

Arms races between social parasites and their hosts: geographic patterns of manipulation and resistance

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The evolutionary interactions between permanently social parasitic species and their hosts are of special interest because social parasites are not only closely dependent on, but are also closely related to, their hosts. The small European slavemaker *Harpagoxenus sublaevis* has evolved several characters that help manipulate its host. In this study we investigated adaptations of this social parasite to its local hosts and the geographic pattern of host resistance in two main host species from three different populations. In behavioral experiments, we examined whether host colonies from three geographically distant *Leptothorax acervorum* populations varied in their ability to defend the nest against social parasites. Naive colonies from the unparasitized English population killed attacking slavemakers more often than did host colonies from two parasitized populations. We also found strong interpopulation variation in the ability of the slavemaker to manipulate host behavior. *H. sublaevis* uses the Dufour gland secretion to induce intracolony fights and, in general, this “propaganda” substance was most effective against local hosts. Our results suggest that the social parasite is leading the arms race in this aspect. Similar experiments uncovered differences between two populations of the second host species *L. muscorum* and could demonstrate that nest defense in both host species is similarly efficient. In *L. acervorum*, monogynous colonies were more successful in nest defense, whereas social structure had no impact in *L. muscorum*. Colony size did not affect the efficacy of nest defense in either host species. The caste of the slavemaker had a strong influence on the success of an attack. **Key words:** coevolution, geographic mosaics, host–parasite system, host resistance, slavemaking ants, social parasites. [*Behav Ecol* 14:80–88 (2003)]

Parasitism is a common phenomenon in many animal taxa, from simple platyhelminths to vertebrates such as fish and birds. It reaches a special dimension when the social behavior of another species is exploited (Buschinger, 1993). Avian brood parasites are a good example. Cuckoos and cowbirds lay eggs in nests of different species to avoid the costs of brood care (Rothstein and Robinson, 1998). Social parasitism can be defined as the exploitation of social behaviors by another species (Hölldobler and Wilson, 1990). It occurs in several Hymenopteran families, but is common and widely distributed among ants, where more than 300 socially parasitic species are known (Buschinger, 1993). Social parasite systems differ from most ecto- and endoparasites because host and parasite are, following Emery’s rule, often closely related species (Emery, 1909; Wilson, 1971). The close phylogenetic relationship has strong implications on the coevolutionary interactions.

Coevolution and the arms-race paradigm has been shown to be suitable for various host–parasite systems (Allison, 1982; Anderson and May, 1982; Gandon et al., 1996; Schmid-Hempel, 1998; Thompson and Burdon, 1992). However, close coevolutionary interactions in a stepwise fashion are especially likely to occur when host and parasite exhibit similar generation times and population sizes, as in social parasites. In such a situation, hosts are expected to keep up with the parasite and to evolve resistance characters when parasite pressure is strong. Only few empirical studies have investigated the coevolutionary interactions between social insect

parasites and their hosts (Foitzik et al., 2001; Hare and Alloway, 2001; Lorenzi and Filippone 2000). This is in contrast to the large literature on this subject in avian brood parasites (Davies, 2000; Rothstein and Robinson, 1998). In general, it has been assumed that brood parasites have won the arms race (Dawkins, 1982; Gladstone, 1981; Grasso et al., 1992). Observations of a cuckoo chick fed by step-parents half its size or of *Leptothorax* workers indifferent to the strangulation of their mother by a tiny parasitic *Epimyrma* queen (Hölldobler and Wilson, 1990; Kutter, 1968) appeared to suggest that these hosts are unable to evolve resistance. However, studies on avian systems have revealed the occurrence of concealed defensive mechanisms (e.g., clutch desertion or egg rejection; Davies, 2000; Davies et al., 1996; Lotem et al., 1992; Soler et al. 1999), and a recent study on coevolution in social parasites found indications of arms races and resistance characters in strongly parasitized host populations (Foitzik et al., 2001).

Permanent social parasites have one of two distinct life-history strategies (Buschinger, 1993; D’Ettorre and Heinze, 2001; Kutter, 1968): inquilines are social endoparasites that live in a host colony, often without killing host workers or queens. In contrast, slavemakers live in their own nest, but have to conduct periodic slave raids to replenish their labor force on which they depend throughout their lives. These raids destroy the reproduction and growth of several host nests each year. Often, when the queen or many workers are killed, host colonies eventually perish (Alloway, 1979, 1990; Foitzik and Herbers, 2001; Foitzik et al., 2001; Hasegawa and Yamaguchi, 1994; Kwiat and Topoff, 1984; Mori et al., 1991). Parasite pressure on host populations can be substantial, depending on the number of slavemaker colonies and their raiding frequency. Presence of the North American slavemaker *Protomognathus americanus* is linked to demographic, ecological, behavioral, and genetic changes in nearby *Leptothorax longispinosus* host colonies (Foitzik and Herbers, 2001; Foitzik et al., 2001; Herbers and Foitzik, 2002).

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One of the biggest challenges in coevolutionary theory is to understand how coevolution can occur over broad geographic landscapes (Benkman et al., 2001; Thompson, 1999). Coevolution can be either universal or localized (Foitzik et al., 2001). According to the geographic mosaic theory (Thompson, 1994, 1999), universal coevolution occurs when there are only few possible ways by which host and parasite can adapt to each other. Then both host and parasite will evolve universal strategies depending on the intensity of selection pressure. In coevolutionary hot-spots, the arms race will be very advanced. The host will be equipped with many defenses and the slavemaker with superior parasite adaptations. In other localities, ecological selection pressures are predominant so that both species will not coadapt. According to this model, parasite efficacy is correlated with host defensiveness and depends on historic parasite pressures. In contrast, the model of local coevolution assumes that host and parasite evolve different strategies in different populations. Here, strong geographic differences are expected, and it is not clear a priori how host populations fare in attacks by parasites from different populations. Both models are not mutually exclusive; some adaptations might follow one model and some the other.

Harpagoxenus sublaevis (Nylander, 1852), the species studied here, is an obligatory slavemaker that occurs throughout the boreal region of Western Eurasia. It parasitizes predominately *Leptothorax acervorum* (Fabricius, 1793) and *L. muscorum* (Nylander, 1846), and very rarely parasitizes the patchily distributed *L. gredleri* (Mayr, 1855). Due to the wide distribution and easy laboratory culture of this slavemaking species, many aspects of its biology have been studied (Adlerz, 1896; Bourke, 1988; Bourke et al., 1988; Buschinger, 1968, 1971, 1975; Buschinger and Winter, 1975, 1978; Buschinger et al., 1980; Schumann and Buschinger, 1991; Trivers and Hare, 1976; Vieh Meyer, 1908; Winter and Buschinger, 1986). However, host–parasite coevolution has not been investigated, even though this system allows the test of various hypotheses. For example, we used in this study the occurrence of large-scale, parasite-free host populations of *L. acervorum* to analyze the reaction of naive workers toward a slavemaker in comparison to workers from parasitized populations. Thus, we could study the evolution of behavioral defenses in a host as a reaction to parasite pressure. Furthermore, we examined in behavioral tests whether there was evidence for universal or localized coevolution. To be able to differentiate between these two models, we included all host and parasite species from three different localities. This procedure also allowed us to test whether the social parasite was specialized on different host species in different populations. Parasite specialization can lead to host alternations—that is, oscillation of host species use over time and space (Davies and Brooke, 1989a,b; Thompson, 1999). Particularly, the sympatric occurrence of the two main host species *L. acervorum* and *L. muscorum* in close proximity and over a large part of their distribution could induce host alternations, as has been suggested for avian brood parasites (Davies and Brooke, 1989a,b). Furthermore, the ability of the parasite to manipulate sympatric or allopatric host populations by using a “propaganda” substance (Allies et al., 1986) could indicate whether parasite or host leads the arms race in this respect.

