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Parasite virulence and host resistance in a slave-making ant community

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ABSTRACT

Questions: Does virulence of socially parasitic slave-making ants vary in interactions with different host species? If so, can this be linked to host properties such as nest availability or resistance of host species?

Study system: Our study system included three slave-making ant species, *Polyergus breviceps*, *Formica puberula*, and *F. gynocrates*, and two host species, *F. occulta* and *F.* sp. cf. *argentea*.

Methods: We measured slave-maker virulence by comparing the mortality rates of host nests that were raided by slave-makers to host nests that were not raided. To determine whether slave-makers that were more likely to over-exploit slave resources were more prudent (lower virulence), we compared the percentage of nests that were raided for each host species. To determine whether variation in slave-maker virulence was due to different levels of host resistance, we compared the aggressiveness of the two host species towards slave-makers during slave raids, reasoning that nests of a more aggressive host species would show higher survivorship.

Results: Slave-makers were highly virulent in association with the host, *F.* sp. cf. *argentea*, but more benign in interactions with *F. occulta*. *Formica occulta* was not universally more aggressive against slave-makers than *F.* sp. cf. *argentea*, suggesting that this alone is not a sufficient explanation for the higher survivorship of this species. Slave-makers that specialized on *F. occulta* were at higher risk of over-exploiting resources, indicating that more prudent slave-maker strategies might be selected for in interactions with this host.

Keywords: co-evolution, Formicidae, *Polyergus*, social parasites, virulence.

INTRODUCTION

Parasites exploit every level of biological organization and affect nearly all other organisms. Thus, interactions between parasites and their hosts play a fundamental role in organizing communities and generating biodiversity (Thompson, 1994; Summers *et al.*, 2003). A great deal of theoretical and empirical work has focused on understanding the dynamics of host–parasite

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systems, with the goal of identifying factors that influence the outcome of interactions between parasites and their hosts. Theoretical models and empirical evidence show that parasite virulence (parasite-induced reduction in host fitness) depends on a variety of factors related to host and parasite life history, such that some associations evolve to be more benign, others more lethal, while others produce a range of intermediate outcomes (Anderson and May, 1981; Bull, 1994; Frank, 1996; Galvani, 2003).

Slave-making ants are social parasites that have emerged as a new model system for studying host–parasite co-evolution (Foitzik and Herbers, 2001; Foitzik *et al.*, 2001, 2003; Hare and Alloway, 2001; Blatrix and Herbers, 2003; Zamora-Munoz *et al.*, 2003; Brandt and Foitzik, 2004; Fischer and Foitzik, 2004; Brandt *et al.*, 2005a, 2005b). Slave-makers exploit the labour of closely related host species by incorporating host workers into the slave-maker colony, where the slaves carry out normal worker duties. Queens of obligate slave-makers are unable to independently initiate a new colony, and instead must penetrate a free-living host nest, kill or expel the resident queen(s) and either gain acceptance or expel host workers. The queens then produce their own workers, which replenish the slave supply each year by stealing larvae and pupae from neighbouring host colonies during slave raids. Slave raids can be frequent and destructive, often resulting in host nest mortality, and thus impart strong selection pressure on hosts to evolve resistance (Foitzik and Herbers, 2001; Hare and Alloway, 2001; Blatrix and Herbers, 2003).

Slave-maker virulence, which we measure here by the increase in host nest mortality following slave raids, is ultimately the product of selection pressures on virulence that result from aspects of parasite and host life history, and population structure. For example, more prudent slave-maker strategies should be favoured in host populations characterized by low nest densities and low re-colonization rates, because slave-maker colonies are at risk of over-exploiting slave resources (Brandt *et al.*, 2005a). At the same time, hosts are under strong selection pressure to evolve resistance, and consequently virulence also reflects the resistance to slave raiding of a particular host (i.e. virulence will be lower in an interaction with a more resistant host). Given that different host species are likely to vary in traits such as population density and levels of resistance to slave raiding, we expect slave-maker virulence to vary in association with different hosts. Nevertheless, only one study has demonstrated this by comparing survival of different host species following slave raids by the same slave-maker (Blatrix and Herbers, 2003). Moreover, these comparisons have only been made in myrmicine slave-making systems; analogous studies for formicines, the only other ant sub-family to evolve slave-making, are lacking.

