

## REVIEW

Patrizia D'Ettorre · Jürgen Heinze

**Sociobiology of slave-making ants**

Received: 2 February 2000 / Received in revised form: 21 December 2000 / Accepted: 8 January 2001

**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-

Communicated by T. Czeschlik

P. D'Ettorre  
IRBI, Faculté des Sciences et Techniques,  
Université François Rabelais, Parc de Grandmont,  
37200 Tours, France

J. Heinze (✉)  
Lehrstuhl für Biologie I, Universität Regensburg,  
93040 Regensburg, Germany  
e-mail: juergen.heinze@biologie.uni-regensburg.de  
Tel.: +49-941-9432475, Fax: +49-941-9433304

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 micro-parasites. 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 be 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

**Table 1** List of slave-making ant genera and some basic features of their life history, based on reviews by Buschinger (1986, 1997), Hölldobler and Wilson (1990), Wilson (1971), and others

Species	Host	Colony size		Recruitment during slave raids	Mating	Founding
		Slave makers	Host workers			
<b>Formicinae</b>						
<i>Rossomyrmex</i> <i>R. minuchae</i> <i>R. proformicarum</i>	<i>Proformica</i>	23–200	65–650	carry workers <sup>b</sup>	?	?
<i>Polyergus</i> <i>P. breviceps</i> <i>P. lucidus</i> <i>P. nigerrimus</i> <i>P. rufescens</i> <i>P. samurai</i>	<i>Formica</i>	Several dozen to thousand	Several hundred to thousand	Group recruitment <sup>b</sup>	Mating flight, mating on the ground, during raids	Usurpation, kill host queen but not the host workers, budding?
<i>Raptiformica</i> <i>R. sanguinea</i> and 11 other species	<i>Formica</i>	Several thousand	None to several thousand	Group recruitment <sup>b</sup>	Mating flight, on the ground?	Usurpation, especially of small host colonies, budding, adoption in queenless host colonies
<b>Myrmicinae:</b>						
<b>Formicoxenini</b>						
<i>Chalepoxenus</i> <i>C. muellerianus</i> and 7 other species <sup>a</sup>	<i>L. (Myrafant)</i>	Few dozen	None to several hundred	Tandem running	Mating flight	Usurpation, kill or expel host queen and host workers
<i>Epimyrma</i> <i>E. algeriana</i> <i>E. bernardi</i> <i>E. ravouxi</i> <i>E. stumperi</i> and 8 other species <sup>a</sup>	<i>L. (Myrafant)</i>	Few dozen	None to several hundred	Group recruitment	Mating flight or intranidal mating	Usurpation, kill host queen but not host workers
<i>Harpagoxenus</i> <i>H. candensis</i> <i>H. sublaevis</i> <i>H. zaisanicus</i>	<i>Leptothorax</i> (s.str.)	Few dozen	Several dozen	Tandem running	Sexual calling, female sex pheromones	Usurpation, kill or expel host queen and host workers
<i>Leptothorax</i> <i>L. duloticus</i>	<i>L. (Myrafant)</i>	Few dozen	Several dozen	Group recruitment	?	Usurpation, kill or expel host queen and host workers
<i>Protomognathus</i> <i>Pr. americanus</i>	<i>L. (Myrafant)</i>	Few dozen	Several dozen	Group recruitment	Mating flight	Usurpation, kill or expel host queen and host workers
<b>Myrmicinae:</b>						
<b>Tetramoriini</b>						
<i>Strongylognathus</i> <sup>a</sup> 26 species	<i>Tetramorium</i>	Several hundred	Several thousand	Group recruitment	Mating flight	

<sup>a</sup> Not all species are active slave makers; <sup>b</sup> In formicines, slaves do not take part in slave raids

or to intraspecific parasitism in ants and wasps. The frequent occurrence of parasitic ants in boreal or alpine environments (Kutter 1969; Hölldobler and Wilson 1990) might reflect both the high costs of solitary founding (due to hibernation mortality, Heinze 1993) and perhaps also the high density of host populations due to a generally lowered diversity of ants in boreal habitats (e.g., Kusnezov 1957).

#### Evolution of slave making

The evolutionary origins of slave making itself remain obscure, though they have been extensively discussed for more than 150 years (e.g., Darwin 1859; Wasmann 1905; Wheeler 1910; Buschinger 1970; Wilson 1971; Hölldobler and Wilson 1990). Three behavioral traits have been suggested, either alone or in various combinations, to have led to the evolution of slave raids: predato-

ry behavior, territoriality, and brood transport between separate nests of a multi-nest colony.

Darwin (1859) proposed that the ancestors of slave-raiding ants preyed on the broods of neighboring colonies of other ant species. Some of the broods carried into the predator's nest might have survived by chance and eclosed to workers. Accidental "slave making" may have evolved to regular slavery because of the selective advantage resulting from the work of this "forgotten" prey. However, there is currently little evidence for this hypothesis. It has been occasionally observed that pillaged brood may be eaten (*L. duloticus*: Alloway 1979; but see Buschinger and Pfeifer 1988; *Polyergus breviceps*: Topoff et al. 1984; *F. sanguinea*: Mori et al. 2000a) and that adult workers of the host and/or other ant species are preyed on (*F. wheeleri*: Topoff and Zimmerli 1991; *F. sanguinea*: Mori et al. 2000a). However, slave makers did not evolve in those ant taxa that are specialized ant predators, whereas the Formicoxenini are rich in slave makers but do not prey on ants (Hölldobler and Wilson 1990).

In territorial contests, large colonies may invade neighboring nests of their own species and pillage their broods, which eventually serve as "real slaves" (Hölldobler 1976; Pollock and Rissing 1989). The sporadic occurrence of colonies containing workers from different species suggests that interspecific raids may occasionally occur (Kutter 1957; Alloway 1980). From this and from laboratory observations in which non-parasitic *Leptothorax* raided neighboring colonies in a well-organized way it was concluded that intraspecific territorial encounters are the starting point in the evolution of slave making (Wilson 1975; Alloway 1980; Stuart and Alloway 1982, 1983; Pollock and Rissing 1989; but see Buschinger and Pfeifer 1988). Theoretical considerations and additional field observations suggest, however, that ants with small colony size, such as *Leptothorax*, rarely defend absolute territories (Levings and Traniello 1981). In the field, *Leptothorax* workers have been observed only gently removing intruders from the immediate surroundings of their nests rather than engaging in fierce territorial battles (Dobrzański 1966; Foitzik and Heinze 1998). Violent fights and raiding behavior in experimental arenas have therefore been considered to be laboratory artifacts (Buschinger and Pfeifer 1988). The existence of inter- or intraspecific mixed colonies in *Leptothorax* may be better explained by colony fusion and intraspecific parasitism by founding queens when nest sites are scarce (Foitzik and Heinze 1998). This presumably does not involve brood raiding. Still, the occurrence of intraspecific brood raiding was observed in *Polyergus* (Topoff et al. 1984; Le Moli et al. 1993) and interpreted as a consequence of territorial competition.

Neither the predation nor the territoriality hypothesis explains the simultaneous evolution of slave raiding and parasitic founding. Buschinger (1970) therefore suggested that slave makers evolved from ancestors whose colonies contained several queens (polygyny) and at the same time inhabited several nest sites (polydomy). Para-

sitic founding originated from the return of queens into their maternal colonies and slave raiding evolved from brood transport between different nests of a polydomous colony. Polydomy and polygyny are indeed quite common both in Formicini and Formicoxenini.

Most *Leptothorax* hosts of *Chalepoxenus* and *Epi-myrrma*, however, are monodomous (colonies live in a single nest) and monogynous (colonies have a single queen), and though queen number appears to be a rather flexible trait in social insects (Ross and Carpenter 1991) it seems unlikely that these slave makers evolved from polygynous ancestors. Furthermore, it is unclear how peaceful brood transport could have evolved to bellicose slave raiding.

Merging territoriality and polygyny–polydomy hypotheses, Alloway (1980) and Stuart and Alloway (1983) proposed that slavery arose from territorial battles and brood robbing in polygynous, polydomous species in which new colonies were founded by re-adoption of young queens and budding rather than solitary founding. Explicitly for *Polyergus*, a similar hypothesis was proposed, which includes three behavioral processes: queen take-over, territorial fighting, and olfactory imprinting (Topoff 1990).

#### Phylogeny of social parasites

Slave makers and slaves are typically closely related species (Emery 1909). This might reflect a common speciation pattern: a "preparasite" specialized for exploiting conspecific colonies might become reproductively isolated from the rest of the population it parasitizes, leading to sympatric speciation of a pair of parasite and host species (Buschinger 1990). Subsequently, hosts and parasites might have each radiated into a cluster of separate species, resulting in a diverse group of parasites parasitizing a similarly diverse group of host species. Alternatively, the close phylogenetic relationship may be a consequence of behavioral and ecological constraints. Interspecific parasitism will only be successful if host and parasite mutually understand their communication signals and have similar ecological requirements concerning, food, nest sites, and so forth. Consequently, social parasitism might evolve more easily between closely related species after allopatric speciation (e.g., Wilson 1971).

Several authors have seen slave making as an intermediate step in the evolution from free-living species or temporary parasites to inquilines, queen-tolerant social parasites, which have lost their worker caste (e.g., Wilson 1971). This hypothesis probably reflects the traditional assumption that parasites and hosts co-evolve toward a more benign symbiosis. Empirical and theoretical studies in epidemiology show, however, that this view is often based on circular reasoning and shaky theoretical arguments (May and Anderson 1983; Toft and Aeschlimann 1991). Besides, the occurrence of inquilines in social insect taxa without slave makers suggests

that workerless parasites can evolve directly from non-parasitic ancestors without the intermediate step of slave making (e.g., Buschinger 1990; Bourke and Franks 1991).

Obligate slave making might have evolved from facultative slave raiding and temporary parasitism in Formicinae. However, neither facultative slave makers nor temporary parasites exist in Myrmicinae. A shift from slave making to queen-intolerant, workerless parasitism is well documented only in the genera *Epimyrma* and *Chalepoxenus*, where both active slave raiders and workerless species exist (Buschinger et al. 1988a, b; Buschinger 1989). That here workerless species evolved from slave makers is corroborated by the intermediate “degenerate slave maker” *E. krausseii*, which produces too few workers for efficient slave raiding (Buschinger and Winter 1983; Buschinger 1989). Interestingly, cross-breeding experiments suggest a strong maternal influence on queen/worker ratio (Jessen and Klinkicht 1990). The existence of both active slave makers and queen-tolerant parasites in the genus *Strongylognathus* suggests that here similar evolutionary transitions occurred, though the worker caste has not been lost completely (Sanetra et al. 1998; Sanetra and Buschinger 2000).

