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REVIEW

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Sociobiology of slave-making ants

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Abstract Social parasitism is the coexistence in the same nest of two species of social insects, one of which is parasitically dependent on the other. Though parasitism in general is known to be of crucial importance in the evolution of host species, social parasites, though intriguing, are often considered as a phenomenon of marginal interest and are typically not taken into account in reviews on parasitism. Nevertheless, social parasites are rather common in social bees, wasps, and ants and therefore may offer unique model systems to study a number of fundamental problems in evolutionary biology. Here we review several aspects of the peculiar life history of slave-making ants, which is characterized by socially parasitic founding of colonies and the pillage of broods from neighboring host colonies during slave raids. In particular we focus on the evolution of slave-making habits (dulosis), communication mechanisms between slave makers and their hosts, sex-allocation ratios and reproductive conflict, and the effect of slave makers on host populations.

Keywords Dulosis · Parasitism · Reproductive tactics · Chemical communication · Coevolution

Introduction

Parasitism is currently considered to be one of the most powerful forces driving evolution. Though the term parasitism is difficult to define unambiguously (Cheng 1991; Toft 1991; Schmid-Hempel 1998), it has widely been used to describe relationships among quite different biological entities. Traditionally, parasites are viruses, prokaryotes, or eukaryotes that exploit other such organisms (Toft et al. 1991; Hamilton and Howard 1997; Schmid-Hempel 1998; Poulin and Morand 2000). Recently, however, ultraselfish genetic elements (sex-ratio-distorting cytoplasmatic genes, meiotic drivers, etc.; Majerus et al. 1996; Freeman and Herron 1998) have also been considered to "parasitize" individual genes or complete genomes. At the other end of the range of biological entities, "social parasites" parasitize complete societies.

"Social parasitism" has been defined as the coexistence in the same nest of two species of social insects, one of which is parasitically dependent on the other (Hölldobler and Wilson 1990). As an insect society can be considered as a "superorganism" (Wheeler 1928; Wilson 1971; Jaisson 1985; Hölldobler and Wilson 1990), social parasitism fits the more general definitions of parasitism (Tinaut and Ruano 1999).

Though social parasites are rather common in social bees, wasps, and especially in ants, they are widely unknown to non-specialists and are typically not taken into account in reviews on parasitism (e.g., Toft et al. 1991; Hamilton and Howard 1997; Schmid-Hempel 1998). We believe, however, that rather than being only a fascinating detail in the large range of life histories of social insects, they offer a unique model system to study a number of fundamental problems in evolutionary biology. This appears to be especially true for a particular category of social parasites, the slave-making ants:

1. Slave-making ants are able to exploit the communication system of their hosts and thus provide a special opportunity to explore social signals in general.
2. Slave-making ants are suitable study objects to investigate the mechanisms involved in the formation of a distinct colony odor and the proximate processes of nestmate discrimination and recognition.
3. The life history of slave-making ants leads to distinct, testable predictions from kin-selection theory con-

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cerning sex-allocation ratios and reproductive conflict in animal societies.
4. Slave-making ants and their host species are expected to engage in a co-evolutionary arms race, which might have an important impact on the structure of their populations.

Here we review several aspects of the peculiar life history of slave-making ants, focusing in particular on their evolution, communication between slave makers and their hosts, kin conflict, and the effect of slave-making ants on host populations.

Life history and evolution of slave-making ants

Slave making in ants (dulosis) is a life history combining socially parasitic colony founding by queens and slave raiding by workers. For example, after mating, the queen of the palaearctic slave-maker ant *Harpagoxenus sublaevis* must find a colony of a suitable host ant species, for example, *Leptothorax acervorum*. Here, she attacks or expels its adult residents with the help of her clipper-like mandibles and presumably also chemicals that interfere with the hosts' nestmate recognition system (Buschinger 1968, 1974). After successfully taking over the nest, the *Harpagoxenus* queen starts to reproduce, and host workers, which by then have eclosed from the conquered host brood, take care of her and her offspring. *Harpagoxenus* workers are inefficient in the daily tasks of colony maintenance, brood care, foraging, and so forth, which are all carried out by host workers. Instead, they search for neighboring host colonies, which they attack in highly organized slave raids. The pillaged host pupae later eclose in the slave-maker colony and increase its worker force (Buschinger 1966a, b, 1968, 1974).