METHODS

Natural history of the slavemaker *Harpagoxenus sublaevis*

In the palaeartic slavemaking ant, *H. sublaevis*, most queens are wingless and resemble workers in external morphology (intermorphic queens; Buschinger, 1975; Buschinger and

Winter, 1975, 1978; Winter and Buschinger, 1986). Parasitic queens have therefore limited dispersal capabilities. The life cycle starts with a queen which leaves the nest in summer and attracts males through female calling (Buschinger, 1968). After mating, the queen searches for a host colony and enters the nest (Buschinger, 1974). If the slavemaking queen is successful, she kills or expels all host workers and queens and takes over the nest site with the brood. When the new host workers emerge, they start working in the nest as slaves and raise the parasitic brood. Raids ensure the recruitment of new slaves, which take over all routine chores in the colony. Slavemaker workers, which are produced the next year, conversely, are well equipped for raiding, their main task, with large mandibles that are good for fighting (Buschinger, 1966a,b, 1968, 1974; Buschinger et al., 1980; Vieh Meyer, 1908). If a scout discovers a host nest, it returns to the mother colony and recruits nest mates (Buschinger and Winter, 1977; Buschinger et al., 1980). During the raid, members of the host colony are killed or expelled, and the brood is stolen. In these attacks, *H. sublaevis* uses a “propaganda substance” from the Dufour gland, which induces deadly fights among nest-mate host workers (Allies et al., 1986; Buschinger, 1974; Regnier and Wilson, 1971). The social parasite thus does not sting host workers directly, but uses the sting to apply this secretion onto the cuticle of host workers.

Slavemaker populations

Colonies of the slavemaker *H. sublaevis* were collected in Germany and Russia. In Germany, ants were collected in summer 2000 in pine forests close to Erlangen (11°02' E, 49°35' N), Feucht (11°16' E, 49°20' N), and Abensberg (11°58' E, 48°49' N), Bavaria. In Russia, slavemakers were collected in summer 1999–2000 in a population near Vyrica-Posyolok, 50 km south of St. Petersburg (30.5° E, 59.3° N). The slavemaker *H. sublaevis* does not occur in Great Britain (Radchenko et al., 1999), leaving the potential host population of *L. acervorum* unparasitized.

Host populations

We used host colonies of *L. acervorum* from Germany, Russia, and England. The German colonies were collected in summer 2000 in pine forests near Erlangen, Feucht, and Abensberg. Russian host colonies were obtained in July 2000 from a population near Vyrica-Posyolok (see above). Ants were collected in England in July 2000 at a site in the New Forest, close to the small village of Norleywood, Hampshire (1°30' E, 50°47' N). At all three collection areas the habitat was a pine forest with an undergrowth of heather, blueberries, and ferns. Colonies of all three species inhabit cavities in sticks and logs on the forest floor.

Leptothorax muscorum colonies were collected in the same habitats in Germany and Russia. This species is widely distributed throughout the boreal region of the Palaearctic, but it does not occur on the British Isles (Radchenko et al., 1999).

Ant collection and laboratory maintenance

We transported the ants to the laboratory in Regensburg, censused them, and allowed them to move into artificial nests inside small boxes (10 cm × 10 cm × 1.5 cm) with a moistened plaster floor (Buschinger, 1974; Heinze and Ortius, 1991). During the behavioral tests we kept the ants at room temperature (20°–25°C). Twice weekly all colonies were fed with diluted honey and pieces of cockroaches.

Behavioral tests

General setup for experiments on colony defense

Host colonies from various populations exhibited different demography such as queen number and worker number, which could confound the efficiency of nest defense. Therefore, we chose colonies for the experiments to control for demographic variation. We observed the reaction of host colonies to the introduction of a single slavemaker using a cross-fostering design. Thus, we allowed single slavemakers to enter nests from various host populations. Each host colony and each individual slavemaker was used only once.

The behavioral tests were conducted in arenas of 20.0 cm × 10.0 cm × 5.5 cm with a plaster floor. No food was provided during the experiment. The slavemaker was introduced in the middle of the arena, at about 10 cm from the host nest entrance. We observed the reaction of the host ants and the behavior of the slavemaker for the next 3–9 h, depending on the type of experiment (see below). Every 5 min we noted the number of host workers that were in the nest entrance and that bit the slavemaker. We also recorded the use of the sting by the slavemaker and the host workers and the number of host workers engaged in intracolony fights.

In a final analysis, after 24 h we recorded the number of dead and injured host workers and queens, as well as the number of raided larvae and pupae. *H. sublaevis* slavemakers fight with their strong mandibles and cut off legs or antennae of their opponents. We therefore noted the number of host workers that were injured (i.e., had lost legs or antennae) in fights. We also noted the position of the slavemaker (in the nest site or in the arena) and whether it had survived the encounter without injuries.

Experiments with Leptothorax acervorum

In this test series, we compared the response of host colonies from the unparasitized English population to a *H. sublaevis* slavemaker with the reaction of host colonies from parasitized areas in Germany and Russia. We also investigated the impact of social organization and size of the host colony as well as of slavemaker caste on the behavior during and the outcome of the encounter. We used 34 *L. acervorum* colonies from the 3 host populations and 102 slavemakers; 51 slavemakers came from 7 Russian colonies and the same number of social parasites from 11 German colonies. All slavemakers came from colonies with *L. acervorum* slaves, except three from Germany, which had a high fraction of *L. acervorum* slaves. Single slavemakers were allowed to enter nests from all three host populations. We used each host colony and each individual slavemaker only in one experiment. The experimental setup was observed for a total of 9 h.

From external morphology alone, it is impossible to determine the caste of a *H. sublaevis* slavemaker unambiguously, and thus we used both slavemaker queens and workers in the trials. After the experiments, we killed all slavemakers by freezing and dissected them to record the conditions of the ovaries and the presence of spermatheca. This allowed the caste assignment of individuals. Furthermore, we determined the size of all slavemakers to investigate the impact of body size on the success of an attack. We measured maximum head width, thorax length, and thorax width (Heinze and Buschinger, 1987; Kaspari, 1996). We calculated a mean of three measures for each size parameter that were done with a binocular microscope with ×60 magnification.