In this study, we compare the virulence of different slave-maker–host associations in a community that included three slave-maker species and two host species. The study system consisted of the obligate slave-maker, *Polyergus breviceps*, which has been studied extensively in association with a different host species at an alternative location (Topoff *et al.*, 1984, 1985a, 1985b, 1985c, 1989), two *Formica* slave-makers, *F. puberula* and *F. gynocrates*, and two hosts, *F. occulta* and *F.* sp. cf. *argentea*. At this location, *P. breviceps* enslaves both host species, though individual colonies specialize on only one. *Formica puberula* enslaves *F. occulta*, while *F. gynocrates* enslaves *F.* sp. cf. *argentea*. We were thus able to compare the virulence of a specific slave-maker in interactions with different hosts, as well as the virulence of different slave-makers in interactions with the same host. Comparisons were made in a single location, so that we could exclude differences in parasite and host life history and population structure that would complicate studies of these interactions in different locations.

From previous work in this system we were able to identify differences in the social structure and population biology of the two host species that might have implications for slave-maker virulence. *Formica* sp. cf. *argentea* colonies in this population are polygynous (colonies have multiple queens), polydomous (colonies occupy multiple nest sites), and can produce new nests by colony budding (J. M. Bono *et al.*, unpublished manuscript). In contrast, *F. occulta* colonies are monogynous (J.M. Bono *et al.*, unpublished manuscript), and presumably monodomous [polydomy and colony budding are unusual for monogynous species (Chapuisat *et al.*, 1997)]. Polygynous/polydomous social structure generally results in dense nest aggregations characterized by rapid re-colonization of abandoned nest sites (Pamilo, 1982; Pollock and Rissing, 1989; Chapuisat *et al.*, 1997). Indeed, *F.* sp. cf. *argentea* colonies were more common at our study site, outnumbering *F. occulta* nests 1.5 to 1. These differences in nest availability and re-colonization suggest the possibility that slave-makers specializing on *F. occulta* are at a higher risk of over-exploiting slave resources. To verify this, we compared the proportion of nests that were raided over 2 years of study for each host species. We discuss how these findings relate to differences in slave-maker virulence in association with the two host species.

Because slave-maker virulence can reflect differences in resistance of host species, we also compared the aggressiveness of hosts during slave raids by the three slave-makers. Host aggression is one possible mechanism of resistance, as more aggressive host colonies saved more brood during slave raids by *P. rufescens* (Visicchio *et al.*, 2003) and *Protomagnathus americanus* (Foitzik *et al.*, 2001, 2003). Colonies that save brood have a larger future workforce, which could ultimately result in higher survivorship. Other authors have noted that slave raids by *Polyergus* generally involve less aggression than raids by *Formica* slave-makers (Grasso *et al.*, 1992; Mori *et al.*, 2001). This difference might be explained by the release of propaganda pheromones by *Polyergus* raiders, which has been suggested for one species, *P. rufescens* (Visicchio *et al.*, 2001). Nevertheless, similar pheromones have been identified for some *Formica* slave-makers (Hölldobler and Wilson, 1990), although we do not know whether they are used by *Formica* slave-makers in our study system. Moreover, the effectiveness of these pheromones could vary against different host species. In light of these complications, we do not make specific predictions about the level of aggressiveness for specific slave-maker host pairs, but rather examine the possibility that aggressiveness and survivorship are positively linked (i.e. the more aggressive host overall shows higher survival overall).

METHODS

Study site

Our study site in the foothills of the Rocky Mountains (elevation 2000 m) was 36 km northwest of Fort Collins, Colorado, USA. The system here consists of three slave-makers, *P. breviceps*, *F. gynocrates*, and *F. puberula*, and two host species, *F. occulta* and *F.* sp. cf. *argentea*. *Formica* slave-makers are generally assumed to be facultative (Hölldobler and Wilson, 1990), although we did not find any colonies of either slave-maker at our site living without slaves. The study site included open meadows and sparsely spaced ponderosa pine, spruce, and fir trees. We found colonies of slave-makers and hosts nesting under rocks on southern and south-eastern exposed slopes. *Formica* sp. cf. *argentea* nests were more abundant at this site, outnumbering *F. occulta* colonies 1.5 to 1. We specifically chose to follow the activity of 11 slave-maker colonies at this site (7 *P. breviceps*, 2 *F. puberula*, and 2 *F. gynocrates* colonies). We selected these colonies because they were within an approximately 1-km^2 area that we could easily patrol on a daily basis and be confident that we observed all slave raids. We used survey equipment and global positioning systems (GPS) to generate Universal Transverse Mercator (UTM) coordinates of all host and slave-maker colonies we could find prior to our study within this predetermined area, which were then mapped with Arcview software. We obtained UTM coordinates of additional colonies that were found in 2002 and 2003.

Impact of slave raiding on host nests

We monitored slave-maker colonies every day during the 2002 and 2003 slave-raiding seasons (1 to 30 July for 2002 and 2 July to 17 August for 2003) from 13:00 h until slave raids ended in the evening, usually before 20:00 h. We recorded all slave raids for each monitored colony and the locations of raided host colonies were mapped with Arcview software.