The loss of a worker caste is associated with dramatic changes in the longevity and the reproductive tactics of the parasitic queen, which more or less changes from iteroparity to semelparity (Bourke and Franks 1995). Worker loss might be an adaptive move of the parasite in the arms race with the host, for example, when the host has evolved better defense mechanisms against raiding. Alternatively, it might be an adaptation to environmental changes, such as a decreasing density of host colonies (e.g., Buschinger 1989), or a lowered life expectancy of established parasite colonies, for example, due to a high risk of being parasitized itself. To abolish the production of workers while killing the host queen (as occurs in “degenerate slave makers”) might appear rather maladapted, as this dooms the parasite colony due to the rapid decline of the number of host workers. Queen killing might be seen as an atavism from former slave-raiding times, when the fertile host queen was not needed to replenish the stock of host workers. However, numerous cases exist in which queen-intolerant workerless parasites apparently have evolved directly from non-parasitic ancestors, whereas other workerless species have managed to keep the host queen alive (Buschinger 1990; Heinze 1995). Wilson (1971) suggested that the parasite queen in any case maximizes her total reproductive output under particular ecological conditions (the “big bang” strategy of reproduction).

The differing tolerance toward the host queen in workerless parasites might in fact be shaped by transmission rates and virulence (May and Anderson 1983) or, more generally, by the mortality rates of founding parasite queens and mature parasite colonies (Heinze and Tsuji 1995). If horizontal transmission, that is, invasion of new host colonies by the parasite queen’s daughters, is easy, the queen is selected to divert all the resources of

her host colony immediately into her own offspring and to kill the host queen. On the other hand, if horizontal transmission is difficult, a parasite queen benefits from less strongly exploiting the host colony and allowing vertical transmission, for example, by budding of polygynous host colonies. These two strategies appear to have evolved independently in workerless parasites of the ant *L. acervorum* (Buschinger 1990; Heinze 1995).

New ideas and more research are needed to determine the evolutionary origin of slave-making in ants. As mentioned above, the origin of parasitic founding can probably be understood better by extending and refining models of dispersal tactics in ant queens. The recent findings of intraspecific parasitism in ants (e.g., Tschinkel 1996; Foitzik and Heinze 1998, 2000; Heinze and Keller 2000) and a closer examination of its ecological causes might also shed light on the evolution of interspecific parasitism.

Slave making itself might have evolved from different types of behavior in different groups of ants. There is some evidence for the predation pathway in the Formicini. Future research in Formicoxenini should focus on the presumed territoriality and intraspecific brood raiding of non-parasitic species under natural conditions and the behavioral repertoire involved. Furthermore, as yet it is not evident what distinguishes those taxa in which slave making has evolved from those in which social parasitism is absent. Differences in the mechanisms of brood recognition (see below) or average nest density might be important.

More information is also needed on the phylogeny of parasitic ants and their hosts. Detailed genetic studies on the relationship between social parasites and their hosts, such as those in Tetramoriini (Sanetra and Buschinger 2000), are still an exception. A careful analysis of Formicoxenini with their large number of parasitic genera will be especially rewarding, both concerning the origin of social parasites and the interrelations between slave makers andinquilines. Breeding studies such as those done by Jessen and Klinkicht (1990) as well as more detailed genetic and biochemical analyses might help us to understand better how worker loss evolved in inquilines. They might also shed some light on the genetics of caste differentiation in general.

---

### Host–parasite communication

One of the principal elements in the organization of insect societies is the ability to discriminate nestmates from non-nestmates. The current hypothesis is that members of the same colony share a common specific label (“gestalt odor”; Crozier and Dix 1979), presumably a specific blend of cuticular hydrocarbons and/or fatty acids (Breed 1998; Singer 1998; Vander Meer and Morel 1998; Lahav et al. 1999; Lenoir et al. 1999). Presumably, each individual is able to read the label of other individuals, to compare it with an internal template, and to reject individuals that bear a different label. Because the

characteristic label of each colony changes over time (Vander Meer et al. 1989; Dahbi and Lenoir 1998; Boulay et al. 2000), the template should require an actualization. For a discussion of the origin of the template see, for example, Lenoir et al. (1999).

Nevertheless, the queens of slave-making ants are capable of breaking the colony recognition code and of manipulating the host workers to direct their altruistic behaviors toward the parasites rather than their own relatives. Furthermore, slave makers are capable of integrating workers from different host species within a single nest. Exploring how this is achieved might help us to understand better the mechanisms underlying nestmate recognition and the formation of colony odor in social insects in general.

In different phases of the life history of slave makers, various chemical uses, such as camouflage, appeasement, propaganda, and repellent, and the capability of young workers to imprint on a certain odor appear to be critically important. Several recent studies have focused on similarities in cuticular hydrocarbon signatures of parasite and host, and the usage of Dufour's gland secretions (for reviews see, for example, Dettner and Liepert 1994; Lenoir et al. 2001).

During colony founding, queens of some slave-making ants sooner or later become accepted by the workers of an invaded host colony, presumably because they bear the appropriate recognition labels. In principle, the recognition labels of a slave-maker queen can be similar to those of the hosts due to either camouflage or mimicry (sensu Howard and Akre 1995; see also Dettner and Liepert 1994). Camouflage implies the acquisition of chemicals through social interactions, both passive (accidental contact with host ants and the nest material) and active (allogrooming, trophallaxis). Mimicry, in contrast, is a *de novo* biosynthesis of host-specific chemicals by the parasite. Camouflage and mimicry can be combined when the parasite synthesizes a certain amount of compounds and at the same time acquires other compounds from its hosts (Akino et al. 1999). It would obviously be advantageous for a parasite queen already to have actively mimicked the chemical label of its future hosts before invading their colony. However, because of environmental influences, each host colony possesses its own distinctive and flexible signature, which is a priori unknown to the parasite queen. Mimicry therefore is less likely than camouflage, and although it seems to occur in some myrmecophile and termitophile insects (Howard et al. 1980, 1990; Howard and Blomquist 1982), it has indeed never been reported in parasitic ants.

Slave-maker queens show behavior that might help them actively acquire chemical substances from the host queen and facilitates their adoption by the adult host workers. For example, after injuring or killing the *Formica* host queen, the usurping queen of *Polyergus* self-grooms in close contact to the body of the host queen, rolls on the nest substrate while holding it, and even covers herself with it for several minutes (Topoff et al. 1988; Mori et al. 1995; D'Etterre et al. 1997). The importance of close contact with the host queen is dem-

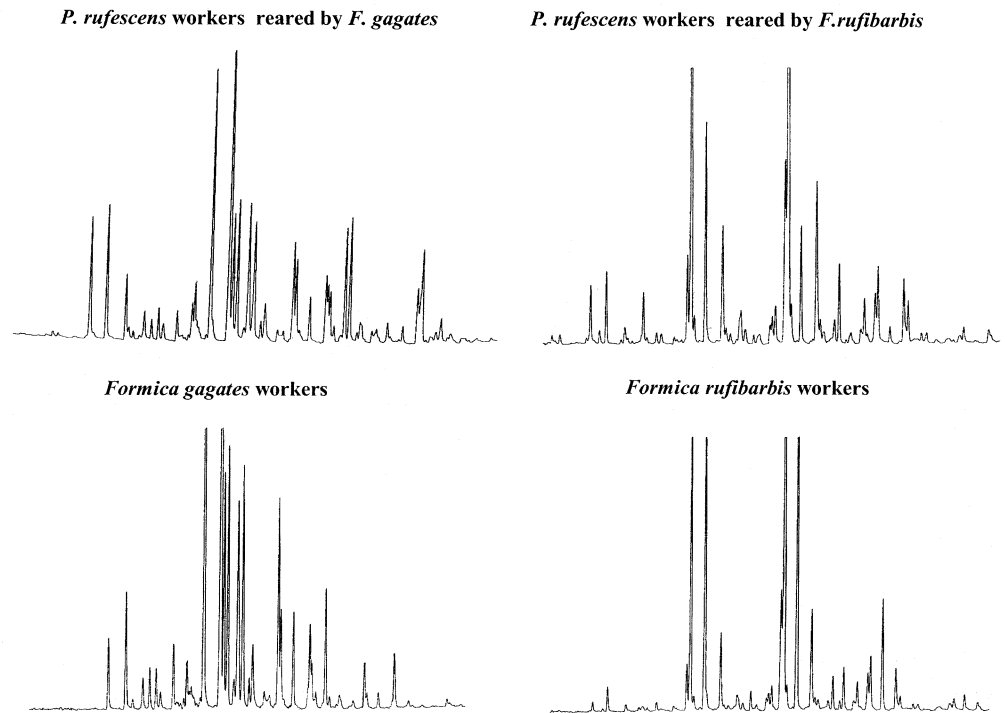
onstrated by the observation that newly mated queens of *P. breviceps* are more easily integrated into host colonies with a queen than into queenless colonies (Topoff et al. 1988; but see Mori et al. 1995), and *Polyergus* queens that have already killed a host queen or have even only been in contact with a dead host queen are more easily accepted when transferred into queenless host colonies (Topoff and Zimmerli 1993). Interestingly, newly mated *P. breviceps* queens do not kill those *Formica* queens that have not yet formed colonies. Presumably, young host queens do not elicit the parasite's aggressive behavior because they do not possess the chemical stimuli typical of mature queens (Zimmerli and Topoff 1994). Moreover, if two *P. rufescens* queens are simultaneously introduced into a host colony, only the one who first approaches and finally kills the host queen is adopted by host workers, whereas the other is killed (D'Etterre et al. 1997). Young *P. rufescens* queens indeed do not possess detectable amounts of cuticular hydrocarbons, but 5 days after adoption by a host colony they show a chemical signature similar to that of the respective host species (D'Etterre and Errard 1998; Lenoir et al. 2001).

