

Raiding Activity of an Obligate (*Polyergus breviceps*) and Two Facultative (*Formica puberula* and *F. gynocrates*) Slave-Making Ants

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Slave-making ants are social parasites that exploit the labor of workers from their host species by keeping them captive in the slave-maker nest. Slave-makers vary in their degree of specialization, ranging from obligate slave-makers that cannot survive without captives, to facultative slave-makers, which are often found living independently. Our study system included one obligate slave-maker, Polyergus breviceps, two facultative slave-makers, Formica puberula and F. gynocrates, and two hosts, F. occulta and F. sp. cf. argentea. We observed all raids conducted during two raiding seasons by seven P. breviceps colonies, two F. puberula colonies, and two F. gynocrates colonies. We report on raiding frequency, average raid distances, and then compare the probability of being raided multiple times in a single raiding season for the two host species. We also report on the spatial distribution of slave raids, which suggests that slave-makers avoid raiding in areas used by other slave-maker colonies. This is the first report of raiding activity for P. breviceps in this location, and the first report of raiding activity of any kind for F. puberula and F. gynocrates.

KEY WORDS: social parasites; raiding behavior; *Polyergus*; *Formica sanguinea*; ants.

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INTRODUCTION

Ant slavery is a form of social parasitism in which colonies of one species exploit the labor of workers of their host species by incorporating them into the slave-maker colony as captives. The life-history of slave-making ants includes two key components: parasitic colony founding by queens and slave-raiding by workers. A newly mated queen is unable to establish colonies independently and instead must enter a free-living host nest, execute or expel the resident queen(s), and either expel or gain acceptance from the host workers. The invading queen then begins laying eggs that are cared for by the host workers. Each year, slave-making workers raid neighboring host colonies to steal developing brood, which eclose in the slave-maker nest and perform normal worker duties. Although only about 50 of 11,000 ant species are slave-makers, this behavior has evolved at least 10 times independently, and is particularly common in the myrmicine tribe Formicoxenini and the formicine tribe Formicini (D'Ettorre and Heinze, 2001).

Slave-making ants are either obligate or facultative, reflecting the extent of dependence on hosts. Obligate slave-makers often have morphological and behavioral specializations that enhance their efficiency as slave-makers while compromising their ability to perform normal worker tasks (Mori and Le Moli, 1988). Thus, they are completely dependent on slaves for survival and are never found living independently. In contrast, facultative slave-maker workers often retain a normal behavioral repertoire, and colonies can function without captives (Mori *et al.*, 2001).

Slave-making ants and their hosts are engaged in a coevolutionary arms race whose pace and trajectory can vary dramatically from one site to another. For example, Foitzik *et al.* (2003) showed that across three sites in Europe, the interaction between *Harpagoxenus sublaevis* and its host *Lep-tothorax acervorum* ranged from mild to highly aggressive. Similarly, strong variation in the interaction between the slave-maker *Protomagnathus americanus* and its three hosts depends on host density, the availability of alternative host species, and geological history (Foitzik *et al.*, 2001; Blatrix and Herbers, 2003; Brandt and Foitzik, 2004). Differing strengths of interactions between slave-makers and hosts is best explained by the geographic mosaic theory of coevolution (Thompson, 1999; Gomulkiewicz *et al.*, 2000), which posits that geographic variation in the intensity of reciprocal selection results from local conditions, gene flow, and broader species composition.

Our study system included one obligate slave-maker, *Polyergus breviceps* and two facultative slave-makers from the *Formica sanguinea* group

(*F. gynocrates* and *F. puberula*). The *Formica sanguinea* group consists of 12 species, one in Eurasia and 11 in North America, which are generally considered to be facultative slave-makers (Hölldobler and Wilson, 1990). However, at least one North American species, *F. subintegra*, is regarded as an obligate slave-maker (Savolainen and Seppa, 1996; Savolainen and Deslippe, 2001).

Our primary objective in this study was to compare slave-raiding activity (frequency of raids, average raid distance, and observations of raid organization) of *P. breviceps*, *F. gynocrates* and *F. puberula* with data from other studies on *Polyergus* and *Formica sanguinea* group slave-makers. Several studies of slave-raiding behavior have been conducted on *P. breviceps* (Wheeler, 1916; Topoff *et al.*, 1984, 1985a,b,c), *P. lucidus* (Talbot, 1967; Coolkwait and Topoff, 1984; Trager and Johnson, 1985), *P. rufescens* (Czechowski, 1975, 1977; Mori *et al.*, 1991, 2001; Lemoli *et al.*, 1994), and *P. samurai* (Hasegawa and Yamaguchi, 1994, 1995). Because slave-makers in different locations often enslave different host species, collecting data from more populations is critical to gaining a better understanding of the life history of these ants and how they coevolve with their hosts. Indeed, our current knowledge of slave-raiding behavior of *P. breviceps* comes almost exclusively from two populations in Arizona, USA (Topoff *et al.*, 1985a,b). Our study system also had the added benefit that we could make comparisons for some parameters (raiding frequency, average raid distance, proportion of raids that failed, proportions of host colonies raided multiple times) for *P. breviceps* colonies that raided different host species in the same location.