Experiments with Leptothorax muscorum

In this test series, we conducted a total of 46 experiments, including 31 German and 15 Russian *L. muscorum* host colonies. The slavemakers came from colonies with *L.*

muscorum slaves. In all experiments we observed the reaction of a host colony to the presence of a German slavemaker and again analyzed the impact of host nest size (number of workers) and social structure (number of queens). Each experimental setup was observed for a total of 3 h.

Experiments on the effect of the “propaganda substance”

In a third test series we investigated the impact of the Dufour gland secretion of *H. sublaevis* on *L. acervorum* colonies from different host populations. We removed a single host worker from a focus nest, marked it on the thorax with quick dry metallic ink pens (Edding), and allowed the paint to dry for 20 min. We killed *H. sublaevis* slavemakers from Germany by freezing and dissected the Dufour gland out of the gaster. With a fine sterile needle we applied the content of the gland onto the gaster of a marked *L. acervorum* host worker and allowed it to reenter its mother colony by walking through a 2-cm long piece of plastic straw. We observed experimental colonies every 30 s for the next 30 min and recorded the behavior of the focal worker and the reaction of nest mates. We differentiated between three behaviors of the marked worker: moving, inactivity, and self-grooming. We recorded the frequency of the following behaviors of nest-mate workers that were directed toward the focal individual: antennating, opening of mandibles, biting, carrying and allo-grooming. Antennating can occur in various contexts, while opening of mandibles, biting, and carrying are behaviors typically involved in nest defense. Opening of mandibles often precedes biting and can be seen as a threat behavior. Carrying behavior is not only involved in nest movement, but *Leptothorax* ants frequently react to the invasion of an alien individual by carrying it out of the nest (Dobrzanski, 1966; Foitzik and Heinze, 1998; Heinze et al., 1996). In our experiments, we closed the nest entrance and thus prohibited the removal of the focus worker. Allo-grooming was considered a friendly reaction, as it is a behavior typically restricted to nest mates.

We deliberately chose experimental colonies with a similar demographic distribution from the different populations. Thus, there was no interpopulational variation in colony size and queen number. However, individual colonies varied considerably in size (25–130 workers), and we therefore analyzed data on observed behaviors (antennating, biting, etc.) per capita. As we did not know how fast the Dufour gland secretion evaporates, we analyzed the data in two ways: first, we investigated the frequency of the focal behaviors in the first 5 min after introduction; and, second, we analyzed the frequency of behaviors throughout the duration of the experiment.

Statistics

The data sets were tested for normal distribution with the Kolmogorov-Smirnov test. As a rule, the data were not normally distributed, and thus we used nonparametric tests for data analysis. We abbreviate the various tests in the results as follows: Mann-Whitney *U* test (MW), Kruskal-Wallis test (KW), Fisher's Exact test (FE), post-hoc Scheffé test (PS), and. The chi-square test and the Spearman rank order correlation are indicated by the χ^2 value and the r_s value, respectively. When multiple tests were performed on the same tables, we corrected the α values according to the sequential Bonferroni method (Rice, 1989). All statistical tests were performed with the program Statistica.

RESULTS

Demography of slavemaker nests

We collected a total of 32 *H. sublaevis* colonies in Germany in 2000. Ten (31%) of these contained only *L. acervorum* slaves,

9 (28%) *L. muscorum* slaves, and 9 (28%) slave workers of both species. One colony consisted of a *Harpagoxenus* queen and *L. acervorum* worker pupae, but no adult slaves. Three times we collected a single slavemaker queen not surrounded by host ants. Slavemaker colonies with *L. acervorum* or *L. muscorum* slaves did not differ in colony size (number of slavemaker or slave workers) or productivity (per capita production of new workers or sexuals; MW: $p > .10$, $n = 10, 9$). All slavemaker colonies contained one queen and on average 15.2 ± 4.4 (SE) slavemaker workers and 55.5 ± 11.6 slaves. Six *H. sublaevis* colonies were collected in Russia in 1999. We found an additional five colonies in summer 2000, and only for those we can report demographic data at time of collection. All 5 colonies had a single queen, but only 3 of them also contained between 2 and 16 slavemaker workers and between 0 and 83 *L. acervorum* slaves. The demographic composition of slavemaker nests from Germany and Russia did not differ in the number of queens, slavemaker workers, or slaves (MW: $p > .10$, $n = 32, 5$).

In the Russian and the German populations the host species *L. acervorum* and *L. muscorum* coexist, and we found slavemaker–host nest ratios between 1:15 and 1:5. The composition of the Formicoxenine ant communities differed strongly between Germany and Russia (G test: $\chi^2_2 = 13.74$, $p < .005$). We found higher relative slavemaker frequencies in Germany ($\chi^2_1 = 5.69$; $p < .02$) and a higher fraction of *L. muscorum* host colonies in Germany compared to Russia ($\chi^2_1 = 7.69$; $p < .006$). In Russia, we did not find enslaved *L. muscorum* workers, and pooling over both slavemaker populations *H. sublaevis* appeared to slightly prefer *L. acervorum* ($\chi^2_1 = 3.89$; $p = .049$). This preference was not significant in our subsets from Germany (FE: $df = 1$, $p = .13$) or Russia alone (FE: $df = 1$, $p = .17$). A larger proportion of German slavemaker colonies appeared to contain *L. muscorum* slaves compared to Russian social parasite nests (FE: $df = 1$, $p = .07$).

Experiments with *L. acervorum*

Colony demography of host populations

We collected 222 *L. acervorum* colonies; 78 colonies in Germany (G), 53 colonies in Russia (R), and 91 colonies in England (E). We found a significant difference in worker number between German and Russian colonies, the latter containing more workers (KW: $H_2 = 11.06$, $p < .025$; PS: G–R: $p < .02$, G–E: $p > .20$, R–E: $p > .20$). We uncovered interpopulational variation in social structure. In Germany, colonies were more likely to be monogynous (72%) than colonies from the two other populations (R, 54%; E, 55%; KW: $H_2 = 11.00$, $n = 67, 53, 81$ for G, R, E, respectively; $p < .01$; PS: G–R: $p < .005$, G–E: $p > .30$, R–E: $p = .07$). Although we did not map the host populations, we noted that colony densities differed between the three populations. Although all English colonies were collected in an area with more than 2 nests/m², colony densities were much lower both in Germany and Russia (< 0.5 /m²).

Nest defense experiments

Influence of sympatry or allopatry of host and parasite. We analyzed whether the results of the experiments depended on sympatry or allopatry of slavemaker and host. We could compare this only for the experiments including German and Russian hosts. Overall, we found only one difference: host workers tried to sting slavemakers from the same population less often than slavemakers from another population (MW: $U = 393.5$; $p < .025$, $n = 34, 34$).