In addition, *Polyergus* queens apply substances from the Dufour's gland onto the body of the resident host queen. These secretions, which in *P. rufescens* predominantly consist of decyl butanoate (D'Etterre et al. 2000, unpublished manuscript), have a repellent effect on *Formica* workers and have been suggested to render the host queen unattractive to her own workers. They can also elicit attacks (Topoff et al. 1988; Mori et al. 1995; D'Etterre et al. 1997). Mori et al. (2000b, c) found that Dufour's gland secretions drastically lowered the degree of overt attacks from host workers against the usurping *P. rufescens* queen herself and suggested that they act as an appeasement signal. Nevertheless, this appeasement phenomenon and the observed reduced aggression could be due to the repellent effect of decyl butanoate on host workers (D'Etterre et al. 2000).

It therefore appears that *P. rufescens* queens use a dual chemical strategy to usurp host nests successfully: (1) lack of a distinct chemical profile (*chemical insignificance*, cf. Lenoir et al. 1999) and acquisition of chemicals from the host queen, and (2) employment of Dufour's gland secretions to appease or deter potential host aggressors (Topoff et al. 1988; D'Etterre et al. 2000; Mori et al. 2000b).

The queens of other slave-making ants may employ similar strategies. For example, *Epimyrma* queens feign death when approached by host workers and sit for days in close contact with the *Leptothorax* host queen, slowly killing her by throttling (Buschinger 1989). In contrast, queens of *Harpagoxenus sublaevis* attack and aggressively expel adult workers and queens from the conquered host colony. During colony founding they use "propaganda" pheromones from the Dufour's gland to confuse the host workers and induce fighting among them (Buschinger 1974; Allies et al. 1986; for other ants see Franks et al. 1990; Heinze et al. 1998).

**Fig. 1** Gas chromatograms of the cuticular hydrocarbons in *Polyergus rufescens* slave-maker workers reared by two different host species (*Formica gagates* and *Formica rufibarbis*) and of host workers



In established colonies of slave-making ants, such as *H. sublaevis* (Kaib et al. 1993), *P. samurai* (Yamaoka 1990), and *P. breviceps* (Howard and Akre 1995), slave makers and hosts share the same cuticular hydrocarbon profile, without considerable quantities of substances specific only to the slave maker. *P. samurai* parasitizes two different Japanese host species, *F. japonica* and *F. hayashi*, and shows the same cuticular hydrocarbon pattern as the host present in the colony (Yamaoka 1990). Similarly, *H. sublaevis* occurs in mixed colonies with *L. acervorum* and *L. muscorum* and its cuticular hydrocarbon profile closely matches that of the respective host species. In colonies in which *H. sublaevis* lives together with workers from two host species, a hydrocarbon pattern results combining substances from both host species (Heinze et al. 1994). These results strongly suggest chemical camouflage. Similarly, aggression tests suggest that *F. sanguinea* slave makers acquire species-specific substances from enslaved *F. polyctena* (Czechowski 1993).

In contrast, the cuticular hydrocarbon profiles of *P. rufescens* workers and its *Formica* hosts do not closely correspond. Instead, the slave makers apparently produce some substances and simultaneously modify the relative amounts of cuticular hydrocarbons to match the hosts' profile better (Habersetzer and Bonavita-Cougourdan 1993; Bonavita-Cougourdan et al. 1996, 1997). These authors suggested that *P. rufescens* workers are able to actively adjust their cuticular profile to the social environment. *P. rufescens* workers, coming from the same mother colony but adopted as cocoons by different *Formica* species, show a cuticular pattern similar to that of the rearing species (D'Etterre, unpublished results, Fig. 1). Further studies are needed to clarify the underlying mechanisms.

In addition, *Protomognathus americanus* were believed to mark their slaves with chemical substances and thus to prevent them from returning to host colonies (Alloway and Keough 1990; see below). Chemical analyses have not yet been done, but this would mean that host workers show substances on their cuticles that are derived from the slave makers.

In conclusion, behavioral observations and chemical analyses indicate that those slave-maker queens that are tolerated by adult host workers probably do not bear a specific cuticular label but instead attempt to disguise themselves with substances from their hosts. The close correspondence between the cuticular hydrocarbon patterns of several of the few investigated slave makers and their respective hosts similarly suggests that the slave makers mask themselves with host substances probably acquired by allogrooming and/or trophallaxis (for the role of the postpharyngeal gland in colony odor see, for example, Lahav et al. 1999; Lenoir et al. 1999), though an active synthesis of some compounds has not yet been completely ruled out.

According to Jaisson (1985), "slave-making ants use a pre-existing ethogenetic phenomenon in a heterospecific direction," that is, by "sensory exploitation" (Ryan 1990) they make use of mechanisms of communication in their hosts that evolved for other purposes. In general, ants develop species- and colony-specific cuticular signatures only after the first hours of their adult life (cuticular chemical insignificance of young ants; Lenoir et al. 1999). Furthermore, young workers do not show aggressive behavior, are comparatively immobile, and produce highly conserved substances that induce grooming by older workers not only of the same, but also of other species. This all obviously facilitates the integration of

young ants into their colonies (Jaisson 1985). At the same time, specific chemical labels may be transferred from adult ants onto the blank cuticle of the callows by intensive grooming. During this period of early adult life, it appears that individuals imprint to the odor of both their adult nestmates and brood in any colony in which they eclose (e.g., Stuart 1988; Jaisson 1991). In most cases, this will be the colony of their mother, and all adult nestmates and brood will be more or less closely related. Hence, it normally is adaptive for a worker to take care of those individuals it encounters in the nest where it ecloses. Slave makers, however, benefit from this peculiarity: both slave-maker workers and host workers eclosing from the raided brood imprint to the present social environment, obtain the colony label, and thus are easily integrated into the mixed colony, and the host workers are manipulated to work for individuals to which they are not related.

Imprinting to the odor of the host species strongly influences the host choice of young queens during colony foundation and also the orientation of raids by workers of some slave-making ants. Young queens and raiding parties of *Chalepoxenus muellerianus*, *P. lucidus*, and *P. rufescens* almost exclusively usurp or raid nests of the host species already present in their maternal nest, even if other suitable host species are available (Goodloe and Sanwald 1985; Goodloe et al. 1987; Buschinger et al. 1988a; Mori et al. 1994a; Schumann and Buschinger 1995). This maternal "cultural transmission" of host specificity resembles the formation of gentes in cuckoos (e.g., Marchetti et al. 1998; Gibbs et al. 2000) and might eventually lead to the genetic separation of different strains, especially if the communication between sexuals relies in part on cuticular hydrocarbon profiles. On the other hand, colonies of species such as *E. ravouxi*, *H. canadensis*, and *H. sublaevis* may at the same time contain workers from two or more host species (e.g., Buschinger and Winter 1983; Schumann and Buschinger 1991; Heinze et al. 1992, 1994). The fate of these mixed colonies depends on the compatibility of the different host species. *Leptothorax muscorum* hosts were found to accept *L. acervorum* pupae but not vice versa (Schumann and Buschinger 1991), leading to a decrease in the frequency of slave-maker colonies with only *L. muscorum* hosts. Furthermore, aggressive interactions were observed when the two host species occurred in unequal numbers in the slave-maker colony: the majority began to expel the minority. This was reflected also in cuticular hydrocarbon patterns, which in these cases differed considerably between nestmates belonging to different host species (Heinze et al. 1994).

During slave-raids, workers of *F. subintegra*, *F. pergandei*, *H. sublaevis*, and probably other slave-making species use "propaganda substances," which disorientate the host workers (Regnier and Wilson 1971; Buschinger 1974; Franks and Partridge 1993). In addition, *H. sublaevis* workers apply these substances to the host brood to make them unattractive to their relatives. Slave-maker-specific substances might also be used to mark adult

host workers to prevent them from absconding from the slave-maker colony. Host workers from *Pr. americanus* colonies were attacked by their former, unparasitized nestmates when re-introduced into their natal colonies (Alloway and Keough 1990).

Finally, Mori and co-workers (Zimmerli and Mori 1993; Mori et al. 1996) suggested the existence of inter-specifically attractive brood pheromones in *Polyergus*. Similarly, callows of *P. rufescens* excrete droplets of a clear fluid from the anus that appear to be highly attractive to the *Formica* hosts and might act as an appeasement signal (D'Ettore and Errard 1999; see also Stuart 1981 for *Protomognathus americanus*).

---

### Sociogenetics of slave-making ants

The special life history of slave-making ants is thought to affect in a distinct way the outcome of conflict between queens and workers concerning the allocation of resources toward male and female sexuals and also concerning the origin of males (Trivers and Hare 1976). Slave-making ants therefore have been considered to provide a unique opportunity to test specific predictions from inclusive fitness theory (Hamilton 1964).

Due to haplodiploid sex determination in Hymenoptera, workers in monogynous and monandrous (single mating by the queen) societies with completely sterile workers obtain equal fitness payoff from both sexes only if they invest 3 times more in female than in male sexuals. The queen, in contrast, benefits most from a 1:1 allocation ratio (Trivers and Hare 1976). Female-biased sex-investment ratios in non-parasitic, monogynous species suggest worker control (reviewed by Bourke and Franks 1995). In slave-making ants, the host workers completely take over brood care, and so slave-maker workers can less easily enforce their own interests by manipulating resource allocation to male or female larvae. Hence, the slave-maker queen rather than the slave-maker workers might be in control of sex ratios. To demonstrate queen control unambiguously, however, has been more complicated than originally thought. With sex-allocation theories having become more and more refined over the past few years, slave-making ants have somewhat lost their role as outstanding, simple model systems.

As expected with queen control, sex-investment ratios were indeed found to be quite even in *Epimyrma ravouxi*, *Harpagoxenus sublaevis*, *Leptothorax duloticus*, and *Formica subnuda* (Bourke 1989; Bourke and Franks 1995; Savolainen and Deslippe 1996). In contrast, sex allocation was female biased in the facultative slave makers *F. sanguinea* and exhibited strong, unexplained variation at the colony level (Pamilo and Seppä 1994). Similarly, sex ratios varied considerably between and within populations of *H. canadensis*, *L. duloticus*, and *Protomognathus americanus*, with 6 of 11 data sets supporting neither queen nor worker control (Herbers and Stuart 1998).