Several studies have been conducted on the slave raiding activity of other *Formica sanguinea* group slave-makers (Czechowski, 1975; Topoff and Zimmerli, 1991; Czechowski and Rotkiewicz, 1997; Mori *et al.*, 2001), but, to our knowledge, there is no information on the raiding activity of *F. gynocrates* or *F. puberula*. Because facultative slave-makers might represent a crucial link in the evolution of obligate slave-making behavior (Mori *et al.*, 2001), the collection of data on more facultative slave-makers is critical.

A final objective of this study was to compare the spatial distribution of slave raids and to monitor interactions among slave-maker colonies themselves. This diverse slave-maker/host community provides an excellent system for studying both intraspecific and interspecific slave-maker interactions.

METHODS

We studied slave-raiding activity of three slave-makers, *Polyergus breviceps*, *Formica gynecrates*, and *Formica puberula* in interactions with two host species, *F. occulta* and *F. sp. cf. argentea*. Our 1 km² study site was in the foothills of the Rocky Mountains, at an elevation of approximately 2000 m, 36 km northwest of Fort Collins, Colorado USA. The study site included open meadows and sparsely spaced ponderosa pine, spruce, and fir trees. Prior to the study we found and marked all colonies of slave-makers and hosts nesting under rocks and stones, which were abundant on southern and south-eastern exposed slopes. At this location *P. breviceps* enslaves both host species, but individual colonies specialize on only one host. *Formica gynecrates* enslaves *F. sp. cf. argentea*, while *F. puberula* enslaves *F. occulta*. As they are members of the *F. sanguinea* group, the *Formica* slave-makers are assumed to be facultative. However, we found no colonies of either slave-maker at our study site or in the immediate vicinity that did not have captives ($N=3$ for *F. gynecrates*; $N=4$ for *F. puberula*). We did observe *Formica* slave-makers participating in activities outside of the nest such as nest maintenance, indicating that they are not “behaviorally degenerate” like *Polyergus* species. Although we do not know the exact age of any of these slave-maker colonies, all were at least two years old at the beginning of the study (they were marked during an earlier study at the same location).

Raiding Observations

Our study was conducted over two raiding seasons (July–August, 2002, and 2003). We monitored seven *P. breviceps* colonies, two *F. gynecrates* colonies, and two *F. puberula* colonies every day during the slave raiding season from 13:00 h until slave raids ended in the evening, usually before 20:00 h; additional nearby colonies were watched casually but are excluded here because we were unable to observe them in detail. We recorded all slave raids for each monitored colony and the location of host colonies using global positioning systems (GPS). We generated maps of raiding ranges with Arcview software. These maps included only raids that were successful because the majority of failed raids did not appear to reach a target nest and locations were thus ambiguous. For a small number of raids ($N=12$ for *P. breviceps*; $N=15$ for *Formica* slave-makers) we used a digital video camera to film raiding columns. We counted the number of raiders passing the camera during the first 15 min of a raid and we counted the number of pupae brought back for 15 min after the first worker returned with pupae.

These data were originally collected for another purpose, but nevertheless give a rough idea of the number of raiders participating in raids, the rate at which pupae were retrieved, and the amount of time before the first raider emerged with pupae.

Data Analysis

We used mixed model ANOVAs (SAS, proc mixed) to compare the total number of raids and average raid distance for *P. breviceps* colonies that raided different host species. We included host species, year, and host species-year interaction term as fixed effects and colony nested within host species as a random effect. We log-transformed values of average raid distance to normalize the data distribution, but no transformation was necessary for total raids. We eliminated terms from the model that were not significant ($\alpha = 0.10$). If we found no differences between colonies that raided different host types, we used General Linear Models to evaluate intercolonial differences in the number of raids or average raid distance. We included three factors in these models: colony, year and their interaction. Terms were eliminated from the model when they were not significant ($\alpha = 0.10$).

We used the *G*-test of independence (with Williams' correction) to compare the proportion of raid failures (raids that did not result in brood capture) for *P. breviceps* colonies that raided different host species and to compare the proportion of colonies that were raided more than one time during a given year. We also used the *G*-test of independence (with Williams' correction) to compare the proportion of raid failures and the proportion of colonies that were raided more than once in a year for slave-makers that raided the same host species.