Of the approximately 10,000 species of ants, only a tiny minority of about 50 are active slave makers (Table 1). However, slave making apparently has evolved independently more than ten times, with peculiar hot spots in the myrmicine tribe Formicoxenini and the formicine tribe Formicini. Slave making normally is obligatory, but it is facultative in *Formica* (*Raptiformica*), where the slave-maker workers are still able to accomplish daily tasks and where colonies without host ants are quite common (Wheeler 1910). Whereas most slave makers raid only host broods, slave-making *Strongylognathus* also enslave adult host workers ("eudulosis"; Kutter 1969). The occurrence of eudulosis has also occasionally been observed in *Polyergus rufescens* (Mori et al. 1991; Le Moli et al. 1993).

Similarities in life history have led to the evolution of convergent morphology and behavior (e.g., sickle-shaped mandibles in *Polyergus* and *Strongylognathus*; broad heads with strong mandibles in *Harpagoxenus* and *Protomognathus*; scouting and well-organized raiding behavior). Nevertheless, considerable variation exists in colony size, reproductive strategies, and communication (e.g., Buschinger et al. 1980; Buschinger 1986; Franks and Bourke 1988; Hölldobler and Wilson 1990; Ruano and Tinaut 1999; Table 1). For example, species and genus-specific recruitment (tandem running and carrying of workers), fighting tactics (stinging, throttling, piercing the head capsule), and chemical weapons (propaganda, repelling and pacifying substances) have evolved. Some of these differences might be explained by phylogenetic constraints: colonies of formicoxenine slave makers, as well as those of their hosts, typically consist of only a few dozen individuals. Mass recruitment or large nuptial flights therefore are unlikely.

It is difficult to describe slave making in ants using the conventional terminology of parasitism and symbiosis. Obviously, successful colony founding by a slave-maker queen, sooner or later, leads to the death or at least the "sterilization" of the host colony. Its impact on the host therefore resembles more that of parasitoid flies or wasps (Godfray 1994) than that of macro- or microparasites. Similarly, at least in formicoxenine ants, colonies of the host species are probably completely destroyed by slave raids (Foitzik and Herbers 2001a, b) and slave raiding here is thus more similar to predation. In contrast, in some formicines, host colonies may survive an individual raid and may therefore by raided repeatedly during their biological cycle (e.g., in *P. rufescens*; Mori et al. 1991). Here, the effect of slave raids on a host colony more strongly resembles that of typical pathogens or parasites. Brood parasitism in birds, to which social parasitism has been compared (Davies et al. 1989), also differs in certain respects. For example, brood parasitism typically affects an individual host nest only during a single brood period.

The question of how slave-making ants have evolved comprises several aspects, which are more easily discussed separately (e.g., Buschinger 1986): (1) which ecological conditions have favored the evolution of parasitic founding, (2) which ecological conditions have favored the evolution of slave raiding, and (3) from which ancestors did slave makers evolve?

Evolution of parasitic founding

Parasitic founding is not restricted to slave-making ants but instead is rather widespread in social insects, so we will not discuss it here in detail. Furthermore, models explaining the enormous intra- and interspecific variation of reproductive tactics of queens of social insects and particularly ants (Herbers 1993; Bourke and Heinze 1994; Bourke and Franks 1995; Heinze and Tsuji 1995) might perhaps be extended to include parasitic founding.

In social parasites, queens avoid the unsafe phase of solitary colony founding by exploiting the work force and the security provided by an already established colony of another species. Interspecific parasitic founding thus can be seen as an adaptation to conditions where independent founding is not very successful due to high queen mortality and/or nest site limitation. It therefore could be considered as analogous to the return of young queens to their native nests in polygynous social insects