1993). Some authors have suggested that parasitic castrators divert energy and nutrients away from host reproduction into parasite growth and reproduction (Strambi *et al.* 1982; Hurd 1993). In this sense, the behavioural physiology of parasitic castration may resemble intrinsic (non-parasitic) caste determination mechanisms in social insects, which frequently involve nutritional differences among individuals (Wheeler 1986; Hunt 1991). In other words, the mechanisms by which parasitic castration translates into helping or worker-like behaviour in hosts may already be in place before the host-parasite relationship arises.

West-Eberhard (1981) and Jeanne (1991) have suggested that behavioural differentiation among social insect reproductive castes (i.e. queens and workers) is driven by individual differences in reproductive value. In general, when indirect reproductive value (RV_i) exceeds direct reproductive value (RV_d), helping behaviour is favoured over attempting to reproduce. Parasites may act as a mechanism favouring reproductive division of labour by causing or enhancing differences in RV_d among group members (figure 1). All else being equal, infected individuals' RV_d is decreased relative to uninfected individuals' RV_d . Parasitically castrated individuals that are not killed in the course of infection may have alternative reproductive options available; in eusocial or incipiently social species, infected individuals may be able to recoup some fitness by aiding relatives' reproductive efforts, that is, they may retain some RV_i . The strength of the parasite's effect on RV_d depends on the degree to which host fecundity is lowered; in the case of total castrators, host $RV_d = 0$, and all of the host's fitness options are through helping (RV_i). The degree to which RV_i is also lowered by parasitic infection is an empirical question, and will depend in part on the pathology associated with the infection.

Reproductive division of labour caused by parasitic castrators has the added benefit of helping groups to

Figure 1. Effects of partial parasitic castrators on the expression of helping behaviour in a population of facultatively or primitively eusocial hosts. Without parasites (a), the host population exhibits variation in some measure of relative capacity to succeed in direct reproduction (e.g. nest-founding) versus indirect reproduction (e.g. joining founded nests as helpers). Here, the measure of relative reproductive capacity is the ratio of direct to indirect reproductive value, following West-Eberhard (1981). For individuals with reproductive capacity above a population-specific critical ratio, direct reproduction is favoured (open area under curve), and for individuals below the critical ratio, helping behaviour is favoured (shaded area). When parasitic castrators enter the population (b), RV_d of infected females decreases. If RV_i is retained by infected individuals, the distribution of individuals between the favoured reproductive strategies will shift, with helping behaviour favoured in a greater proportion of the parasite-infected population.

avoid infection of all members. In some cases, parasite transmission within the group (e.g. at the nest) may be especially rare; for example, when infective stages of the parasite are broadcast on plant material by foragers (Kathirithamby 1989; Durrer & Schmid-Hempel 1994) or when infection results from attacks by an adult, free-living parasite stage (Alford 1968, 1975; Schmid-Hempel 1995). The reproductives (e.g. queens) would then be unlikely to become infected, because they remain at the nest and are less exposed to sources of infection. In temperate bumble bee (*Bombus*) species, queens of early-season nesters are at low risk of

infection by insect parasitoids relative to their own workers and to late-season queens, whose active flying season overlaps the reproductive season of dipteran parasitoids (Alford 1975).

3. PARASITE TRANSMISSION WITHIN HOST GROUPS

A number of species of parasites are transmitted to adult social insects when they are away from the nest. In these host-parasite systems, transmission within host groups is probably infrequent. Transmission of microsporidian protozoans can occur via ingestion of faeces and venereally (Weiser 1985). Many eusocial Hymenoptera avoid defecating in or near their nests (although this is not the case with termites), and copulation typically occurs away from the nest as well. Conopid flies and braconid wasps oviposit directly into foraging adult hosts (Alford 1975). Female strepsipteran parasitoids produce large numbers of infective triungulin larvae, which they broadcast into the environment while protruding partially from their host's body (Kathirithamby 1989). Parasitic nematodes often infect hosts from soil or water (Wülker 1975).

Several aspects of parasite evolutionary history can restrict transmission within social groups of hosts. When the parasite uses non-social as well as social species as hosts, selection for efficient transmission within social groups may be weak. Social insects can be incidental hosts to certain parasites, which means that the parasite may not complete its life cycle (reproduce) in a given host species (Alford 1975). A related explanation for restricted transmission within colonies involves phylogenetic inertia; even parasites specific to social hosts presumably evolved from parasites of non-social species, where intra-group transmission is irrelevant. These species may not have had enough time to adapt to social hosts via efficient intra-group transmission (Dobson 1988). In addition, insects often serve as intermediate hosts for parasites. Such parasites' fitness depends on transmission to a later definitive host species, rather than on transmission within social groups of the intermediate host.