We wanted to determine whether raiding distance increased for colonies as the raiding season progressed. Because colonies started raiding and stopped raiding on different dates we could not do a simple correlation analysis for raid distance and raid number. Instead we did separate correlations (Pearson) for each colony for each year; to determine whether there was a general trend for these correlations to be positive we used a *G*-goodness of fit test under the hypothesis that 50% of the correlations should be positive. Finally, we also used correlation analysis to determine whether the average raid distance was positively correlated with the number of raids conducted by a colony (i.e. do colonies that raid more frequently also raid over longer distances?).

RESULTS

Raid Descriptions

We observed a total of 175 raids against 143 different colonies over two field seasons (74 in 2002 and 101 in 2003). Although the first raids occurred on nearly the same date in 2002 and 2003 (July 1st and 2nd respectively), the duration of the raiding season was longer in 2003, spanning into mid August, while the 2002 season lasted only until late July. Raids occurred on nearly all days during the active period unless it rained.

Polyergus breviceps raids were characteristic of *Polyergus* raids described by others (Czechowski, 1975, 1977; Mori *et al.*, 1991, 2001; Lemoli *et al.*, 1994). Activity of *P. breviceps* workers commenced in the late afternoon as individuals began circling around the nest area, and raids began when scouts returned. Raiders left the nest *en masse*, forming a dense raiding column that moved toward the host nest. By examining video footage, we estimated that the number ants participating in raids ranged in the hundreds to more than a thousand [three colonies: Pb 2: 860 (1 raid only); Pb 3: 295–1116; Pb 4: 82 (1 raid only); Pb 6: 756–1133; Pb 10: 692–908]. Generally, most raiders had passed the monitoring point by 15 min, and thus, these ranges are good estimates of total raiders participating. When raiders arrived at the target colony they immediately searched for entrances to the nest and penetrated the host colony when an entry point was found. Raiders generally emerged from the nest carrying pupae or large larvae; the first raider carrying pupae reached the camera on the return trip at an average of 29 min after the raid began (Range: 14–45 min). In the next 15 min raiders brought back an average of 152 captive immatures (Range: 17–448). Raids rarely lasted for more than 1 h.

Formica puberula and *F. gynocrates* raids were similar to those described for closely related *F. sanguinea* (Czechowski, 1977; Czechowski and Rotkiewicz, 1997; Mori *et al.*, 2000, 2001). The beginning of a raids were less conspicuous than that of *P. breviceps*, as raiders left the home nest gradually rather than *en masse*. Rather than forming a raiding column moving in one direction, individuals moved back and forth along the route to the host colony in a manner characteristic of that described for *F. sanguinea* (Czechowski, 1977). The slow build-up of individuals participating in slave raids is exemplified by the low numbers of raiders leaving the slave-maker nest during the first 15 min of a raid (Fp 2: 78–123; Fg 5: 60–124). Although these figures are low, numbers continued to build up over the course of the raid with several hundred to a thousand raiders participating by the

end. Raiders sometimes spent considerable time digging near the host colony before finally penetrating and stealing brood, which is suggested by the average time of 62 min for the first raider to reach the camera with brood (Range: 12–155 min). Over the next 15 min, raiders brought back an average of 14 (Range: 1–40) immatures. Raiders stole mostly large larvae and pupae, but were also seen carrying fully-pigmented adult ants in the pupal position and, on one occasion, alate females that appeared to be alive. Raids commonly lasted for several hours and so the average amount of brood retrieved in the first 15 min is not a reliable estimate of the total number of brood stolen. The overall picture that emerges is that the *Formica* slave-makers were generally less efficient slave raiders than *P. breviceps*.