To assess the impact of slave raids on host colony fitness, we compared the survivorship, colony size, and sexual investment of nests that were raided with that of control nests. Control nests, 11 for *F. occulta* and 12 *F.* sp. cf. *argentea*, were randomly selected from nests that had been marked before the study but not raided during the 2002 season. We are confident that none of these nests were raided because we monitored them daily during the raiding season. We collected these colonies in addition to colonies that had been raided during the 2002 raiding season (the summer prior). We excluded raided nests that lay under large boulders or whose exact location was uncertain. We recorded whether control colonies and raided colonies were present or absent; a random sample of those that were present were completely excavated. Colonies that were not present were assumed to have died. Topoff *et al.* (1985a, 1985b) reported that colonies of a different host (*F. gnava*) frequently emigrated to new nest sites on days following a slave raid or after experimenter-induced disturbance. We therefore monitored host nests on days following slave raids but never observed a colony move in 2 years of study. Moreover, we commonly disturbed nests to take samples and again never observed colony emigration. Taken together, these observations suggest that the two hosts in our study system do not emigrate as commonly as *F. gnava* and we are thus confident in our estimates of nest mortality.

After collection, ants were sorted from the soil and then frozen. We censused colonies by counting the number of workers and the number of reproductive adults and pupae. Measuring sexual investment (dry weight of sexuals) was complicated by the fact that colonies had both reproductive pupae and adults. Therefore, we calculated the population average weight of each reproductive class (male adults, male pupae, queen adults, queen pupae), and multiplied those averages by the respective number of individuals produced by each colony to estimate total sexual investment for a colony.

To increase sample size for survival comparisons, in June 2004 we also assessed the survival of colonies that were raided during the 2003 raiding season. We recorded presence/absence of ants at previously occupied nest sites but did not excavate nests; if we did not find ants at the surface, we dug at least 20 cm deep in the area where the nest had been. Nest collections are summarized in Table 1.

We compared the survival of raided nests versus unraided nests using Fisher's exact tests. Several *F. occulta* nests were raided more than once during a raiding season, so we assigned nests to one of three categories: nests that were not raided, nests raided once, and nests

Table 1. Summary of colony collections for each slave-maker/host pair

Slave-maker/host	Number of colonies collected in 2003	Number of colonies collected in 2004
P. breviceps/*F. occulta*	6	13
F. puberula/*F. occulta*	7	6
P. breviceps/*F.* sp. cf. *argentea*	10	15
F. gynocrates/*F.* sp. cf. *argentea*	5	2

Note: Collections in 2003 were of colonies that were raided in 2002 and collections in 2004 were of colonies that were raided in 2003.

raided more than once. No *F.* sp. cf. *argentea* nests were raided multiple times, so we did not split the analysis for this species. We compared colony size and sexual investment of raided versus unraided colonies using Kruskal-Wallis tests. A general problem shared with other studies of rare species is that data analysis is hampered by limited statistical power associated with small sample sizes (Ellison and Agrawal, 2005). We were more concerned with Type II than Type I errors, and so report below results of one-tailed tests with $\alpha = 0.10$ (*a priori* predictions were that raided colonies would have lower survival, smaller colony size, and lower sexual investment). We used two-tailed Fisher's exact tests to compare the survival of host nests raided by different slave-makers because we could not make *a priori* predictions.

Host resource exploitation

To compare the risk of over-exploiting slave resources for slave-makers that raided different host species, we first needed to establish which host nests in the population qualified as being 'available' to a particular slave-maker colony (i.e. close enough to the slave-maker colony that the probability of being raided was relatively high). To do this, we generated polygons that connected the outermost locations for slave raids made by each colony. We then mapped the locations of host nests that we had marked before the study over these polygons. For each slave-maker colony we counted the number of host nests (of the species on which it specialized) that were within its polygon. We then calculated the percentage of these that were raided during the 2 years of study. These nests were certainly not the only host nests within these polygons, as slave-maker colonies frequently raided cryptic nests that we had not found. However, because they were marked before the study, we were able to use them to calculate the relative proportion of raided to unraided nests for each host species. We compared these proportions using a *G*-test of independence.

Aggressiveness during slave raids

To compare aggressiveness during slave raids, we observed interactions between slave-making ants and hosts during 53 randomly selected slave raids (15 for *P. breviceps*/*F.* sp. cf. *argentea*, 13 for *P. breviceps*/*F. occulta*, 13 for *F. gynocrates*/*F.* sp. cf. *argentea*, and 12 for *F. puberula*/*F. occulta*). We began recording aggressive interactions when the first host worker appeared outside the nest. From this point, we counted the number of aggressive interactions at 5-min intervals for up to 1 h (12 total observations or until the raid ended). We considered an encounter to be aggressive when ants were clasped together and clearly fighting. Encounters were never ambiguous – ants either interacted in a clearly aggressive manner, or avoided contact altogether.