Influence of host colony origin. During the experiments, host workers from all three populations were observed to attack

and to immobilize the slavemaker. German colonies positioned significantly more guards in the host nest entrance than host colonies from the other two populations (KW: $H_2 = 9.01$, all $n = 34$; $p < .015$ for trend; PS: G–R: $p < .05$, G–E: $p < .01$, R–E: $p > .80$). In the first 3 h after introduction of the slavemaker, the number of workers immobilizing the slavemaker by biting was lowest in Russian colonies, but did not differ between German and English colonies (KW: $H_2 = 8.87$, all $n = 34$; $p < .015$ for trend; PS: G–R: $p = .16$, G–E: $p > .70$, R–E: $p < .03$). English host workers tried to sting the slavemaker more often (KW: $H_2 = 5.85$, all $n = 34$; $p = .053$; PS: G–R: $p > .75$, G–E: $p < .02$, R–E: $p < .08$).

When looking at the outcome after 24 h, the survival rate of host workers and queens did not differ between the various host populations (KW: $H_2 = 6.38$, all $n = 34$; $p = .88$). However, colonies from the English (50%) population managed to kill the slavemaker more often than colonies from the German (24%) or the Russian (26%) population (G test: $\chi^2_2 = 6.44$, $p < .05$, CS: G–R: $p > .75$, G–E: $p < .025$, R–E: $p < .05$).

Influence of the social structure of host colonies. When analyzing the impact of the social structure, we pooled over host populations. Monogynous and polygynous colonies did not differ in their behavior during the experiments (MW: $p > .10$, $n = 62, 40$ for monogynous and polygynous, respectively). Nevertheless, we found a significant difference in the efficacy of nest defense. After 24 h, monogynous colonies (44%) had killed the slavemaker more often than polygynous colonies (18%; $\chi^2_1 = 7.42$; $p < .007$). Over all host populations, colony size was not different between colonies that were able to kill the slavemaker and those that were not (MW: $U = 1093.5$; $p = .66$, $n = 68, 34$ for killed, did not kill, respectively).

Influence of slavemaker origin. During the experiments, slavemakers from the two populations showed no obvious differences in their behavior. However, the Russian host population reacted differently to slavemakers from Russia or Germany in that workers tried to sting German slavemakers more often than Russian slavemakers ($\chi^2_1 = 6.10$; $p < .015$ for trend). We found no such differentiation in the German and English hosts (CS: $p > .20$). All five slavemakers that took over the host colony within 24 h came from the Russian population (FE: $p = .08$).

We found interpopulational variation in the reaction to the Dufour gland secretion. Pooling over host populations, host workers confronted with a Russian slavemaker engaged in more intracolony fights than when confronted with a German slavemaker (MW: $U = 982.5$; $p < .035$, $n = 51, 51$). However, when testing within populations this effect was found only in the German population. German host colonies started more intracolony fights when confronted with a Russian slavemaker than when attacked by a sympatric social parasite (MW: $U = 67.0$; $p < .008$, $n = 17, 17$). Russian or English host colonies did not change their fighting behavior in response to slavemaker origin (MW: $p > .30$, $n = 17, 17$). Slavemaker origin also did not influence the proportion of host workers that were killed during the experiment.

Pooling over host populations, we found a positive association between the frequency of usage of the sting and the relative proportion of host workers that were killed ($r_s = .24$, $p < .018$ for trend, $n = 101$). These killings were mostly the result of intracolony fights because, first, we found a tight association between host worker death and aggressive behaviors between nest mates ($r_s = .42$, $p < .0001$, $n = 101$), and, second, the number of times the slavemakers used their sting to apply the propaganda substance was positively correlated with the number of fights ($r_s = .39$, $p < .0001$, $n = 102$). Again, host and slavemaker origin had an impact on the

Table 1
The correlation between the rate of Dufour's gland application and the frequency of intracolony fights

Origin of slavemaker colonies	Origin of host colonies		
	Germany	Russia	England
Germany	$r_s = .11$, $p = .68$	$r_s = .40$, $p = .11$	$r_s = .35$, $p = .17$
Russia	$r_s = .32$, $p = .21$	$r_s = .79$, $p < .0002^*$	$r_s = .49$, $p < .05$

The results of Spearman rank correlations are given; $n = 17$ in all cases.

* Significant p values after Bonferroni correction.

reaction. Although we did not find an association for any of the host populations in reaction to the behavior of German slavemakers, Russian slavemakers used the Dufour gland secretion to manipulate Russian and, to a slighter extent, English *L. acervorum* colonies to attack their own nest mates (Table 1).

Influence of slavemaker caste. The caste of the slavemaker greatly influenced the outcome of the encounters. Through dissections we found that 25 slavemakers used in the experiments had a spermatheca and thus were intermorphic queens; 5 of these queens were mated. Seventy-five individuals were slavemaker workers. The caste of two slavemakers could not be determined. Slavemaker queens (8%) were killed less often by the host colony than slavemaker workers (43%; $\chi_1^2 = 10.04$; $p < .002$). In addition, we found that four of five slavemakers that successfully invaded a host colony were mated queens.

Our measurements showed that slavemakers queens were only slightly larger than workers (Table 2). Although thorax length and width differed significantly (MW: $p < .02$ for trend, $n = 23$, 74 for queens, workers, respectively), we could not find a difference in head width (MW: $p > .20$). Although several body size parameters were linked to slavemaker caste, size did not influence the survival rate of slavemakers overall (MW: $p > .50$, $n = 65$, 32). The body size of *H. sublaevis* was larger in Russia (MW: $p < .05$ for trend, $n = 48$, 49).

Experiments on the effect of the propaganda substance

We found strong interpopulational differences in the reaction of *L. acervorum* colonies to the Dufour gland secretion from German slavemakers applied to a nest-mate host worker. First, the focal individual behaved differently. Introduced Russian and English workers moved around more in their mother nest. In contrast, German workers were mostly inactive (Table 3; PS for inactivity; G–R: $p < .02$, G–E: $p < .07$, R–E: $p > .55$).

Host colonies from different populations varied in their aggressive reaction to the propaganda substance (Table 4). Consistently, host colonies from Russia reacted less aggressively than German or English host colonies (Figure 1; PS for biting; G–R: $p < .11$, G–E: $p > .60$, R–E: $p < .03$). Furthermore, German host colonies groomed the focal worker much more often in the first 5 min of the experiment than colonies from Russia or England (G test: $\chi_2^2 = 10.61$, $p < .005$; G–R: $p < .02$, G–E: $p < .015$, R–E: $p > .80$).

We did not find behavioral differences between monogynous and polygynous host colonies (MW: $p > .15$, $n = 13$, 26 for monogynous, polygynous, respectively), and host workers did not react differently to the Dufour gland secretion of slavemaker workers or queens (MW: $p > .10$, $n = 12$, 28 for secretions of workers, queens, respectively).

Table 2
Mean head width, thorax length, and thorax width of intermorphic queens and workers of the slavemaker *Harpagoxenus sublaevis*

	Head width (mm)	Thorax length (mm)	Thorax width (mm)
Queens	0.79 ± 0.006	1.16 ± 0.008	0.50 ± 0.005
Workers	0.78 ± 0.004	1.14 ± 0.007	0.48 ± 0.004

A total of 74 workers and 23 queens were dissected and measured. Means \pm SEs are given.