Though it is not our aim to review in detail all factors that potentially affect sex allocation in social insects, we



will examine at least those that appear to be important in slave makers (for detailed reviews see Bourke and Franks 1995; Pamilo and Crozier 1996). These include polygyny, polyandry (multiple mating), worker reproduction, local resource, and local mate competition. For example, the sociogenetic structure of slave-maker colonies is still incompletely known, and probably not all of the assumptions made by original sex-allocation models – monogyny, monandry, and worker sterility – are met. Monogyny appears to be the rule in slave-making ants, excepting *E. algeriana*, *Polyergus breviceps*, and facultative slave-making *Formica* (Buschinger et al. 1990; Savolainen and Seppä 1996). However, the mating frequency of queens is currently known from genetic data only for *H. sublaevis* and *Pr. americanus*, which are both monandrous (Bourke et al. 1988; Foitzik and Herbers 2001a), and for *F. sanguinea*, where queens may mate multiply (Pamilo 1981; Pamilo and Seppä 1994). Behavioral observations suggest single mating in *P. breviceps* (Topoff and Greenberg 1988) and *Rossomyrmex minuchae* (F. Ruano and A. Tinaut, personal communication), and occasional multiple mating in several *Formica* (e.g., Kannyowski 1963), *P. rufescens* (Mori et al. 1994b), and *P. lucidus* (Marlin 1971). Multiple mating by itself might lead to a more balanced sex-allocation ratio under worker control.

Male production by slave-maker workers might similarly increase investment in males. Workers of most slave-making ants are capable of producing their own male offspring in colonies without a queen. Correcting for male production by workers in these queenless colonies, Bourke (1989) still found support for queen control in *E. ravouxi* and *H. sublaevis*. However, at least in *Pr. americanus*, workers have been demonstrated to produce males both in colonies with and without a queen, which considerably affects their interests concerning sex allocation and weakens the case for queen control (Foitzik and Herbers 2001a).

Additional complications arise in those species where some queens are wingless, as in *H. sublaevis* (Buschinger and Winter 1975) and *P. samurai* (Terayama et al. 1993), or where queens do not disperse on the wing, as in other species of *Polyergus* (Topoff and Greenberg 1988; Mori et al. 1994a). Here, young queens search on foot for suitable host colonies in the surroundings of their maternal colony and thus compete with their sisters and their mothers for the same host nests. This local resource competition might again select for a male-biased sex-allocation ratio (Foitzik and Herbers 2001a, but see Bourke et al. 1988). In contrast, in species where sibmating occurs in the nest, as in *E. bernardi* (Buschinger 1989), local mate competition might increase female bias.

Moreover, in contrast to previous assumptions, slave-maker workers might have the power to manipulate sex allocation. *L. duloticus* workers were observed grooming the brood and exchanging food with larvae (Wilson 1975), and *Chalepoxenus muellerianus* workers regularly begged food from larvae (Heinze 1996a, b). Thus,

they appear to be capable of cannibalizing brood, and the fundamental hypothesis of the incapability of slave makers to manipulate sex allocation is therefore not applicable for all species.

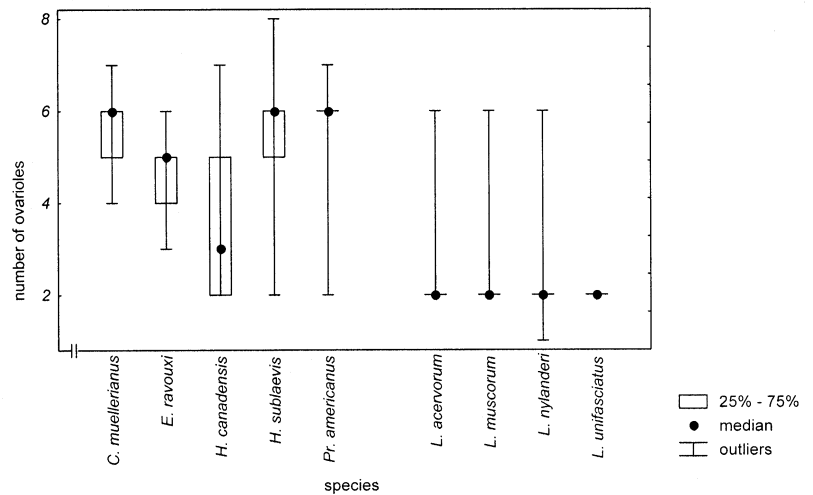
Finally, the third party in the colonies of slave-making ants, the host workers that do most of the brood care, have been considered to be indifferent to the sex ratio of the brood they rear, because they are equally unrelated to both sexes (Trivers and Hare 1976). Nevertheless, if they were selected to rear a particular, adaptive sex ratio in their native colonies, they might simply attempt to bias sex allocation in the same way when they are enslaved. Sex allocation in slave-maker colonies would then follow the pattern in non-parasitized colonies of the host species. Population-level sex-investment ratios of *Pr. americanus* indeed reflect those of the host population (Herbers and Stuart 1998). This might suggest that slave-maker queens cannot easily override sex-ratio preferences of their hosts.

Sex-ratio data in slave-making ants are much less unambiguous evidence for queen control than initially thought. Additional data, preferably on primary sex ratio of queen-laid eggs, secondary sex ratio, and the origin of males, are needed to clarify who is in control of sex allocation. Workers of *Tetramorium* and presumably also those of its slave maker *Strongylognathus* do not possess ovaries and therefore are obligatorily sterile (Buschinger, cited in Nonacs and Tobin 1992). Hence, sex allocation in *Strongylognathus* might be of particular interest.

Assuming that slave-maker workers have indeed less power to skew sex allocation than workers in non-parasitic ants, they might attempt to counterbalance this decrease in inclusive fitness through an increase in their direct fitness by selfishly producing their own sons (Bourke 1988). Similarly, allospecific brood care by unrelated host workers might allow female larvae of social parasites to control their own ontogeny to a greater extent than in non-parasitic species. Nonacs and Tobin (1992) concluded that a worker caste will only be retained in social parasites under conditions that increase the fitness of being a worker relative to becoming a sexual, for example, with worker production of males. This assumes that becoming a worker is less rewarding in terms of inclusive fitness in slave-making ants than in non-parasitic relatives and that the inclusive fitness gained from slave raiding is lower than that gained from “normal work” in non-parasites. Whether this is true for slave makers is doubtful, though it certainly applies for parasitic species where workers engage in neither brood care nor slave raids (e.g., degenerate slave makers, Buschinger and Winter 1983).

Several observations might suggest that slave-maker workers are more “selfish” than workers of related non-parasitic species. First, slave-maker workers tend to have more complex ovaries than workers of their hosts and related species. This has been shown in Formicoxenini (Heinze 1996a; Fig. 2) and appears to be the case also in Formicini. For example, workers of *P. rufescens* have 6–12 ovarioles per ovary (Beck 1972) in contrast

**Fig. 2** Number of ovarioles in workers of slave-making formicoxenine ants and their *Leptothorax* hosts (based on Heinze 1996b)



to workers of *F. rufibarbis*, which typically have 1–4 (Hohorst 1972). More complex ovarian anatomy is not a mere epiphenomenon of larger worker size or a less-pronounced caste dimorphism in slave-making species, because it occurs also in genera, such as *Epimyrma*, where workers are much smaller than host workers and the two female castes differ greatly in external morphology. Second, whereas in most non-parasitic *Leptothorax*, worker–worker reproductive conflict becomes evident only after the queen is removed (Heinze et al. 1997; but see Cole 1981), slave makers interact aggressively and form dominance hierarchies in the presence of the queen (Wilson 1975; Franks and Scovell 1983; Bourke 1988; Heinze 1996b). Finally, genetic data show that in *Pr. americanus*, workers produce most of the males in queenright colonies (Foitzik and Herbers 2000a).

An alternative explanation for increased selfishness is that slave-maker workers are selected to out-reproduce their hosts. Host workers are often more numerous than slave-maker workers in mixed colonies and might divert a large part of the colony's resources into the production of their own males (Heinze 1996b). Aggression of slave-maker workers toward their hosts has repeatedly been observed (e.g., Le Masne 1970), and in *H. sublaevis* attacks were predominantly directed against host workers with well-developed ovaries (Heinze et al. 1994). Only *Polyergus* males were produced in queenless mixed colonies of *Polyergus* and *Formica* (Hung 1973; P. D'Etterre, unpublished research), but host males occasionally eclose in colonies of slave-making Formicoxenini (Heinze 1996a, b). It is currently unknown whether they were reared from raided brood or from eggs laid by enslaved workers, nor whether and how host male production affects the total sexual output of the slave-maker colony. In analogy to paying a staying incentive (optimal skew theory, Reeve and Ratnieks 1993; Keller and Reeve 1994), slave makers might permit host workers to reproduce to keep them from absconding from the colony or to prevent host rebellions [as hypothesized by Hölldobler (1976) in an intraspecific case].

Most of what we currently know about kin conflict in slave-making ants is from Formicoxenini (for an exception see Hung 1973). Data from other taxa might help us to understand better apparent worker selfishness in slave-making ants.

### Host response and coevolution

Typically, parasites have a shorter generation time and higher effective population size than their hosts and therefore can quickly evolve countermeasures to the acquisition of resistance by their hosts. Social parasites differ from other types of parasites in a number of important ways that might affect the pattern of coevolution. They are more closely related to their hosts than other parasites and therefore might be better capable of “tracking” the evolution of countermeasures by the host species (Davies et al. 1989). On the other hand, the generation time of slave makers is similar to, or even longer than, that of their hosts, and their population size is typically smaller. Slave makers might therefore react more slowly to defensive changes in their hosts than other parasites. In addition, genetic drift might affect the slave makers more strongly than their hosts – indeed, whereas  $F_{ST}$  values calculated from allozyme frequencies were close to zero for populations of *Leptothorax acervorum* throughout Europe (Heinze et al. 1995), two German populations of its slave maker *Harpagoxenus sublaevis* differed significantly in allele frequencies (Heinze, unpublished research). It might therefore be more difficult for slave makers to optimize their life history and they might suffer a higher risk of local extinction.