We observed no aggressive interactions in a large number of raids, and consequently could not normalize the data. Therefore, we split the analysis into two parts: (1) we used Fisher's exact tests to look for differences in the occurrence of at least one aggressive encounter during a raid, and (2) for those raids with aggression, we used mixed-model analyses of variance (SAS, proc mixed) to compare log-transformed means of the average number of aggressive interactions per observation (i.e. the average of the 12 observations) for each species pair. We refer to this measure as 'aggression intensity'. The analysis of variance (ANOVA) model included the following fixed effects: (1) slave-maker/host pair, (2) observer identity, (3) and an observer × slave-maker/host pair interaction term. Slave-maker colony nested within slave-maker/host pair was included as a random effect. We eliminated the interaction term when it was not significant ($\alpha = 0.10$). We made *a priori* comparisons with the Lsmeans procedure in SAS proc mixed.

RESULTS

Impact of slave raiding on host nests

Formica occulta nests that were raided only once by *P. breviceps* or *F. puberula* did not suffer higher mortality than nests that were not raided (20% for nests raided once by *P. breviceps* vs. 27% for control nests, Fisher's exact test, one-sided $P = 0.509$; 44% for nests raided once by *F. puberula* vs. 27% for control nests, Fisher's exact test, $P = 0.370$; Fig. 1A, B). Mortality rates for nests that were raided more than once were much higher, however, with 75% of nests raided multiple times by *P. breviceps* not surviving (Fisher's exact test, one-sided $P = 0.071$ for comparison of nests raided once vs. more than once; one-sided $P = 0.143$ for comparison of controls with nests raided more than once; Fig. 1B). All nests raided multiple times by *F. puberula* did not survive (Fisher's exact tests, one-sided $P = 0.098$ for

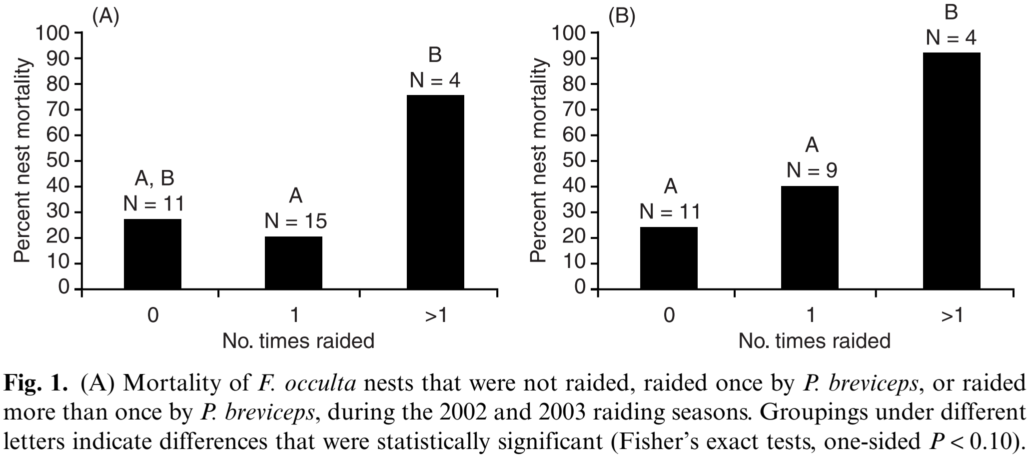

Fig. 1. (A) Mortality of *F. occulta* nests that were not raided, raided once by *P. breviceps*, or raided more than once by *P. breviceps*, during the 2002 and 2003 raiding seasons. Groupings under different letters indicate differences that were statistically significant (Fisher's exact tests, one-sided $P < 0.10$). (B) Mortality of *F. occulta* nests that were not raided, raided once by *F. puberula*, or raided more than once by *F. puberula*, during the 2002 and 2003 raiding seasons. Groupings under different letters indicate differences that were statistically significant (Fisher's exact tests, one-sided $P < 0.10$).

comparison of nests raided once vs. more than once; one-sided $P = 0.026$ for unraided vs. nests raided more than once; Fig. 1B). There were no differences in survival of nests raided by different slave-makers (Fisher's exact test, $P = 0.356$ for comparison of nests raided once by *P. breviceps* vs. *F. puberula*; $P > 0.999$ for nests raided more than once).