Experiments with *L. muscorum*

Colony demography of the populations

In Germany, we collected 62 *L. muscorum* colonies and 17 *H. sublaevis* slavemaker nests containing *L. muscorum* slaves. Thus, the slavemaker–host nest ratio was 1:3.7. Eight of the slavemaker colonies (47.1%) also contained *L. acervorum* slaves. In our year 2000 collections in Russia, we found 24 *L. muscorum* colonies, none of which contained the social parasite. Thus, parasite pressure on the host species *L. muscorum* is higher in Germany than in Russia ($\chi_1^2 = 4.95$; $p < .03$). There are strong differences in colony demography between the two host populations. In Russia, *L. muscorum* colonies were more likely to be polygynous (MW: $U = 220.5$; $p < .005$, $n = 33$, 24 for R, G, respectively), and were smaller, containing fewer workers, fewer worker pupae, and fewer larvae (MW: $p < .001$).

Nest defense experiments

As a general rule, *L. muscorum* colonies reacted with aggression toward the social parasite. Host workers tried to bite and sting the slavemaker and often immobilized it by biting its limbs. However, colonies from Russia and Germany did not differ in their efficiency to kill an attacking slavemaker ($\chi_1^2 = 0.25$; $p > .60$). Although the same proportion of Russian or German host workers were killed during the experiments (MW: $U = 220.0$; $p > .70$, $n = 31$, 15 for R, G, respectively), more *L. muscorum* workers from the Russian population were injured (i.e., lost limbs during fights; MW: $U = 140.0$; $p < .03$).

In contrast to what we found for *L. acervorum*, monogynous and polygynous *L. muscorum* colonies did not differ in their efficacy to kill the slavemaker ($\chi_1^2 = 1.30$; $p = .25$). Colony size (i.e., number of workers) was closely linked to the frequency of the host colony to immobilize the slavemaker during the experiments ($r_s = .49$; $p < .001$, $n = 46$). However, just as for *L. acervorum*, colony size did not influence the likelihood with

Table 3
Interpopulation differences in the behaviour of *Leptothorax acervorum* workers, onto whose gaster the Dufour gland secretion of a German slavemaker was applied, after reintroduction into its mother colony

Behavior	Within the first 5 min		During the entire test (30 min)	
	H	p	H	p
Inactive	6.95	.031*	5.63	.060
Moving	6.40	.041	6.60	.037
Self-grooming	0.68	.716	2.10	.350

A total of 40 behavioral tests were performed and analyzed with a Kruskal-Wallis test.

* Significant p values after Bonferroni correction.

Table 4
Interpopulation variation in the reaction of *Leptothorax acervorum* colonies to a worker coated with Dufour gland secretion of a German slavemaker

Behavior	Within the first 5 min		During the entire test (30 min)	
	<i>H</i>	<i>p</i>	<i>H</i>	<i>p</i>
Antennating	2.26	.324	1.81	.405
Opening of mandibles	6.68	.036*	6.04	.049
Biting	8.33	.016*	6.34	.042
Carrying	5.55	.080	8.95	.011*

German and English colonies behaved much more aggressively compared to Russian colonies (see Figure 1). A total of 40 behavioral tests were performed and analyzed with a Kruskal-Wallis test.

* Significant *p* values after Bonferroni correction.

which the slavemaker was killed during the experiment (MW: $U = 218.0$; $p > .60$, $n = 31$, 15 for workers that survived, were killed, respectively).

Comparison of nest defense between the two host species

To analyze whether the efficacy of nest defense differed between the two host species, we compared the experiments including both German slavemakers and German and Russian host colonies. *L. acervorum* and *L. muscorum* host colonies did not differ in their efficiency to defend their nest against the social parasite. The slavemaker *H. sublaevis* was killed as often by *L. acervorum* as by *L. muscorum* host colonies ($\chi^2_1 = 1.28$; $p = .26$). Although *L. muscorum* workers are by far smaller, the same fraction of the host workers was killed during the experiments (MW: $U = 615.5$; $p = .11$, $n = 46$, 34 for *L. acervorum*, *L. muscorum*, respectively).

DISCUSSION

The results of our behavioral experiments with *L. acervorum* are summarized in Tables 5 and 6. Although all host colonies

recognized the slavemaker as an enemy and attacked it, different *L. acervorum* populations varied in their ability to defend their nest against the social parasite *H. sublaevis*. Naive colonies from the unparasitized English population were more successful in killing the slavemaker than colonies from two parasitized host populations in Russia and Germany. Two behavioral differences can explain how English *L. acervorum* colonies were able to defend their nest so efficiently: workers immobilized the slavemaker more often by biting in the first 3 h after introduction, and they tried to sting the slavemaker more frequently.

Nest defense was certainly not enhanced by the demographic colony composition. English *L. acervorum* colonies are frequently polygynous, which generally lowers defensiveness (Breed and Bennet, 1987; Hölldobler and Wilson, 1977; Morel et al., 1990; this study) and are often smaller than host colonies from the other two populations. Thus, the question remains why English colonies are ultimately so much better in defending their nest against the social parasite. We found three possible explanations for this phenomenon. English colonies might have evolved these resistance characters at a time when *L. acervorum* host populations on the British Isles were parasitized by *Harpagoxenus*. Due to the absence of historical distribution data on ant species, we cannot test this hypothesis. Another explanation is based on the colony odor of slavemaker and host. *L. acervorum* populations from the British Isles are geographically isolated, and their cuticular hydrocarbon profile might have changed through genetic drift to become different from mainland populations. We found that host colonies attacked slavemakers from the same population less often than allopatric slavemakers. This could be caused by an adaptation of the slavemaker to mimic the cuticular hydrocarbon profile in order to sneak into host colonies without triggering aggression. *H. sublaevis* slavemakers acquire a colony odor similar to that of their host species (Heinze et al., 1994; Kaib et al., 1993). Thus, it is possible that English *L. acervorum* colonies attacked the social parasite so heavily not because this population evolved resistance, but because the social parasite is well adapted to its local host. In addition to being an adaptation in the context of social parasitism, high aggressiveness could have evolved on a different background. We collected *L. acervorum*