It has been questioned whether slave makers are common enough to be a strong selective force for their hosts (Dawkins 1982; Davies et al. 1989). However, in some populations, more than 10% of all host colonies were successfully usurped by slave-maker queens, and in addition, established slave-maker colonies affect numerous other host colonies by raiding their broods. Individual colonies of *Polyergus* may conduct up to 50 raids in one summer

(Cool-Kwait and Topoff 1984; Mori et al. 1991; Hasegawa and Yamaguchi 1994), and 26 raids of *Formica sanguinea* occurred during a period of 78 days of observation (Mori et al. 2000a). Foitzik and Herbers (2001b) estimated that in some populations almost half of all colonies of *L. longispinosus* are raided by *Protomognathus americanus* per year. Though most information on parasite–host dynamics is anecdotal, there is evidence that intensive parasitism may eventually lead to local extinction of the host (Yasuno 1964; Zamora et al., unpublished manuscript). Countermeasures against usurpation, slave-raiding, and being enslaved should therefore be selected, even if resistance may be costly to the unparasitized host. Such countermeasures might include sociometric changes, for example, higher queen number or larger colony size, better defense mechanisms, such as more efficient recognition systems, fighting techniques and nest evacuation strategies, and others.

It is currently unclear, however, whether resistance against social parasites has indeed evolved and if the genotype of a host colony determines whether it is parasitized or not. Colonies of formicoxenine hosts are probably destroyed by just a single slave raid (Foitzik and Herbers 2001b), but colonies of some formicines may be raided repeatedly. Here, however, nothing is known about how frequently a host colony is raided and whether the probability of being raided or usurped is affected by the host's genotype or other parameters, for example, whether a slave-maker colony exists in the vicinity or how conspicuous or exposed the host nest is, compared to other host colonies in the same population.

As shown above, slave makers use camouflage and chemical weapons to break into host colonies. Still, by evolving a more efficient recognition system, insect societies might be better protected against being parasitized. If the hosts were capable of recognizing slave makers as specific enemies, they might react in a more appropriate way to raiding parties and usurping queens, that is, by immediate attack or escape from the raided nest with their brood (Marlin 1969; Le Moli et al. 1994). However, they might also be more prone to making mistakes, such as preventing their own nestmates from entering the nest. The more aggressive reaction of workers of *L. longispinosus* to workers of *Pr. americanus* than to workers of the non-parasitic *L. ambiguus* has been seen as such a specific enemy recognition (Alloway 1990). However, this observation might also be explained by ants reacting more aggressively toward distantly rather than closely related species (Errard 1987). Detailed experiments on enemy recognition and especially on the behavior of workers from different host populations (Zamora et al., unpublished manuscript) to slave makers might help to clarify whether coevolution occurs in this respect.

Polygyny could potentially protect a host colony against being usurped by a slave-maker queen (Herbers 1986): to eliminate several host queens obviously is more difficult than to kill only a single queen. However, queens of *Epimyrma stumperi* have been observed to throttle one host queen after the other in polygynous colonies of *L. tuberum* (Kutter 1969), and at least in facultatively polygynous *L. longispinosus*, queen numbers were

not larger in populations with slave makers than without (Herbers 1986). Furthermore, most host species of *Epimyrma*, *Chalepoxenus*, and *Strongylognathus* are obligatorily monogynous (see above). In a pioneering study on the impact of *Pr. americanus* on populations of its host *L. longispinosus*, Foitzik and Herbers (2001b) found that host colonies in parasitized populations were less likely to be polygynous, had fewer workers, and had a higher relatedness among worker broods than in populations without slave makers. These differences might result from parasite pressure itself, that is, host colonies being raided early in their development and therefore never reaching large size or being able to readopt daughter queens. Alternatively, workers in monogynous host colonies might have a more homogeneous colony odor than workers from polygynous colonies and therefore might react more strongly to alien ants, preventing an easy usurpation. Slave makers might also benefit from already existing regional differences in host sociometry, that is, they may preferentially settle in areas with small, monogynous host colonies (Foitzik and Herbers 2001b).

Queens of several slave-maker species appear to prefer to invade small, incipient rather than large host colonies (A. Buschinger, cited in Hölldobler and Wilson 1990, p. 458; Ito and Higashi 1990). Parasitic founding – and presumably also slave raiding – might therefore select for rapid colony growth in the host (Savolainen et al. 1996). Slave-maker queens, however, have found ways to usurp even very large host colonies. Newly mated *Polyergus* queens participate in the slave raids and take advantage of the confusion induced by the slave makers' propaganda substances or alarm pheromones of the host workers to establish themselves in the leftovers of raided *Formica* colonies (Topoff et al. 1988; Mori et al. 1995). Furthermore, several related queens may simultaneously penetrate into the same host colony, thus dividing the defensive actions of resident workers among themselves (D'Ettorre et al. 1997).

When a host colony cannot avoid being usurped or raided during its lifetime, it might benefit from producing sexuals early instead of investing in colony growth for a long time. Results from a study on colony size and the reproductive strategy of the host ant *F. podzolica* did not, however, unambiguously fit either hypothesis (Savolainen et al. 1996). Furthermore, it will be difficult to determine whether differences in sociometric parameters between unparasitized and parasitized host populations have evolved as ways to resist parasitism or instead are caused by environmental conditions that also favor parasites. For example, increased investment in colony growth might be a strategy against raiding or usurpation, but on the other hand, slave makers might benefit from especially raiding the large colonies.

The capacity of larvae to imprint on the odor of their natal nest might make an ant species unsuitable for slave makers (e.g., Davies et al. 1989). An ant worker pillaged as pupa after preimaginal imprinting might identify slaver-maker brood as alien and refuse to care for them.

This phenomenon, its role in the phylogenetic distribution of slave-making ants, and the interrelations between larval conditioning and learning during imaginal stages require more investigation because as yet it has been demonstrated only in two ant genera that do not serve as hosts (Isingrini et al. 1985; Carlin and Schwartz 1989).

Once host workers have been enslaved, the evolution of resistance appears to be unlikely, because a new genotype in the host workers, which leads to rebellion against the slave makers and/or emigration from the slave-maker colony, would have few options to be transmitted (Gladstone 1981). However, the potential of host workers to produce their own males or to recruit related queens from neighboring colonies was not taken into account. Czechowski (1990, 1994) reported "slave emancipation" in experimentally manipulated colonies of *F. sanguinea*. One year after adding exceptionally large numbers of host pupae (*F. polyctena*) to mixed colonies, the slave makers had disappeared and the former hosts had adopted conspecific queens. However, *F. polyctena* is not a typical host of *F. sanguinea* and the outcome of the experiment therefore could be due to the incompatibility of chemical signals between the two species. Still, in some species attacks of host workers against slave makers have repeatedly been observed (e.g., Wilson 1975).

Numerous ways exist in which coevolution between slave makers and their hosts might have occurred. Several lines of research might be especially rewarding in the future. First, a comparative analysis of colony structure of hosts in parasitized and unparasitized populations might reveal consistent differences in growth rate and size at maturity. Second, a detailed investigation of the interactions between slave makers and hosts from parasitized and non-parasitized host populations in experimental encounters might help to determine whether behavioral adaptations, such as specific enemy recognition, do exist. The pair *H. sublaevis*-*L. acervorum* is an especially appropriate system for such a study. Both species inhabit large parts of boreal Eurasia (e.g., Buschinger 1997; Radchenko et al. 1999), but some host populations appear not to have been parasitized for many generations. For example, *H. sublaevis* is absent from the British Isles, despite the presence of dense host populations. The British ant fauna is depauperate and lacks common European species such as *L. muscorum*, *F. polyctena*, and *Camponotus herculeanus* (Collingwood 1971). Perhaps the typically wingless queens of *H. sublaevis* could not manage to recolonize these islands after the last glaciation. *L. acervorum* in England might therefore have been protected from the slave makers for several thousand years and might have lost special adaptations against raiding or parasitic founding.

## Perspectives

Though slave-making ant species have been studied for more than 150 years, many problems are still open, the

most prominent obviously being the evolution of slave raiding itself. Recent investigations have given contradictory results concerning, for example, the mechanisms of chemical integration of slave makers and their hosts in a mixed society, the pattern of sex allocation in slave makers, and coevolution between social parasite and host. Obviously, more data are needed on the ontogeny of colony odor, preimaginal imprinting, and the role of the post-pharyngeal gland in natural mixed colonies, and on chemical weapons used during colony foundation and raiding. Strategies of chemical manipulation, similar to those employed by parasitic ants, have recently been shown to occur also in non-parasitic species (Heinze et al. 1998) and it is likely that other phenomena as yet known only in parasitic ants are of more general importance.

Combined chemical, genetic, and behavioral investigations might clarify whether cultural transmission of host preference plays a role in the choice of mating partners and may eventually lead to sympatric speciation. Clear theoretical predictions and empirical information on host-parasite dynamics, such as local extinction rates, and differences in sociometry and life history between parasitized and unparasitized host populations might help us understand whether hosts and parasites engage in a coevolutionary arms race. Detailed comparisons of host populations parasitized by active slave makers, degenerate slave makers, and workerless parasites may allow us to differentiate between the impact parasitic founding and slave raiding have on host populations, and to determine the benefits from losing a worker caste.

Empirical studies on slave-making ants are challenging because of the lack of a theoretical basis, and they are difficult per se due to the rarity of slave makers and their patchy distribution. Considering that almost all slave-making ant species are listed as threatened by the World Conservation Union (IUCN), investigations on their behavior, population structure, and genetic variability may help us learn more about how endangered they really are and if and how they can better be protected. Presumably, intensive field studies will also reveal the existence of additional slave-making species and clarify the life history of several species in which the possibility of slavery has been reported (e.g., Bernstein 1978).

**Acknowledgements** Our work was supported by a Marie-Curie Fellowship (Proposal no. ERB4001GT975111) to P.D., by the Deutsche Forschungsgemeinschaft (He 1623/7-2) to J.H., and in part by program PROCOPE (Project no. 98033) to Jerome Casas. We would like to thank Christine Errard and Alain Lenoir for their helpful comments on the manuscript.