Formica occulta nests that survived raids by either slave-maker had fewer workers than control nests (Kruskal-Wallis, one-sided $P = 0.018$; Table 2), and sexual production was reduced (Kruskal-Wallis, one-sided $P = 0.049$; Table 2). While 55% of nests that were not raided produced sexuals, only one raided colony produced any sexuals, and this was just one male.

Compared with controls, *Formica* sp. cf. *argentea* mortality was higher when nests were raided by *P. breviceps* or *F. gynocrates* (17% for controls vs. 48% for nests raided by *P. breviceps*, Fisher's exact test, one-sided $P = 0.067$; 17% for controls vs. 57% for nests raided by *F. gynocrates*, one-sided $P = 0.095$ for *F. gynocrates*; Fig. 2). Moreover, nests that survived raids had fewer workers than control nests (Kruskal-Wallis, one-sided $P = 0.066$; Table 2). Although there was a trend for raided nests to have lower sexual investment, differences were not statistically distinguishable, possibly because of low power (Kruskal-Wallis, one-sided $P = 0.252$; Table 2). There were no differences in survival for nests raided by the two slave-makers (Fisher's exact test, $P > 0.999$).

Table 2. Median colony size (number of workers) and sexual investment for raided host nests (raided in 2002) and control nests

	Median control colony size (*N*) [Q1, Q3]	Median raided colony size (*N*) [Q1, Q3]	*P*-value	Median control sex investment (mg) (*N*) [Q1, Q3]	Median raided sex investment (mg) (*N*) [Q1, Q3]	*P*-value
F. sp. cf. *argentea*	116.5 (12) [101, 137.5]	61 (7) [49, 155]	0.018	0 (12) [0, 30.1]	0 (7) [0, 8.6]	0.252
F. occulta	186 (11) [82, 599]	58 (7) [40, 122]	0.066	4.3(11) [0, 203.2]	0 (7) [0, 0]	0.049

Note: One-sided *P*-values are from Kruskal-Wallis tests.

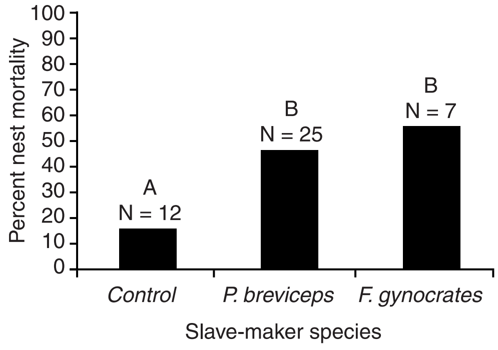

Fig. 2. Mortality for *F.* sp. cf. *argentea* nests that were not raided, raided by *P. breviceps*, or raided by *F. gynocrates* during the 2002 and 2003 raiding seasons. Groupings under different letters indicate differences that were significantly different (Fisher's exact tests, one-sided $P < 0.10$).

While median colony size (measured by number of workers) of *F. occulta* control colonies was larger than that of *F.* sp. cf. *argentea* colonies (186 workers for *F. occulta* vs. 116.5 for *F.* sp. cf. *argentea*; Table 2), this difference was not statistically distinguishable (Kruskal-Wallis, $P = 0.400$).

Host resource exploitation

Slave-makers that specialized on *F. occulta* raided a higher proportion of pre-marked host nests than slave-makers that specialized on *F.* sp. cf. *argentea* (24/26 for colonies specializing on *F. occulta*, 9/19 for colonies specializing on *F.* sp. cf. *argentea*; *G*-test, $P = 0.001$).

Aggressiveness during slave raids

Slave-maker/host pairs differed in the occurrence of aggression during slave raids (Fisher's exact test, $P = 0.038$). Subsequent tests showed that results reflected only pairwise differences between *F. puberula*/*F. occulta* and *P. breviceps*/*F. occulta* and between *F. puberula*/*F. occulta* and *P. breviceps*/*F.* sp. cf. *argentea* (Fisher's exact test, $P = 0.047$ and $P = 0.015$ respectively; Fig. 3A). For raids with aggression, slave-maker/host pairs showed strong differences in aggression intensity (mixed-model ANOVA, $P = 0.010$ for slave-maker/host pair, $P = 0.002$ for observer identity; interaction term was eliminated). Comparisons of least square means revealed more aggression for the pair *F. puberula*/*F. occulta* than all other pairs ($P = 0.002$ for comparison with *P. breviceps*/*F. occulta*; $P = 0.015$ for comparison with *P. breviceps*/*F.* sp. cf. *argentea*; and $P = 0.046$ for comparison with *F. gynocrates*/*F.* sp. cf. *argentea*; Fig. 3B), while differences between other pairings were not statistically distinguishable.