Host behavioural patterns may also play a role in preventing the spread of parasite infections within groups (Möller *et al.* 1993). Schmid-Hempel (1995) has suggested that patterns of parasite transmission within larger insect societies could be affected by division of labour. For example, if subsets of the worker force (e.g. age cohorts) interact with each other more often than they do with other colony members, then parasite transmission in colonies could be greater within than among these subsets. Genotypic diversity within social groups could also serve to limit the spread of parasites (Hamilton 1987; Sherman *et al.* 1988), with transmission more likely among close relatives (e.g. offspring of one queen in a polygynous society, or members of one patriline in a polyandrous society). Results of empirical studies addressing this hypothesis are equivocal (Schmid-Hempel & Schmid-Hempel 1993). Keller (1995) has argued that the evolution of different morphological worker castes in ants could diminish the

spread of parasites within colonies. The same case can be made for the evolution of queen/worker dimorphism; spread of parasitic castrators from workers to queens could select for divergent physiology and morphology among reproductive castes. In some eusocial species, physical contact between adult workers and queens is minimal (Akre & Reed 1983), which may limit inter-caste parasite transmission.

4. MECHANISMS OF PARASITIC CASTRATION IN INSECTS

Most studies of the effects of parasites on insect reproduction have been conducted on solitary species, but the physiological mechanisms of castration documented in non-social species can indicate the types of interactions that may occur between parasites and eusocial or incipiently social hosts. Parasites of insects often reduce host fecundity with minor or no effects on survival. Reproductive effects range from complete castration (destruction of host reproductive tissues) to minor reductions in egg production (reviewed and tabulated in Hurd 1993; Lawrence & Lanzrein 1993) and disruption of mating behaviour (Hurd 1990; Hurd & Parry 1991). Castration can occur by direct or indirect effects on the host's gonadal tissue (Baudoin 1975). Many parasites of insects regulate their hosts' physiology by altering host endocrine function; effects on juvenile hormone (JH) and ecdysteroids are especially common (Lawrence 1986). Parasites that infect the adult stage are probably most relevant to discussions of parasitic castration, although effects on reproduction that carry over from non-lethal infections earlier in life (Karbon & English-Loeb 1997) could also play a role. The importance of such infections in social insects is largely unknown.

Microsporidian protozoans infect many insect hosts; infections are often non-lethal and result in decreased host fecundity (Hurd 1993). Many microsporidians reside in specific host tissues, with the fat body (the site of egg yolk protein synthesis) a common target (Weiser 1976). Eugregarines (Protozoa, Phylum Apicomplexa) are a family of castrating parasites found in insect guts and body cavities. Some species of gregarines may be restricted to the adult stages of their hosts (Clopton & Janovy 1993), where effects on host reproduction are likely to be greatest. Gregarines often invade the fat body, where they are likely to influence nutritional status and a number of endocrine functions (Liu *et al.* 1974; Lawrence 1986). Parasitic nematodes frequently reduce fecundity of insect hosts via effects on the fat body and/or corpora allata (site of JH production), implying endocrine disruption (Wülker 1975). Longevity of strepsipteran hosts is rarely compromised, but partial or complete host castration is usually achieved, accompanied by changes in haemolymph proteins (Salt 1927, 1931; Strambi *et al.* 1982).

5. PARASITIC CASTRATORS IN INSECT SOCIETIES

The fact that many parasites reduce fecundity in solitary insect hosts implies that social behaviour is not a necessary outcome of parasitic castration. I predict

that parasitic castrators are especially likely to favour social evolution in incipiently and primitively eusocial species. In these species, many or all potentially cooperating individuals have a range of reproductive options open to them, from direct reproduction to helping (worker) behaviour, or a mix of the two. Sociality—for example, nest sharing—is facultatively expressed in many taxa, including sweat bees (Eickwort & Kukuk 1987), orchid bees (Dressler 1982), and wasps (Cowan 1991). Furthermore, overt conflict over access to direct reproduction is evident within colonies of many primitively eusocial species (bumble bees: van Honk *et al.* 1981; Owen & Plowright 1982; wasps: Gadagkar 1991). A number of parasites of adults, some or all of which may function as parasitic castrators, have been recorded in social insects and their solitary relatives (wasps: Gadagkar 1991; D. Cowan, personal communication; bees: Wcislo *et al.* 1994; Schmid-Hempel 1995; W. Wcislo, personal communication). Many of the same taxa of parasitic castrators found in well-studied, solitary insects also infect social insect hosts. Examples include Strepsiptera, parasitic wasps and flies, nematodes, and various protozoans (Durrer & Schmid-Hempel 1994; Wcislo & Cane 1996). Infection rates are variable in space and time but can be high, especially in tropical regions (Richards 1978; S. O'D., unpublished data).