## References

- Akino T, Knapp JJ, Thomas JA, Elmes GW (1999) Chemical mimicry and host specificity in the butterfly *Maculinea rebeli*, a social parasite of *Myrmica* ant colonies. *Proc R Soc Lond B* 266:1419-1426
- Allies AB, Bourke AFG, Franks NR (1986) Propaganda substances in the cuckoo ant *Leptothorax kutteri* and the slave-maker *Harpagoxenus sublaevis*. *J Chem Ecol* 127:1285-1293

- Alloway TM (1979) Raiding behaviour in two species of slave-making ants, *Harpagoxenus americanus* (Emery) and *Leptothorax duloticus* Wesson (Hymenoptera: Formicidae). *Anim Behav* 27:202–210
- Alloway TM (1980) The origin of slavery in leptothoracine ants (Hymenoptera: Formicidae). *Am Nat* 115:247–261
- Alloway TM (1990) Slave-species ant colonies recognize slave-makers as enemies. *Anim Behav* 39:1218–1220
- Alloway TM, Keough G (1990) Slave-marking by the slave-making ant *Harpagoxenus americanus* (Emery) (Hymenoptera: Formicidae). *Psyche* 97:55–64
- Beck H (1972) Vergleichende histologische Untersuchungen an *Polyergus rufescens* Latr. und *Raptiformica sanguinea* Latr. *Insectes Soc* 19:301–342
- Bernstein RA (1978) Slavery in the subfamily Dolichoderinae (F. Formicidae) and its ecological consequences. *Experientia* 34:1281–1282
- Bonavita-Cougourdan A, Rivière G, Provost E, Bagnères A-G, Roux M, Dusticier G, Clément J-L (1996) Selective adaptation of the cuticular hydrocarbon profiles of the slave-making ants *Polyergus rufescens* Latr. and their *Formica rufibarbis* Fab. and *F. cunicularia* Latr. slaves. *Comp Biochem Physiol B* 113:313–329
- Bonavita-Cougourdan A, Bagnères A-G, Provost E, Dusticier G, Clément J-L (1997) Plasticity of the cuticular hydrocarbon profile of the slave-making ant *Polyergus rufescens* depending on the social environment. *Comp Biochem Physiol B* 116:287–302
- Boulay R, Hefetz H, Soroker V, Lenoir A (2000) Individuality in hydrocarbon production obliges *Camponotus fellah* workers continual exchange to be integrated in their colony. *Anim Behav* 59:1127–1133
- Bourke AFG (1988) Dominance orders, worker reproduction, and queen-worker conflict in the slave-making ant *Harpagoxenus sublaevis*. *Behav Ecol Sociobiol* 23:323–333
- Bourke AFG (1989) Comparative analysis of sex-investment ratios in slave-making ants. *Evolution* 43:913–918
- Bourke AFG, Franks NR (1991) Alternative adaptations, sympatric speciation and the evolution of parasitic, inquiline ants. *Biol J Linn Soc* 43:157–178
- Bourke AFG, Franks NR (1995) Social evolution in ants. Princeton University Press, Princeton, N.J.
- Bourke AFG, Heinze J (1994) The ecology of communal breeding: the case of multiply-queened leptothoracine ants. *Philos Trans R Soc Lond B* 345:359–372
- Bourke AFG, van der Have TM, Franks NR (1988) Sex ratio determination and worker reproduction in the slave-making ant *Harpagoxenus sublaevis*. *Behav Ecol Sociobiol* 23:233–245
- Breed MD (1998) Chemical cues in kin recognition: criteria for identification, experimental approaches, and the honey bee as an example. In: Vander Meer RK, Breed MD, Espelie K, Winston ML (eds) *Pheromone communication in social insects. Ants, wasps, bees and termites*. Westview Press, Boulder, Colo., pp 57–77
- Buschinger A (1966a) Untersuchungen an *Harpagoxenus sublaevis* Nyl. (Hym., Formicidae) I. Freilandbeobachtungen zu Verbreitung und Lebensweise. *Insectes Soc* 13:5–16
- Buschinger A (1966b) Untersuchungen an *Harpagoxenus sublaevis* Nyl. (Hym., Formicidae) II. Haltung und Brutaufzucht. *Insectes Soc* 13:311–322
- Buschinger A (1968) Untersuchungen an *Harpagoxenus sublaevis* Nyl. (Hymenoptera, Formicidae) III. Kopula, Koloniegründung, Raubzüge. *Insectes Soc* 15:89–104
- Buschinger A (1970) Neue Vorstellungen zur Evolution des Sozialparasitismus und der Dulosis bei Ameisen (Hym., Formicidae). *Biol Zentralbl* 88:273–299
- Buschinger A (1974) Experimente und Beobachtungen zur Gründung und Entwicklung neuer Sozietäten der sklavenhaltenden Ameise *Harpagoxenus sublaevis* Nyl. *Insectes Soc* 21:381–406
- Buschinger A (1986) Evolution of social parasitism in ants. *Trends Ecol Evol* 1:155–160
- Buschinger A (1989) Evolution, speciation and inbreeding in the parasitic ant genus *Epimyrma* (Hymenoptera, Formicidae). *J Evol Biol* 2:265–283
- Buschinger A (1990) Sympatric speciation and radiative evolution of socially parasitic ants – heretic hypotheses and their factual background. *Z Zool Syst Evol Forsch* 28:241–260
- Buschinger A (1997) Socially parasitic formicoxenine ants from Western Europe – a review (Hymenoptera, Formicidae). *Proc Int Coll Soc Insects* 3–4:1–9
- Buschinger A, Pfeifer E (1988) Effects of nutrition on brood production and slavery in ants (Hymenoptera, Formicidae). *Insectes Soc* 35:61–69
- Buschinger A, Winter U (1975) Der Polymorphismus der sklavenhaltenden Ameise *Harpagoxenus sublaevis*. *Insectes Soc* 22:333–362
- Buschinger A, Winter U (1983) Population studies of the dulotic ant, *Epimyrma ravouxi*, and the degenerate slavemaker, *E. krausseii* (Hymenoptera: Formicidae). *Entomol Gener* 8:251–266
- Buschinger A, Ehrhardt W, Winter U (1980) The organization of slave-raids in dulotic ants – a comparative study (Hymenoptera; Formicidae). *Z Tierpsychol* 53:245–264
- Buschinger A, Ehrhardt W, Fischer K, Ofer J (1988a) The slave-making ant genus *Chalepoxenus* (Hymenoptera, Formicidae) I. Review of literature, range, slave species. *Zool Jahrb Syst* 115:363–401
- Buschinger A, Cagniant H, Ehrhardt W, Heinze J (1988b) *Chalepoxenus brunneus*, a workerless “degenerate slave-maker” ant (Hymenoptera: Formicidae). *Psyche* 95:253–263
- Buschinger A, Jessen K, Cagniant H (1990) The life history of *Epimyrma algeriana*, a slave-making ant with facultative polygyny (Hymenoptera, Formicidae). *Zool Beitr NF* 33:23–49
- Carlin NF, Schwartz PH (1989) Pre-imaginal experience and the nestmate brood recognition in the carpenter ant, *Camponotus floridanus*. *Anim Behav* 38:89–95
- Cheng TC (1991) Is parasitism symbiosis? A definition of terms and the evolution of concepts. In: Toft CA, Aeschlimann A, Bolis L (eds) *Parasite-host associations. Coexistence or conflict?* Oxford University Press, Oxford, pp 15–36
- Cole BJ (1981) Dominance hierarchies in *Leptothorax* ants. *Science* 212:83–84
- Collingwood CA (1971) A synopsis of the Formicidae of north Europe. *Entomologist* 104:150–176
- Cool-Kwait E, Topoff H (1984) Raid organization and behavioral development in the slave-making ant *Polyergus lucidus* Mayr. *Insectes Soc* 31:361–374
- Crozier RH, Dix MW (1979) Analysis of two genetic models for the innate components of colony odor in social Hymenoptera. *Behav Ecol Sociobiol* 47:217–224
- Czechowski W (1990) Autonomization of slaves from mixed colonies of *Formica sanguinea* Latr. & *F. polyctena* Foerst. (Hymenoptera, Formicidae). *Mem Zool* 44:55–63
- Czechowski W (1993) Do colonies of *Formica sanguinea* Latr. (Hymenoptera, Formicidae) take over an odour discriminator from their slaves? *Przeł Zool* 37:273–276
- Czechowski W (1994) Emancipation of slaves in *Formica sanguinea* Latr. colonies (Hymenoptera, Formicidae). *Ann Zool* 45:15–26
- Dahbi A, Lenoir A (1998) Nest separation and the dynamics of the Gestalt odor in the polydomous ant *Cataglyphis iberica* (Hymenoptera, Formicidae). *Behav Ecol Sociobiol* 42:349–355
- Darwin C (1859) *The origin of species by means of natural selection*. Murray, London
- Davies NB, Bourke AFG, Brooke M de L (1989) Cuckoos and parasitic ants: interspecific brood parasitism as an evolutionary arms race. *Trends Ecol Evol* 4:274–278
- Dawkins R (1982) *The extended phenotype*. Oxford University Press, Oxford
- Dettner K, Liepert C (1994) Chemical mimicry and camouflage. *Annu Rev Entomol* 39:129–154
- D’Ettorre P, Errard C (1998) Chemical disguise during colony founding in the dulotic ant *Polyergus rufescens* Latr. (Hymenoptera, Formicidae). *Insect Soc Life* 2:71–77