The general picture that emerged from these data is that aggression was consistently higher for the *F. puberula*/*F. occulta* pair than for any other pairing. There was also a consistent trend (both in the occurrence of aggression and the aggression intensity) for higher aggression for the *F. gynocrates*/*F.* sp. cf. *argentea* pair when compared with any pairs that included *P. breviceps*, though the differences were not statistically significant.

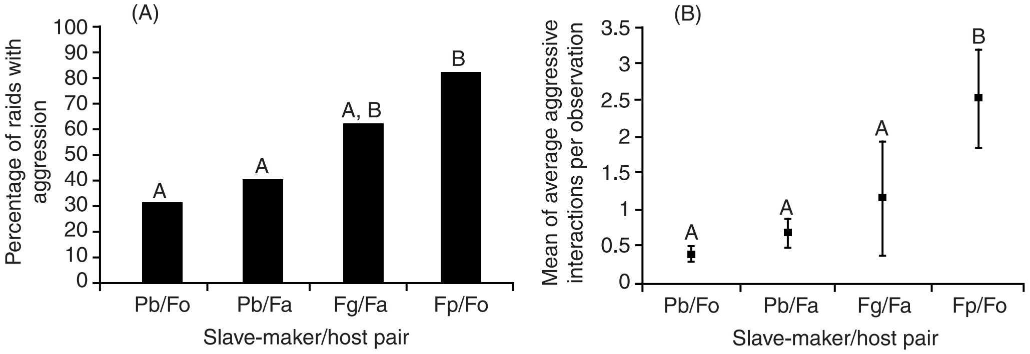

Fig. 3. (A) Percentage of slave raids that had at least one aggressive encounter for each slave-maker/host pair. Groups under different letters indicate pairs that were significantly different (Fisher's exact tests, $P < 0.05$). (B) Mean number of aggressive encounters per observation (error bars represent standard errors) during raids for each slave-maker/host pair. Means grouped under different letters indicate that they were significantly different (mixed-model ANOVA, Lsmeans; $P < 0.05$).

DISCUSSION

The general pattern that emerged from comparisons of slave-maker virulence on the two host species was that slave-makers were more virulent in associations with *F.* sp. cf. *argentea* than with *F. occulta*. This pattern suggests that slave-maker virulence depends, to a large extent, on properties of the host species, as noted for many host–parasite interactions (Bull, 1994; Dybdahl and Storfer, 2003). In fact, the same slave-maker, *P. breviceps*, while relatively benign in association with one host (*F. occulta*), was highly virulent in association with another host (*F.* sp. cf. *argentea*).

Interestingly, slave-makers that specialized on *F. occulta* were also at a higher risk of over-exploiting host resources, which is consistent with the theoretical prediction that lower virulence is favoured when the risk of over-exploiting resources is high (Brandt *et al.*, 2005a). Not only were *F. occulta* nests less common at this site, but slave-makers that specialized on the rarer species raided a much higher percentage of pre-marked nests than slave-makers that specialized on *F.* sp. cf. *argentea* (92% vs. 47%). Clearly, if raids commonly resulted in the death of *F. occulta* nests, then slave-makers would rapidly deplete slave resources unless nest re-colonization rates were high. In contrast, *F.* sp. cf. *argentea* nests were more common and, consequently, pre-marked nests were less likely to be raided. Moreover, re-colonization rates are likely to be higher for this species because of its polygynous/polydomous social structure (Pamilo, 1982; Pollock and Rissing, 1989; Chapuisat *et al.*, 1997). These data suggest that the social structure of host species has important implications for the evolution of slave-maker virulence.

Our results are consistent with previous studies that have shown more prudent slave-maker behaviours and higher survival of raided colonies of the myrmicine host, *Temnothorax longispinosus*, in populations characterized by lower nest densities (Foitzik *et al.*, 2001; Blatrix and Herbers, 2003). However, Blatrix and Herbers (2003) found that the slave-maker *Protomagnathus americanus* was highly virulent in association with a rare host (*T. ambiguus*), which seemingly contradicts these expectations. In contrast to slave-makers in our study system that specialized on only one host species, *P. americanus* colonies enslave both *T. ambiguus* and the more common host, *T. longispinosus.* Consequently, selection for prudence in interactions with *T. ambiguus* is probably weak because the fitness of *P. americanus* depends much more strongly on interactions with its primary host at this site, *T. longispinosus* (Blatrix and Herbers, 2003).

Although single slave raids did not result in higher mortality for *F. occulta* nests, it is important to emphasize that slave raids were still costly for these colonies. Surviving nests had reduced worker numbers compared with controls and also invested less in sexual offspring. In addition, *F. occulta* nests that were raided more than once during a single season had elevated mortality rates compared with control and singly raided nests. Previous work suggests that slave-makers commonly raid *F. occulta* nests more than once in a single season, as 39% of raided nests were attacked more than once (J.M. Bono *et al.*, unpublished manuscript). Thus, while the magnitude of costs associated with slave raiding was lower for *F. occulta* than for *F.* sp. cf. *argentea*, slave raids were, nonetheless, costly for both species.