Spatial Distribution of Raids and Interactions Between Slave-Maker Colonies

The spatial distribution of successful raids during 2002 and 2003 is shown in Fig. 1. These distributions suggest that slave-maker colonies do not raid in random directions. In some cases, the absence of raids in a particular area can probably be explained by a lack of host colonies in the area. For example, colony Fp 2 conducted almost no raids in the area to the west of the nest, which is probably explained by the fact that this area was an open meadow with few rocks for host colonies to nest under. In other cases, the spatial distribution of raids suggests that slave-makers avoid raiding in areas used by other slave-maker colonies. For example, colonies Fg 5 and Pb 3, despite being close enough for raiding ranges to overlap, did so rarely. The most overlap was between colonies Pb 8 and Pb 6 in 2003, but it is interesting to note that these colonies temporally segregated their raiding activities. They raided on a total of 30 days over two seasons, but raided on the same day only twice (Pb 8 raided more at the beginning of the season and Pb 6 later in the season). On one of these occasions (2002) Pb 8 traveled near Pb 6 and encountered circling workers prior to the onset of a raid. This resulted in large-scale aggression, and interestingly, Pb 8 did not raid again for the rest of the season. We did observe Pb 6 and Fp 2 raiding columns cross on one occasion in 2003, which again resulted in large-scale aggression. Here, it is interesting that Fp 2 was raiding extremely far from its home nest (54.9 m) and Pb 6 was raiding in a direction that it had not raided over the two seasons. Finally, on three occasions we observed one slave-maker colony attempt to raid another (Fp 2 raided Pb 6; Fp 2 raided Pb 3; and Pb 6 raided Pb 3). In all cases, large-scale fights ensued and no

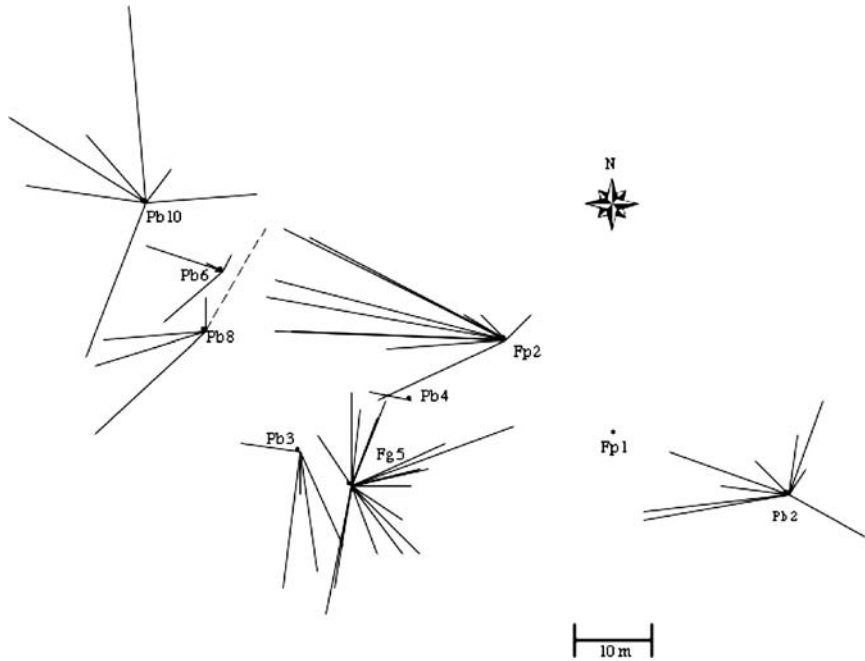


Fig. 1. Spatial distribution of slave raids in (a) 2002 and (b) 2003. Raids that involved confrontations between slave-maker colonies are represented by dashed lines (crossed lines do not necessarily indicate that raiding columns crossed because raids may have been on different days). Two colonies (Pb 12 and Fg 12) are excluded from these figures because they were distantly located from the other colonies.

brood were ever stolen. Because these were failed raid attempts, they are not depicted in Fig. 1.

Comparison of Raid Characteristics

The number of raids conducted by each slave-maker colony are summarized in Table I. Intercolonial comparisons for *P. breviceps* revealed clear differences in the number of colonies raided (GLM, $P = 0.019$), but differences in raiding frequency were not related to the ant host species raided by each *P. breviceps* colony (Mixed model ANOVA, $P = 0.42$ for host species). There was also a strong suggestion that colonies raided more in 2003 than 2002 (GLM, $P = 0.06$ for year). Four colonies (Pb 4, Pb 12, Fp 1, and Fg 12) did not raid successfully in one of the two years, even though