- D'Ettorre P, Errard C (1999) Trophallaxie proctodéale chez la fourmi esclavagiste *Polyergus rufescens*. Actes Coll Insectes Soc 12:61–64
- D'Ettorre P, Mori A, Le Moli F (1997) Haplometrotic colony founding by the slave-making ant *Polyergus rufescens* Latr. (Hymenoptera, Formicidae). Ital J Zool 64:49–53
- D'Ettorre P, Errard C, Ibarra F, Francke W, Hefetz A (2000) Sneak in or repel your enemy: Dufour's gland repellent as a strategy for successful usurpation in the slave-maker *Polyergus rufescens*. Chemoecology 10:135–142
- Dobrzański J (1966) Contribution to the ethology of *Leptothorax acervorum* (Hymenoptera: Formicidae). Acta Biol Exp 26:71–78
- Emery C (1909) Über den Ursprung der dulotischen, parasitischen und myrmekophilen Ameisen. Biol Centralbl 29:352–362
- Errard C (1987) Phylogenesis/biotope interactions among Formicidae. Behav Proc 14:35–47
- Foitzik S, Heinze J (1998) Nestsite limitation and colony take over in the ant, *Leptothorax nylanderi*. Behav Ecol 9:367–375
- Foitzik S, Heinze J (2000) Intraspecific parasitism and split sex ratios in a monogynous and monandrous ant. Behav Ecol Sociobiol 47:424–431
- Foitzik S, Herbers JM (2001a) Colony structure of a slavemaking ant: I. Intra-colony relatedness, worker reproduction and polydomy. Evolution, in press
- Foitzik S, Herbers JM (2001b) Colony structure of a slavemaking ant: II. Frequency of slave raids and impact on the host population. Evolution, in press
- Franks NR, Bourke AFG (1988) Slaves of circumstance. New Scientist 119:45–49
- Franks NR, Partridge LW (1993) Lanchester battles and the evolution of combat in ants. Anim Behav 45:197–199
- Franks NR, Scovell E (1983) Dominance and reproductive success among slave-making worker ants. Nature 304:724–725
- Franks NR, Blum M, Smith RK, Allies AB (1990) Behavior and chemical disguise of cuckoo ant *Leptothorax kutteri* in relation to its host *Leptothorax acervorum*. J Chem Ecol 16:1431–1444
- Freeman S, Herron JC (1998) Evolutionary analysis. Prentice Hall, Upper Saddle River, N.J.
- Gibbs HL, Sorenson MD, Marchetti K, Brooke M de L, Davies NB, Nakamura H (2000) Genetic evidence for female host-specific races of the common cuckoo. Nature 407:183–186
- Gladstone DE (1981) Why there are no ant slave rebellions. Am Nat 117:779–781
- Godfray HCF (1994) Parasitoids: behavioural and evolutionary ecology. Princeton University Press, Princeton, N.J.
- Goodloe L, Sanwald R (1985) Host specificity in colony-founding by *Polyergus lucidus* queens (Hymenoptera: Formicidae). Psyche 927:297–302
- Goodloe L, Sanwald R, Topoff H (1987) Host specificity in raiding behavior of the slave-making ant *Polyergus lucidus*. Psyche 94:39–44
- Habersetzer C, Bonavita-Cougourdan A (1993) Cuticular spectra in the slave-making ant *Polyergus rufescens* and the slave species *Formica rufibarbis*. Physiol Entomol 18:160–166
- Hamilton WD (1964) The genetical evolution of social behavior I, II. J Theor Biol 7:1–52
- Hamilton WD, Howard JC (eds) (1997) Infection, polymorphism and evolution. Chapman & Hall, London
- Hasegawa E, Yamaguchi T (1994) Raiding behavior of the Japanese slave-making ant *Polyergus samurai*. Insectes Soc 41:279–289
- Heinze J (1993) Life history strategies of subarctic ants. Arctic 46:354–358
- Heinze J (1995) The origin of workerless parasites in *Leptothorax* (s.str.) (Hymenoptera: Formicidae). Psyche 102:195–214
- Heinze J (1996a) Reproductive hierarchies among workers of the slave-making ant, *Chalepoxenus muellerianus*. Ethology 102:117–127
- Heinze J (1996b) The reproductive potential of workers in slave-making ants. Insectes Soc 43:319–328
- Heinze J, Keller L (2000) Alternative reproductive strategies: a queen perspective in ants. Trends Ecol Evol 15:508–512
- Heinze J, Tsuji K (1995) Ant reproductive strategies. Res Populat Ecol 37:135–149
- Heinze J, Stuart RJ, Alloway TM, Buschinger A (1992) Host specificity in the slave-making ant, *Harpagoxenus canadensis* M.R. Smith. Can J Zool 70:167–170
- Heinze J, Ortius D, Hölldobler B, Kaib M (1994) Intracolony discrimination among heterospecific slaves of the ant, *Harpagoxenus sublaevis*. Behav Ecol Sociobiol 35:75–83
- Heinze J, Lipski N, Hölldobler B, Bourke AFG (1995) Geographical variation in the genetical and social structure of the ant, *Leptothorax acervorum*. Zoology 98:127–135
- Heinze J, Puchinger W, Hölldobler B (1997) Worker reproduction and social hierarchies in *Leptothorax* ants. Anim Behav 54:849–864
- Heinze J, Oberstadt B, Tentschert J, Hölldobler B, Bestmann HJ (1998) Colony specificity of Dufour gland secretions in a functionally monogynous ant. Chemoecology 8:169–174
- Herbers JM (1986) Effects of ecological parameters on queen number in *Leptothorax longispinosus* (Hymenoptera: Formicidae). J Kans Entomol Soc 58:675–686
- Herbers JM (1993) Ecological determinants of queen number in ants. In: Keller L (ed) Queen number and sociality in insects. Oxford University Press, Oxford, pp 262–293
- Herbers JM, Stuart RJ (1998) Pattern of reproduction in slave-making ants. Proc R Soc Lond B 265:875–887
- Hohorst B (1972) Biometrische Untersuchungen an *Formica (Serviformica) rufibarbis* Fabricius (Hymenoptera: Formicidae). Insectes Soc 19:405–407
- Hölldobler B (1976) Tournaments and slavery in a desert ant. Science 192:912–914
- Hölldobler B, Wilson EO (1990) The ants. Harvard University Press, Cambridge Mass.
- Howard RW, Akre RD (1995) Propaganda, crypsis and slavemaking. In: Cardé RT, Bell WJ (eds) Chemical ecology in insects II. Chapman & Hall, London, pp 364–429
- Howard RW, Blomquist GJ (1982) Chemical ecology and biochemistry of insect hydrocarbons. Annu Rev Entomol 27:149–172
- Howard RW, McDaniel CA, Blomquist GJ (1980) Chemical mimicry as an integrating mechanism: cuticular hydrocarbons of a termitophile and its host. Science 210:431–433
- Howard RW, Stanley Samuelson DW, Akre RD (1990) Biosynthesis and chemical mimicry of cuticular hydrocarbons from the obligate predator, *Microdon albicomatus* Novak (Diptera: Syrphidae) and its ant prey, *Myrmica incompleta* Provancher (Hymenoptera: Formicidae). J Kans Entomol Soc 63:437–443
- Hung ACF (1973) Reproductive biology in dulotic ants: preliminary report (Hymenoptera: Formicidae). Entomol News 84:253–259
- Isingrini M, Lenoir A, Jaisson P (1985) Preimaginal learning as a basis of colony-brood recognition in the ant *Cataglyphis cursor*. Proc Natl Acad Sci U S A 82:8545–8547
- Ito F, Higashi S (1990) Temporary social parasitism in the enslaving ant species *Formica sanguinea* Latreille: an important discovery related to the evolution of dulosis in *Formica* ants. J Ethol 8:33–35
- Jaisson P (1985) Social behaviour. In: Kerkut GA, Gilbert LI (eds) Comprehensive insect physiology, biochemistry and pharmacology. Pergamon Press, Oxford, pp 673–694
- Jaisson P (1991) Kinship and fellowship in ants and social wasps. In: Hepper PG (ed) Kin recognition. Cambridge University Press, Cambridge, pp 60–93
- Jessen K, Klinkicht M (1990) Hybridization in the social parasitic ant genus *Epimyrma* (Hymenoptera, Formicidae). Insectes Soc 37:273–293
- Kaib M, Heinze J, Ortius D (1993) Cuticular hydrocarbon profiles in the slave-making ant *Harpagoxenus sublaevis* and its hosts. Naturwissenschaften 80:281–285
- Kannowski PB (1963) The flight activities of formicine ants. Symp Genet Biol Ital 12:74–102
- Keller L, Reeve HK (1994) Partitioning of reproduction in animal societies. Trends Ecol Evol 9:98–102