The higher survival of *F. occulta* compared with *F.* sp. cf. *argentea* could result if the former species has behavioural adaptations, such as higher aggressiveness towards slave-makers, that make it more resistant to slave raiding. Host specificity by slave-makers complicates the interpretation of our aggression results because we do not have data for all possible pairings. Nevertheless, these comparisons indicate that differences in the aggressiveness of host species cannot account for the universally higher survival of *F. occulta. Formcia occulta* was often highly aggressive during raids by *F. puberula*, which suggests that this might have contributed to higher survivorship in interactions with this slave-maker species. However, *F. occulta* was no more aggressive than *F.* sp. cf. *argentea* during *P. breviceps* raids, even though nest mortality was clearly different between these hosts (a summary of host survival and aggressiveness is presented in Table 3). Thus, differences in aggressiveness of the two hosts is not an entirely sufficient explanation for why *F. occulta* colonies showed higher survivorship; clearly, other factors must also contribute to this outcome.

The fact that both host species were relatively more aggressive in interactions with the *Formica* slave-makers than with *P. breviceps* is consistent with the observations of others who have noted that *Polyergus* slave raids generally involve less aggression than raids by *Formica* slave-makers (Grasso *et al.*, 1992; Mori *et al.*, 2001). *Polyergus rufescens* raiders deploy propaganda pheromones that confuse host workers and reduce aggression during slave raids (Visicchio *et al.*, 2001). Our aggression results suggest that *P. breviceps* might also use such chemicals, though others have attributed the panic reactions of host ants during *P. breviceps* raids to alarm pheromones released by the hosts themselves (Topoff *et al.*, 1989). Furthermore, our results imply that *F. puberula* and *F. gynocrates* either do not use propaganda pheromones, or, if they do, they are less effective at inducing panic behaviour in the hosts.

Host aggressiveness is just one possible mechanism of resistance to slave raiding and certainly other factors that we did not study could have contributed to the observed survival differences between the two host species. For example, *F. occulta* workers might be better at escaping with brood during slave raids. This could be evaluated easily in the future by comparing the number of brood that host workers salvage during slave raids with the number lost to slave-makers.

We found clear differences in slave-maker virulence in interactions with different hosts in our study system. By using a comparative approach, we were able to link these differences to attributes of hosts that might select for different levels of slave-maker virulence. This study thus highlights the value of slave-making ant systems that include multiple slave-makers and multiple hosts for understanding the evolution of parasite virulence and host resistance in complex communities.

Table 3. Relative survival of host colonies and relative amount of aggression during slave raids for different host–parasite associations

Slave-maker/host association	Aggression during raids	Host nest survival
P. breviceps/F. occulta	Low	High
F. puberula/F. occulta	High	High
P. breviceps/F. sp. cf. *argentea*	Low	Low
F. gynocrates/F. sp. cf. *argentea*	Medium	Low

Note: Overall, there is not a clear link between survival and aggressiveness of host colonies during raids.

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REFERENCES

Anderson, R.M. and May, R.M. 1981. The population dynamics of micro-parasites and their invertebrate hosts. *Phil. Trans. R. Soc. Lond. B*, **291**: 451–524.

Blatrix, R. and Herbers, J.M. 2003. Coevolution between slave-making ants and their hosts: host specificity and geographical variation. *Molec. Ecol.*, **12**: 2809–2816.

Brandt, M. and Foitzik, S. 2004. Community context and specialization influence coevolution between a slavemaking ant and its hosts. *Ecology*, **85**: 2997–3009.

Brandt, M., Foitzik, S., Fischer-Blass, B. and Heinze, J. 2005a. The coevolutionary dynamics of obligate ant social parasite systems – between prudence and antagonism. *Biol. Rev.*, **80**: 251–267.

Brandt, M., Heinze, J., Schmitt, T. and Foitzik, S. 2005b. A chemical level in the coevolutionary arms race between and ant social parasite and its hosts. *J. Evol. Biol.*, **18**: 576–586.

Bull, J.J. 1994. Perspective – virulence. *Evolution*, **48**: 1423–1437.

Chapuisat, M., Goudet, J. and Keller, L. 1997. Microsatellites reveal high population viscosity and limited dispersal in the ant, *Formica paralugubris. Evolution*, **51**: 475–482.

Dybdahl, M.F. and Storfer, A. 2003. Parasite local adaptation: red queen versus suicide-king. *Trends Ecol. Evol.*, **18**: 523–530.