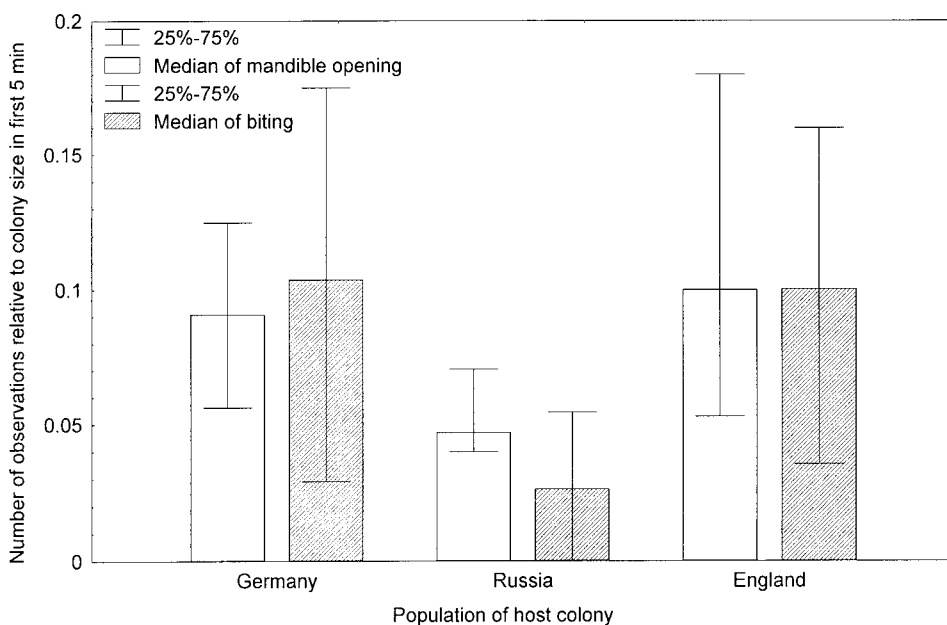


Figure 1
Leptothorax acervorum colonies from Russia reacted less aggressively to nest-mate workers coated with the Dufour gland secretion of a German slavemaker. The chemical substance in the Dufour gland of this slavemaker is used as a propaganda substance, and its application generally leads to intracolony aggression within host colonies.

colonies in England in an area with exceptionally high nest density (>2 nests/m²). Due to many encounters with non-nest-mate workers and high intraspecific competition, this population might have developed a good nest mate recognition system and high aggression against conspecifics. These adaptations could also help in the defense against the slavemaker. We have additional data consistent with this hypothesis. *L. acervorum* colonies from England were very aggressive to their own nest mates treated with the Dufour gland secretion. Possibly, this high aggressiveness could prevent colonization by the slavemaker.

There are several indications that German *L. acervorum* colonies might have evolved resistance characters. They positioned more guards in the nest entrance than colonies from the other two populations, and they were very effective at immobilizing the slavemaker by biting. Furthermore, in the nest defense experiments host colonies were not manipulated to fight more against nest mates as a response to frequent application of the Dufour gland secretion by the social parasite as were colonies from the other populations. In the Dufour gland experiments, we found that German host workers more often groomed nest mates treated with the Dufour gland secretion. This grooming behavior could help lower the impact of the propaganda substance because it allows fast removal of the secretion from the cuticle. We found a difference in the same direction for the second host species, *L. muscorum*. Here, a larger proportion of the German host workers survived the slavemaker attack unharmed. The German host populations are more severely parasitized by the slavemaker than the Russian populations. Therefore, the relative strength of parasite pressure versus ecological selection pressure might lead to the evolution of resistance only in more severely parasitized populations, as was shown for host populations of *P. americanus* (Foitzik et al., 2001). Germany might represent a coevolutionary hot-spot (Thompson, 1999) for the host populations, however, for the social parasites, we found advanced parasite strategies in the Russian and not in the German slavemakers.

Allies et al. (1986) showed that *L. acervorum* workers can be manipulated by the social parasite with the propaganda substance from the Dufour gland to fight against their own nest mates. Here, we showed that the slavemaker can manipulate different host populations, even nonparasitized ones. However, we did find differences in the reaction to slavemakers from different populations. Host workers fought more often against their own nest mates in response to the Dufour gland secretion from Russian slavemakers. It is interesting that they also tried to sting Russian slavemakers less often. This indicates that the Dufour gland secretion from Russian social parasites is both very powerful, because it leads to many intercolonial fights, and very effective, because the slavemaker is attacked less often.

In addition to differences between slavemaker populations, we found strong interaction effects indicating localized coevolution (Foitzik et al., 2001; Thompson, 1999). In general, *L. acervorum* populations reacted more severely to the propaganda substance of the local slavemaker population, both in Russia and in Germany. The ability of a slavemaker to manipulate its local host indicates that at least in this aspect the slavemaker is winning the arms race. Another result supports this notion. Host workers tried to sting allopatric slavemakers more often than sympatric social parasites. If host populations have evolved an enemy recognition mechanism, they should instead attack their local slavemaker more severely. Thus, our results can be explained with strong differences in colony odor between the two populations that allow host colonies to identify the allopatric slavemakers faster than sympatric intruders.

Table 5

Summary of behavioral differences between *Leptothorax acervorum* colonies from various populations in the nest defense and Dufour gland experiments

Test series	Behavior	Germany	Russia	England
Nest defense	No. of host guards in nest entrance	+	–	–
	No. of host workers biting the parasite	+	–	+
	No. of host workers stinging the parasite	–	–	+
	Likelihood of slavemaker to be killed	–	–	+
Dufour gland	Inactivity of focal worker	+	–	–
	Aggressive reaction of focal nest	+	–	+
	Grooming of focal worker by nest mates	+	–	–

In this table only the effects of host population are given. Impact of sympatry of allopatry of slavemaker and host on the behaviors are shown in Table 6. For statistical tests, see text. + means more, – means less.

H. sublaevis appears to parasitize both host species at similar rates, and our experiments show comparable efficacy of nest defense in *L. acervorum* and *L. muscorum*. Both species showed the same ability to kill the slavemaker, and a similar proportion of their worker force was killed during the attacks. In addition, we found in the German population that slavemaker nests with *L. acervorum* or *L. muscorum* slaves have a similar productivity. Thus, from our data we have no indication that the social parasite should specialize on one host species. In contrast to the North American social parasite system that was analyzed recently (Foitzik et al., 2001), the two main host species of *H. sublaevis* have a similar distribution and occur in most habitats at similar frequencies. This should disrupt a close arms race between parasite and host (Thompson, 1999) because three species are involved in the interaction instead of two.

Caste of the slavemaker had a strong impact on the success rate of the attack. Intermorphic slavemaker queens were rarely killed and more often successful in colony takeover than slavemaker workers. Although we found slight size differences between both castes, body size did not influence the survival rate directly. Thus, the survival of slavemaker queens was not related to size or to a more powerful Dufour gland secretion, since we did not find differences in the effect of the propaganda substance from both castes. Most of the slavemaker queens used in the experiments were presumably young and had a different motivation when attacking a host nest. As a rule, *H. sublaevis* queens are on their own during colony takeover, whereas parasite workers normally recruit the help of others before they raid a host nest (Buschinger and Winter, 1977; Buschinger et al., 1980).