- Kusnezov N (1957) Numbers of species of ants in faunas of different latitudes. *Evolution* 11:298–299
- Kutter H (1957) Zur Kenntnis schweizerischer Coptoformicaarten (Hym., Form.) 2: Mitteilung. *Mitt Schweizer Entomol Ges* 30: 1–24
- Kutter H (1969) Die sozialparasitischen Ameisen der Schweiz. *Vierteljahresschr Naturforsch Ges* 113:1–62
- Lahav S, Soroker V, Vander Meer RK, Hefetz A (1999) Direct behavioral evidence for hydrocarbons as ant recognition discriminators. *Naturwissenschaften* 86:249–249
- LeMasne G (1970) Recherches sur la biologie des fourmis parasites. Le comportement agressif des ouvrières de *Chalepoxenus*. *C R Acad Sci Paris D* 271:1119–1121
- Le Moli F, Grasso DA, D’Ettorre P, Mori A (1993) Intraspecific slavery in *Polyergus rufescens* Latr. (Hymenoptera Formicidae): field and laboratory observations. *Insectes Soc* 40:433–437
- Le Moli F, Mori A, Grasso DA (1994) Behavioural ecology of the obligatory slave-making ant, *Polyergus rufescens* Latr. (Hymenoptera, Formicidae). A review. *Mem Zool* 48:133–146
- Lenoir A, Fresneau D, Errard C, Hefetz A (1999) Individuality and colonial identity in ants: the emergence of the social representation concept. In: Detrain C, Deneubourg JL, Pasteels JM (eds) *Information processing in social insects*. Birkhäuser, Basel, pp 219–236
- Lenoir A, D’Ettorre P, Errard C, Hefetz A (2001) Chemical ecology and social parasitism in ants. *Annu Rev Entomol* 46: 573–599
- Levings SC, Traniello JFA (1981) Territoriality, nest dispersion, and community structure in ants. *Psyche* 88:265–319
- Majerus M, Amos W, Hurst G (1996) Evolution. The four billion year war. Longman, Harlow
- Marchetti K, Nakamura H, Gibbs HL (1998) Host race formation in the common cuckoo. *Science* 282:471–472
- Marlin JC (1969) The raiding behavior of *Polyergus lucidus* in central Illinois (Hymenoptera: Formicidae). *J Kans Entomol Soc* 42:108–115
- Marlin JC (1971) The mating, nesting and ant enemies of *Polyergus lucidus* Mayr (Hymenoptera: Formicidae). *Am Midl Nat* 86:181–189
- May RM, Anderson RM (1983) Epidemiology and genetics in the coevolution of parasites and hosts. *Proc R Soc Lond B* 219:281–313
- Mori A, Grasso DA, Le Moli F (1991) Eco-ethological study on raiding behaviour of the European Amazon ant, *Polyergus rufescens* Latr. (Hymenoptera: Formicidae). *Ethology* 88:46–62
- Mori A, D’Ettorre P, Le Moli F (1994a) Mating and post-mating behaviour of the European Amazon ant, *Polyergus rufescens* (Hymenoptera, Formicidae). *Boll Zool* 61:203–206
- Mori A, Grasso DA, D’Ettorre P, Le Moli F (1994b) Specificity in host choice by the slave-making ant *Polyergus rufescens* Latr. (Hymenoptera Formicidae). *Ethol Ecol Evol* 3:S89–S93
- Mori A, D’Ettorre P, Le Moli F (1995) Host nest usurpation and colony foundation in the European Amazon ant, *Polyergus rufescens* Latr. (Hymenoptera: Formicidae). *Insectes Soc* 42:279–286
- Mori A, D’Ettorre P, Le Moli F (1996) Selective acceptance of parasitic brood by hosts in the evolution of slavery in ants (Hymenoptera: Formicidae). *Insectes Soc* 43:391–400
- Mori A, Grasso DA, Le Moli F (2000a) Raiding and foraging behavior of the blood-red ant, *Formica sanguinea* Latr. (Hymenoptera, Formicidae). *J Insect Behav* 13:421–438
- Mori A, Grasso DA, Visicchio R, Le Moli F (2000b) Colony founding in *Polyergus rufescens*: the role of the Dufour’s gland. *Insectes Soc* 47:7–10
- Mori A, Visicchio R, Sledge MF, Grasso DA, Le Moli F, Turillazzi S, Spencer S, Jones GR (2000c) Behavioural assays testing the appeasement allomone of *Polyergus rufescens* queens during host-colony usurpation. *Ethol Ecol Evol* 12:315–322
- Nonacs P, Tobin JE (1992) Selfish larvae: development and the evolution of parasitic behavior in the Hymenoptera. *Evolution* 46:1605–1620
- Pamilo P (1981) Genetic organization of *Formica sanguinea* populations. *Behav Ecol Sociobiol* 9:45–50
- Pamilo P, Crozier RH (1996) *Evolution of social insect colonies*. Oxford University Press, Oxford
- Pamilo P, Seppä P (1994) Reproductive competition and conflicts in colonies of the ant *Formica sanguinea*. *Anim Behav* 48:1201–1206
- Pollock GW, Rissing SW (1989) Intraspecific brood raiding, territoriality, and slavery in ants. *Am Nat* 133:61–70
- Poulin R, Morand S (2000) The diversity of parasites. *Q Rev Biol* 75:277–293
- Radchenko AG, Czechowski W, Czechowska W (1999) The tribe Formicoxenini (Hymenoptera, Formicidae) in Poland – a taxonomic review and keys for identification. *Ann Zool* 49:129–150
- Reeve HK, Ratnieks FLW (1993) Queen-queen conflicts in polygynous societies: mutual tolerance and reproductive skew. In: Keller L (ed) *Queen number and sociality in insects*. Oxford University Press, Oxford, pp 45–85
- Regnier FE, Wilson EO (1971) Chemical communication and “propaganda” in slave-making ants. *Science* 172:267–269
- Ross KG, Carpenter JM (1991) Phylogenetic analysis and the evolution of queen number in eusocial Hymenoptera. *J Evol Biol* 4:117–130
- Ruano F, Tinaut A (1999) Raid process, activity pattern and influence of abiotic conditions in the slave-making ant *Rossomyrmex minuchae* (Hymenoptera, Formicidae). *Insectes Soc* 46:341–347
- Ryan MJ (1990) Sexual selection, sensory systems and sensory exploitation. *Oxf Surv Evol Biol* 7:157–195
- Sanetra M, Buschinger A (2000) Phylogenetic relationships among social parasites and their hosts in the ant tribe Tetramoriini (Hymenoptera: Formicidae). *Eur J Entomol* 97:95–117
- Sanetra M, Felger S, Buschinger A, Zimmermann FK (1998) On the evolutionary history of social parasites in the ant tribe Tetramoriini (Hymenoptera: Formicidae). In: Schwarz MP, Hogendoorn K (eds) *Proceedings of the XIII International Congress IUSI*. IUSI, Adelaide, Australia, p 413
- Savolainen R, Deslippe RJ (1996) Slave addition increases sexual production of the facultative slave-making ant *Formica subnuda*. *Behav Ecol Sociobiol* 38:145–148
- Savolainen R, Seppä P (1996) Genetic relatedness among worker nestmates of three formicine slave-making ants. *Insectes Soc* 43:31–36
- Savolainen R, Vepsäläinen K, Deslippe RJ (1996) Reproductive strategy of the slave ant *Formica podzolica* relative to raiding efficiency of enslaver species. *Insectes Soc* 43:201–210
- Schmid-Hempel P (1998) *Parasites in social insects*. Princeton University Press, Princeton, N.J.
- Schumann RD, Buschinger A (1991) Selective acceptance of alien host species pupae by slaves of the dulotic ant, *Harpagoxenus sublaevis* (Hymenoptera, Formicidae, Myrmicinae). *Ethology* 88:154–162
- Schumann RD, Buschinger A (1995) Imprinting effects on host selection behavior of slave-raiding *Chalepoxenus muellerianus* (Finzi) workers (Hymenoptera: Formicidae). *Ethology* 90:243–251
- Singer TL (1998) Roles of hydrocarbons in the recognition systems of insects. *Am Zool* 38:394–405
- Stuart RJ (1981) Abdominal trophallaxis in the slave-making ant, *Harpagoxenus americanus* (Hymenoptera: Formicidae). *Psyche* 88:331–334
- Stuart RJ (1988) Development and evolution in nestmate recognition systems of social insects. In: Greenberg G, Tobach E (eds) *Evolution of social behavior and integrative levels*. Erlbaum, Hillsdale, N.J., pp 177–195
- Stuart RJ, Alloway TM (1982) Territoriality and the origin of slave making in lepto thoracine ants. *Science* 215:1262–1263
- Stuart RJ, Alloway TM (1983) The slave-making ant, *Harpagoxenus canadensis* M.R. Smith, and its host-species, *Leptothorax muscorum* (Nylander): slave raiding and territoriality. *Behaviour* 85:58–90

- Terayama M, Yamaguchi T, Hasegawa E (1993) Ergatoid queens of slave-making ant *Polyergus samurai* Yano (Hymenoptera, Formicidae). *Jpn J Entomol* 61:511–514
- Tinaut A, Ruano F (1999) Parasitismo social. *Bol Soc Ent Aragon* 26:727–740
- Toft CA (1991) An ecological perspective: the population and community consequences of parasitism. In: Toft CA, Aeschlimann A, Bolis L (eds) *Parasite-host associations. Coexistence or conflict?* Oxford University Press, Oxford, pp 319–343
- Toft CA, Aeschlimann A (1991) Introduction: coexistence or conflict? In: Toft CA, Aeschlimann A, Bolis L (eds) *Parasite-host associations. Coexistence or conflict?* Oxford University Press, Oxford, pp 1–12
- Toft CA, Aeschlimann A, Bolis L (eds) (1991) *Parasite-host associations. Coexistence or conflict?* Oxford University Press, Oxford
- Topoff H (1990) Slave-making ants. *Am Sci* 78:520–528
- Topoff H, Greenberg L (1988) Mating behavior of the socially-parasitic ant *Polyergus breviceps*: the role of the mandibular glands. *Psyche* 95:81–87
- Topoff H, Zimmerli E (1991) *Formica wheeleri*: Darwin's predatory slave-making ant? *Psyche* 98:309–317
- Topoff H, Zimmerli E (1993) Colony takeover by a socially parasitic ant, *Polyergus breviceps*: the role of chemicals obtained during host-queen killing. *Anim Behav* 46:479–486
- Topoff H, LaMon B, Goodloe L, Goldstein M (1984) Social and orientation behavior of *Polyergus breviceps* during slave-making raids. *Behav Ecol Sociobiol* 15:273–279
- Topoff H, Cover S, Greenberg L, Goodloe L, Sherman P (1988) Colony founding by queens of the obligatory slave-making ant, *Polyergus breviceps*: the role of the Dufour's gland. *Ethology* 78:209–218
- Trivers RL, Hare H (1976) Haplodiploidy and the evolution of the social insects. *Science* 191:249–263
- Tschinkel WR (1996) A newly-discovered mode of colony founding among fire ants. *Insectes Soc* 43:267–276
- Vander Meer RK, Morel L (1998) Nestmate recognition in ants. In: Vander Meer RK, Breed M, Winston M, Espelie KE (eds) *Pheromone communication in social insects*. Westview Press, Boulder, Colo., pp 79–103
- Vander Meer R, Slaiwanchik D, Lavine B (1989) Temporal changes in colony cuticular hydrocarbons patterns of *Solenopsis invicta*. Implications for nestmate recognition. *J Chem Ecol* 15:2115–2125
- Wasmann E (1905) Ursprung und Entwicklung der Sklaverei bei den Ameisen. *Biol Zentralbl* 25:117–127, 129–144, 273–292
- Wheeler WM (1910) *Ants: their structure, development and behavior*. Columbia University Press, New York
- Wheeler WM (1928) *The social insects: their origin and evolution*. Kegan Paul, Treanch, Trubner, London
- Wilson EO (1971) *The insect societies*. Harvard University Press, Cambridge, Mass.
- Wilson EO (1975) *Leptothorax duloticus* and the beginnings of slavery in ants. *Evolution* 29:108–119
- Yamaoka R (1990) Chemical approach to understanding interaction among organisms. *Physiol Ecol Jpn* 27:31–52
- Yasuno M (1964) The study of the ant population in the grassland at Mt. Hakkôda III. The effect of the slave making ant, *Polyergus samurai*, upon the nest distribution pattern of the slave ant, *Formica fusca japonica*. *Sci Rep Tôhoku Univ Ser IV Biol* 30:167–170
- Zimmerli E, Mori A (1993) The role of an attractive brood pheromone in the obligatory slavemaking ant, *Polyergus breviceps* (Hymenoptera: Formicidae). *J Insect Behav* 6:761–770
- Zimmerli E, Topoff H (1994) Queens of the socially parasitic ant *Polyergus* do not kill queens of *Formica* that have not formed colonies (Hymenoptera: Formicidae). *J Insect Behav* 77:119–121