Ellison, A.M. and Agrawal, A.A. 2005. The statistics of rarity. *Ecology*, **86**: 1079–1080.

Fischer, B. and Foitzik, S. 2004. Local co-adaptation leading to a geographical mosaic of coevolution in a social parasite system. *J. Evol. Biol.*, **17**: 1026–1034.

Foitzik, S. and Herbers, J.M. 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, C.J., Hunjan, D.N. and Herbers, J.M. 2001. Coevolution in host–parasite systems: behavioural strategies of slave-making ants and their hosts. *Proc. R. Soc. Lond. B*, **268**: 1139–1146.

Foitzik, S., Fischer, B. and Heinze, J. 2003. Arms races between social parasites and their hosts: geographic patterns of manipulation and resistance. *Behav. Ecol.*, **14**: 80–88.

Frank, S.A. 1996. Models of parasite virulence. *Q. Rev. Biol.*, **71**: 37–78.

Galvani, A.P. 2003. Epidemiology meets evolutionary ecology. *Trends Evol. Ecol.*, **18**: 132–139.

Grasso, D.A., Mori, A. and LeMoli, F. 1992. Analysis of the aggression between slave and slave-making (facultative and obligatory) ant species. *Ethol. Ecol. Evol.*, **2**: 81–84.

Hare, J.F. and Alloway, T.M. 2001. Prudent *Protomognathus* and despotic *Leptothorax duloticus*: differential costs of ant slavery. *Proc. Natl. Acad. Sci. USA*, **98**: 12093–12096.

Hölldobler, B. and Wilson, E.O. 1990. *The Ants*. Cambridge, MA: The Belknap Press of Harvard University Press.

Mori, A., Grasso, D.A., Visicchio, R. and Le Moli, F. 2001. Comparison of reproductive strategies and raiding behaviour in facultative and obligatory slave-making ants: the case of *Formica sanguinea* and *Polyergus rufescens. Insect. Soc.*, **48**: 302–314.

Pamilo, P. 1982. Genetic population structure in polygynous *Formica* ants. *Heredity*, **48**: 95–106.

Pollock, G.B. and Rissing, S.W. 1989. Intraspecific brood raiding, territoriality, and slavery in ants. *Am. Nat.*, **133**: 61–70.

Summers, K., McKeon, S., Sellars, J., Keusenkothen, M., Morris, J., Gloeckner, D. *et al*. 2003. Parasitic exploitation as an engine of diversity. *Biol. Rev.*, **78**: 639–675.

Thompson, J.N. 1994. *The Coevolutionary Process*. Chicago, IL: University of Chicago Press.

Topoff, H., Lamon, B., Goodloe, L. and Goldstein, M. 1984. Social and orientation behavior of *Polyergus breviceps* during slave-making raids. *Behav. Ecol. Sociobiol.*, **15**: 273–279.

Topoff, H., Inezpagani, M., Mack, L. and Goldstein, M. 1985a. Behavioral ecology of the slave-making ant, *Polyergus breviceps*, in a desert habitat. *Southwest. Nat.*, **30**: 289–295.

Topoff, H., Lamon, B., Goodloe, L. and Goldstein, M. 1985b. Ecology of raiding behavior in the western slave-making ant *Polyergus breviceps* (Formicidae). *Southwest. Nat.*, **30**: 259–267.

Topoff, H., Pagani, M., Goldstein, M. and Mack, L. 1985c. Orientation behavior of the slave-making ant *Polyergus breviceps* in an oak-woodland habitat. *J. NY Entomol. Soc.*, **93**: 1041–1046.

Topoff, H., Cover, S. and Jacobs, A. 1989. Behavioral adaptations for raiding in the slave-making ant, *Polyergus breviceps. J. Insect Behav.*, **2**: 545–556.

Visicchio, R., Castracani, C., Mori, A., Grasso, D.A. and Le Moli, F. 2003. How raiders of the slave-making ant *Polyergus rufescens* (Hymenoptera Formicidae) evaluate a target host nest. *Ethol. Ecol. Evol.*, **15**: 369–378.

Visicchio, R., Mori, A., Grasso, D.A., Castracani, C. and Le Moli, F. 2001. Glandular sources of recruitment, trail, and propaganda semiochemicals in the slave-making ant *Polyergus rufescens. Ethol. Ecol. Evol.*, **13**: 361–372.

Zamora-Munoz, C., Ruano, F., Errard, C., Lenoir, A., Hefetz, A. and Tinaut, A. 2003. Coevolution in the slave–parasite system *Proformica longiseta–Rossomyrmex minuchae* (Hymenoptera: Formicidae). *Sociobiology*, **42**: 299–317.