We also found a strong influence of host nest demography on colony defense. Monogynous *L. acervorum* host colonies were better able to defend their nest against the attack of social parasites. In general, monogynous species and colonies are supposed to have a more uniform colony odor and to show higher intercolonial aggression than polygynous ones (Breed and Bennett, 1987; Hölldobler and Wilson, 1977; Morel et al., 1990). In *Leptothorax* ants, however, only differences between colonies with a queen and those without have been found, showing that the presence of a queen leads to

Table 6

Influence of sympatry and allopatry of the slavemaker on the behavior of *Leptothorax acervorum* colonies from the German and the Russian host population

Slavemaker origin	German hosts		Russian hosts	
	Sympatric	Allopatric	Sympatric	Allopatric
No. of host workers stinging the parasite	–	–	–	+
No. of intracolony fights	–	+	–	–
Positive correlation between sting use and intracolony fights	–	–	+	–

Statistical tests are given in the text.

a higher aggression level (Provost et al., 1993; Stuart and Herbers, 2000). Indeed, in several North American *Leptothorax* species, queen number had no influence on the efficiency of nest defense (Stuart, 1991). Here we showed for the first time in this genus that monogynous colonies are able to defend their nest better against an intruder, in this case against a social parasite.

This finding has some interesting implications. When monogynous colonies are better able to defend their nest against social parasite, there could be selection pressure through social parasitism on host colonies to stay monogynous and to stop adopting daughter queens. This could theoretically lead to a balance between ecological factors, which might promote polygyny to avoid the costs of solitary founding (Bourke and Heinze, 1994; Herbers, 1986), and parasite pressure, which might favor monogyny. The variation in social structure between the three *L. acervorum* host populations is consistent with a balance of different selection pressures. In the parasite-free English population, a large fraction of colonies is polygynous, perhaps because ecological conditions favor this social organization, while in Germany, with many social parasites, the majority of colonies is monogynous. The Russian population has to deal with harsh ecological conditions that promote polygyny and is parasitized by the slavemaker. Here, half of the colonies are polygynous. In *L. longispinosus*, host colonies in the vicinity of *Protomognathus americanus* slavemaker colonies were more often monogynous than in parasite-free areas (Foitzik and Herbers, 2001; Herbers and Foitzik, 2002). Whether this is an effect of the slavemaker or a host reaction to parasite presence is not known. We did not find an effect of social structure on the efficacy of nest defense in *L. muscorum*, for which our data set is smaller.

In both host species, colony size had no impact on the effectiveness of nest defense. In *L. muscorum*, larger colonies were able to detain the slavemaker better, but the survival rate was not influenced by that. In contrast, colony size was shown to influence the defense against other social parasites (Alloway, 1979; Stuart, 1984) and against alien conspecifics (Stuart, 1991).

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REFERENCES

- Adlerz G, 1896. Myrmekologische Studien. III. *Tomognathus sublaevis* Mayr. Bih K Svenska Vet Akad Hanl 21:1–76.
- Allies AB, Bourke AFG, Franks NR, 1986. Propaganda substances in the cuckoo ant *Leptothorax kutteri* and the slave-maker *Harpagoxenus sublaevis*. J Chem Ecol 12:1285–1293.
- Allison AC, 1982. Coevolution between hosts and infectious disease agents, and its effects on virulence. In: Population biology of infectious diseases (Anderson RM, May RM, eds). Berlin: Springer; 245–268.
- Alloway TM, 1979. Raiding behavior of two species of slave-making ants, *Harpagoxenus americanus* (Emery) and *Leptothorax duloticus* (Wesson) (Hymenoptera: Formicidae). Anim Behav 27:202–210.
- Alloway TM, 1990. Slave-species ant colonies recognize slavemakers as enemies. Anim Behav 39:1218–1220.
- Anderson RM, May RM, 1982. Coevolution of hosts and parasites. Parasitology 85:411–426.
- Benkman CW, Holimon WC, Smith JW, 2001. The influence of a competitor on the geographic mosaic of coevolution between crossbills and lodgepole pine. Evolution 55:282–294.
- 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, Heinze J, 1994. The ecology of communal breeding: the case of multiple-queen leptothoracine ants. Phil Trans Roy 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, Bennett B, 1987. Kin recognition in highly eusocial insects. In: Kin recognition in animals (Fletcher JC, Michener CD, eds). New York: John Wiley; 243–285.
- Buschinger A, 1966a. Untersuchungen an *Harpagoxenus sublaevis* Nyl. (Hym., Formicidae). I. Freilandbeobachtungen zur Verbreitung und Lebensweise. Insect Soc 13:5–16.
- Buschinger A, 1966b. Untersuchungen an *Harpagoxenus sublaevis* Nyl. (Hym., Formicidae). II. Haltung und Brutaufzucht. Insect Soc 13:311–322.
- Buschinger A, 1968. Untersuchungen an *Harpagoxenus sublaevis* Nyl. (Hymenoptera, Formicidae). III. Kopula, Koloniegründung, Raubzüge. Ins Soc 15:89–104.
- Buschinger A, 1971. Weitere Untersuchungen zum Begattungsverhalten sozialparasitischer Ameisen (*Harpagoxenus sublaevis* Nyl. und *Doronomyrmex pacis* Kutter (Hym., Formicidae) Zool Anz 187: 184–198.
- Buschinger A, 1974. Experimente und Beobachtungen zur Gründung und Entwicklung neuer Sozietäten der sklavenhaltenden Ameise *Harpagoxenus sublaevis* Nyl. Insect Soc 21:381–406.
- Buschinger A, 1975. Eine genetische Komponente im Polymorphismus der dulotischen Ameise *Harpagoxenus sublaevis*. Naturw 62:238.
- Buschinger A, 1993. Bettel, Raub und Mord: aus dem Leben sozialparasitischer Ameisen. Verh Westd Entomol 7–20.
- 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, Winter U, 1975. Der Polymorphismus der sklavenhaltenden Ameise *Harpagoxenus sublaevis*. Insect Soc 22:333–362.
- Buschinger A, Winter U, 1977. Rekrutierung von Nestgenossen mittels Tandemlaufen bei Sklavenraubzügen der dulotischen Ameise *Harpagoxenus sublaevis*. Insect Soc 24:183–190.
- Buschinger A, Winter U, 1978. Echte Arbeiterinnen, fertile Arbeiterinnen und sterile Wirtsweibchen in Völkern der dulotischen Ameise *Harpagoxenus sublaevis* (Nyl.) (Hym., Form.). Insect Soc 25:63–78.
- Davies NB, 2000. Cuckoos, cowbirds, and other cheats. London: Poyser.
- Davies NB, Brooke MdeL, 1989a. An experimental study of coevolution between the cuckoo, *Cuculus canorus*, and its hosts. I. Host egg discrimination. J Anim Ecol 58:207–224.
- Davies NB, Brooke MdeL, 1989b. An experimental study of coevolution between the cuckoo, *Cuculus canorus*, and its hosts. I. Host egg markings, chick discrimination and general discussion. J Anim Ecol 58:225–236.