Parasitic castrators of social insects do not always induce or augment helping behaviour (Schmid-Hempel & Müller 1991; Horton & Moore 1993). In some cases, it may be disadvantageous for the parasite to allow the host to participate in social activities. Insects that serve as intermediate hosts are especially likely to be behaviourally manipulated by their parasites, with behavioural changes favouring transmission to the next host (Dobson 1988). Behavioural and physiological responses by hosts vary with the species of parasite, and may depend on other factors such as parasite load and host nutritional status (Webb & Hurd 1996). For example, behavioural effects of strepsipteran parasitization on social Hymenoptera vary both among and within host species (Salt 1927, 1931).

A number of parasitic castrators do not prevent helping behaviour in their social insect hosts. *Nosema apis* is a pathogen of honey bees, with dramatic effects on worker behaviour. Behavioural development (age polyethism) is accelerated in infected individuals, which moves the workers away from opportunities for direct reproduction. Infected workers show reduced queen tending behaviour, which may contribute to low rates of queen infection (Wang & Moeller 1970). The braconid wasp, *Syntretus splendidus*, parasitizes adult queen and worker bumble bees. Ovaries degenerate in infected individuals, but this parasite apparently has little effect on worker behaviour until the late stages of infection (Alford 1968, 1975). Shykoff & Schmid-Hempel (1991*b*) showed that the trypanosome parasite *Crithidia bombi* caused reductions in reproductive potential in bumble bee (*Bombus terrestris*) workers. Infected workers had reduced ovary development, and cooperated by working for their colonies longer than non-infected workers. *Crithidia bombi* is apparently

transmitted to new hosts through overwintering gynes (future queens); therefore, negative effects on colony reproduction would be disadvantageous to this parasite (Shykoff & Schmid-Hempel 1991*b*). The authors concluded that reduced conflict over reproduction within colonies could result from worker infection.

6. CONCLUSION

There are a number of insect host–parasite systems that involve both parasitic castration of hosts and low rates of transmission within host social groups. Dobson (1988) noted that parasitic castration of hosts is generally disfavoured in parasites with direct life cycles because it leads to destabilization of host–parasite population dynamic models. However, a number of the documented or potential parasitic castrators of social insects have direct life cycles (nematodes, Strepsiptera, gregarines, and dipteran and hymenopteran parasitoids). When hosts can salvage RV_i by aiding colony (rather than personal) reproduction, host population growth rate may increase when parasites are present (figure 2), and the parasite may still gain from castrating individual hosts. Similarly, virulence (reduction in host reproductive success) is lower in parasitic nematodes of fig wasps when the parasites rely heavily on their current host individual for reproduction than when they have greater opportunities to infect the offspring of other host individuals (Herre 1993).

In order for parasitic castrators to affect reproductive division of labour, the degree and type of damage to the host must allow for the expression of normal working behaviour. This relationship does appear to occur in some insect host–parasite systems. An increased understanding of the role of parasites in

Figure 2. Effects of parasitic castrators on host population fecundity. When parasites are present at low frequency (prevalence), mean host fecundity shown by the curve can increase above the level observed without parasites (horizontal dashed line) because reproduction by host groups (colonies) is augmented by helping behaviour. This population effect will diminish—and may reverse—when parasite prevalence is high. Mean host fecundity will begin to decrease when reproductive gains due to additional helpers are compensated by population losses caused by fewer colonies being founded. Host population growth is expected to be highest at some intermediate level of parasite prevalence or virulence (severity of castration).

promoting social evolution will depend on careful attention to the prevalence and effects of parasitic castrators in natural populations of presocial and primitively eusocial species. At the individual level (within populations or colonies), infected females should be more likely to express cooperative helping behaviour. Whether the severity of the infection correlates with the degree of cooperation may depend on the specific host-parasite system under consideration. At the population level, the frequency with which helpers join new nests rather than found their own, and/or the size of founding groups, should be higher in populations where parasitic castrators are more prevalent. This prediction applies to both cooperation among nest-founders of the same generation, and to the expression of helping at the natal nest by offspring. In primitively eusocial species, overt competition over reproduction should be reduced in colonies with infected workers.

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