- Davies NB, Brooke MdeL, Kacelnik A, 1996. Recognition errors and probability of parasitism determine whether reed warblers should accept or reject mimetic cuckoo eggs. *Proc R Soc Lond B* 263: 925–931.
- Dawkins R, 1982. *The extended phenotype*. Oxford: Oxford University Press.
- D'Ettorre P, Heinze J, 2001. Sociobiology of slave-making ants. *Acta Ethol* 3:67–82.
- Dobrzanski 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 Cbl* 29:352–362.
- Foitzik S, Heinze J, 1998. Colony takeover and nest site limitation in the ant *Leptothorax nyländeri*. *Behav Ecol* 9:367–375.
- Foitzik S, Herbers JM, 2001. Colony structure of a slavemaking ant: II. Frequency of slave raids and impact on the host population. *Evolution* 55:316–323.
- Foitzik S, DeHeer CJ, Hunjan DN, Herbers JM, 2001. Coevolution in host–parasite systems: behavioural strategies of slavemaking ants and their hosts. *Proc R Soc Lond* 268:1139–1146.
- Gandon S, Capowiez Y, Dubois Y, Michalakakis Y, Olivieri I, 1996. Local adaptations and gene for gene coevolution in a metapopulation model. *Proc R Soc Lond B* 263:1003–1009.
- Gladstone DE, 1981. Why there are no ant slave rebellions. *Am Nat* 117:779–781.
- Grasso DA, Mori A, Le Moli F, 1992. Analysis of the aggression between slave and slavemaking (facultative and obligatory) ant species (Hymenoptera: Formicidae). *Ethol Ecol Evol* 2:81–84.
- Hare JF, Alloway TM, 2001. Prudent *Protomognathus* and despotic *Leptothorax duloticus*: differential costs of ant slavery. *Proc Natl Acad Sci USA* 98:12093–12096.
- Hasegawa E, Yamaguchi T, 1994. Raiding behavior of the Japanese slave-making ant *Polyergus samurai*. *Insect Soc* 41:279–289.
- Heinze J, Buschinger A, 1987. Queen polymorphism in a non-parasitic *Leptothorax* species (Hymenoptera, Formicidae). *Insect Soc* 34:28–43.
- Heinze J, Foitzik S, Hippert A, Hölldobler B, 1996. Apparent dearenemy phenomenon and environmental-based recognition cues in the ant *Leptothorax nyländeri*. *Ethology* 102:510–522.
- Heinze J, Ortius D, 1991. Social organization of *Leptothorax acervorum* from Alaska (Hymenoptera: Formicidae). *Psyche* 98:227–240.
- Heinze J, Ortius D, Kaib M, Hölldobler B, 1994. Interspecific aggression in colonies of the slave-making ant *Harpagoxenus sublaevis*. *Behav Ecol Sociobiol* 35:75–83.
- Herbers JM, 1986. Nest site limitation and facultative polygyny in the ant *Leptothorax longispinosus*. *Behav Ecol Sociobiol* 19:115–122.
- Herbers JM, Foitzik S, 2002. The ecology of slavemaking ants and their hosts in north temperate forests. *Ecology* 83:148–163.
- Hölldobler B, Wilson EO, 1977. The number of queens: an important trait in ant evolution. *Naturwissenschaften* 64:8–15.
- Hölldobler B, Wilson EO, 1990. *The ants*. Cambridge: Harvard University Press.
- Kaib M, Heinze J, Ortius D, 1993. Cuticular hydrocarbons profiles in the slave-making ant *Harpagoxenus sublaevis* and its hosts. *Naturwissenschaften* 80:281–285.
- Kaspari M, 1996. Worker size and seed size selection by harvester ants in a Neotropical forest. *Oecologia* 105:397–404.
- Kutter H, 1968. *Die sozialparasitischen Ameisen der Schweiz*. Zurich: Neujahrsbl Naturf Gesell Zürich.
- Kwait E, Topoff H, 1984. Raid organization and behavioral development in the slave-making ant *Polyergus lucidus* Mayr. *Insect Soc* 31:361–374.
- Lorenzi MC, Filippone F, 2000. Opportunistic discrimination of alien eggs by social wasps (*Polistes biglumis*, Hymenoptera Vespidae): a defense against social parasitism? *Behav Ecol Sociobiol* 48: 402–406.
- Lotem A, Nakamura H, Zahavi A, 1992. Rejection of cuckoo eggs in relation to host age: a possible evolutionary equilibrium. *Behav Ecol* 3:128–132.
- Morel L, VanderMeer RK, Lofgren CS, 1990. Comparison of nestmate recognition between monogyne and polygyne populations of *Solenopsis invicta* (Hymenoptera: Formicidae). *Ann Entomol Soc Am* 83:642–647.
- 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.
- Provost E, Riviere G, Roux M, Morgan D, Bagnères AG, 1993. Change in the chemical signature of the ant *Leptothorax lichtensteini* bondroit with time. *Insect Biochem Mol Biol* 23:945–957.
- Radchenko A, Czechowski W, Czechowska W, 1999. The tribe Formicoxenini (Hymenoptera, Formicidae) in Poland—a taxonomic review and keys for identification. *Ann Zool* 49:129–150.
- Regnier FE, Wilson EO, 1971. Chemical communication and “propaganda” in slave-making ants. *Science* 172:267–269.
- Rice WR, 1989. Analyzing tables of statistical tests. *Evolution* 43: 223–225.
- Rothstein SI, Robinson SK, 1998. *Parasitic birds and their hosts*. Oxford: Oxford University Press.
- Schmid-Hempel P, 1998. *Parasites in social insects*. Princeton, New Jersey: Princeton University Press.
- Schumann R, Buschinger A, 1991. Selective acceptance of alien host species pupae by slaves of the dulotic ant, *Harpagoxenus sublaevis* (Hym., Form., Myrm.). *Ethology* 88:154–162.
- Soler JJ, Soler M, Perez CT, Aragon S, Möller AP, 1999. Antagonistic antiparasite defenses: nest defense and egg rejection in the magpie host of the great spotted cuckoo. *Behav Ecol* 10:707–713.
- Stuart RJ, 1984. Experiments on colony foundation in the slave-making ant *Harpagoxenus canadensis* M. R. Smith (Hymenoptera; Formicidae). *Can J Zool* 62:1995–2001.
- Stuart RJ, 1991. Nestmate recognition in leptothoracine ants: testing for effects of queen number, colony size and species of intruder. *Anim Behav* 42:277–284.
- Stuart RJ, Herbers JM, 2000. Nest mate recognition in ants with complex colonies: within- and between-population variation. *Behav Ecol* 11:676–685.
- Thompson JN, 1994. *The coevolutionary process*. Chicago: University of Chicago Press.
- Thompson JN, 1999. Specific hypotheses on the geographic mosaic of coevolution. *Am Nat* 153:1–14.
- Thompson JN, Burdon JJ, 1992. Gene-for-gene coevolution between plants and parasites. *Nature* 360:121–125.
- Trivers RL, Hare H, 1976. Haplodiploidy and the evolution of the social insects. *Science* 191:249–263.
- Viehmeyer H, 1908. Zur Kolonieggründung parasitischer Ameisen. *Biol Zentralblatt* 28:18–32.
- Wilson EO, 1971. *The insect societies*. Cambridge, Massachusetts: Belknap Press.
- Winter U, Buschinger A, 1986. Genetically mediated queen polymorphism and caste determination in the slave-making ant, *Harpagoxenus sublaevis* (Hymenoptera: Formicidae). *Entomol Gen* 11:125–137.