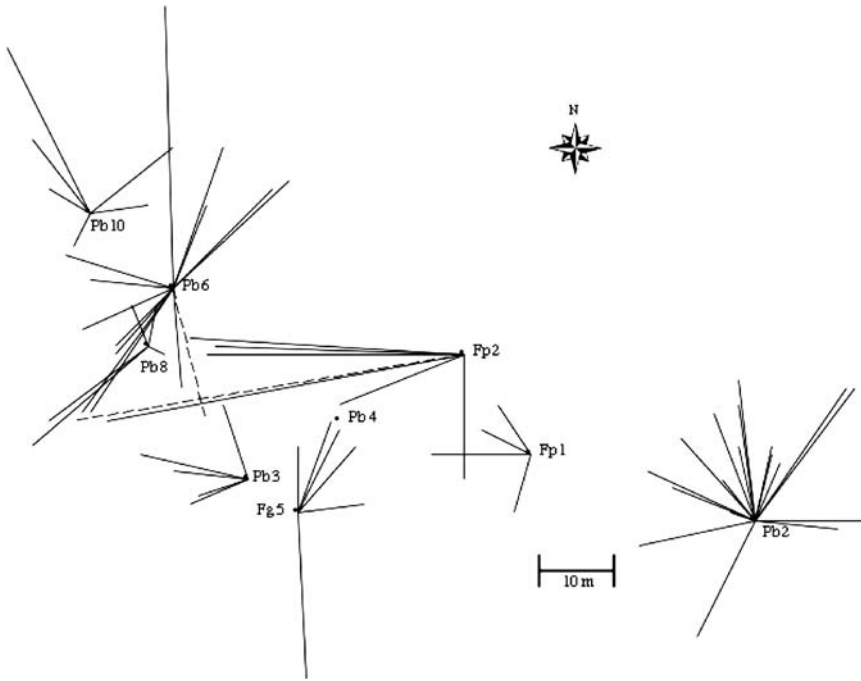


Fig. 1. Continued.

slave-makers were still present in the nest. No host colonies were raided by more than one slave-maker colony.

We found no difference in failure rate of *P. breviceps* colonies that raided different host species (26% for colonies raiding *F. occulta* vs. 23% for colonies raiding *F. sp. cf. argentea*; *G*-test, $P = 0.73$). Thus we pooled all *P. breviceps* data for comparisons with the *Formica* slave-makers, and still found no differences (24% for *P. breviceps*, 21% for *F. puberula*, 13% for *F. gynocrates*; *G*-test, $P = 0.34$).

Polyergus breviceps colonies were more likely to raid *F. occulta* colonies multiple times than *F. sp. cf. argentea* colonies (39% of *F. occulta* colonies raided multiple times, vs. 13% of colonies *F. sp. cf. argentea* multiple times; *G*-test, $P = 0.02$). Compared to *P. breviceps*, the frequency of multiple raids of *F. occulta* colonies by the facultative slave maker *F. puberula* was similar (32%, *G*-test, $P = 0.69$), as was the frequency of multiple raids of *F. sp. cf. argentea* by the facultative slave-maker *F. gynocrates* (8%, *G*-test, $P = 0.55$). Overall, slave-makers that specialized on *F. occulta* were

Table 1. Total Number of Successful Raids, Number of Different Colonies Raided, and Number of Failed Raid Attempts by *P. breviceps* (Pb), *F. pubertula* (Fp), and *F. gynocrates* (Fg) Colonies During 2002 and 2003 Raiding Seasons

Colony	Host type	2002		2003	
		Total successful raids	Different colonies raided	Total successful raids	Different colonies raided
Pb 2	<i>F. sp. cf. argentea</i>	12	10	24	19
Pb 3	<i>F. occulta</i>	9	6	12	6
Pb 4	<i>F. sp. cf. argentea</i>	1	1	0	0
Pb 6	<i>F. occulta</i>	8	5	17	16
Pb 8	<i>F. sp. cf. argentea</i>	6	6	6	6
Pb 10	<i>F. sp. cf. argentea</i>	7	7	9	7
Pb 12	<i>F. sp. cf. argentea</i>	0	0	4	3
Fp 1	<i>F. occulta</i>	0	0	5	5
Fp 2	<i>F. occulta</i>	12	12	16	8
Fg 5	<i>F. sp. cf. argentea</i>	18	17	8	7
Fg 12	<i>F. sp. cf. argentea</i>	1	1	0	0
					8
					10
					0
					6
					4
					3
					1
					1
					4
					1
					1

three times more likely to re-raid a host colony than slave-makers that specialized on *F. sp. cf. argentea* (G -test, $P = 0.01$).

Raid Distances

Average raid distances for each colony are presented in Table II. Comparisons among *P. breviceps* colonies revealed strong differences in average raid distance, with means ranging from 4 m to 19.1 m (GLM, $P = 0.01$). This variation was not explained by different host species raided by the *P. breviceps* colonies (Mixed model ANOVA, $P = 0.59$). Average raid distance was positively correlated with the number of raids conducted by a colony ($r = 0.60$, $P = 0.16$). Despite a strong positive correlation this result was not statistically significant, probably because of low power.

We also found evidence that raid distance increased as the raiding season progressed. When we considered all data (all three slave-makers over both years) 12 of 16 correlation coefficients for raid distance vs. raid number were positive (G -test, $P = 0.04$; Table III). When we considered only *P. breviceps*, this relationship was strong (9/11 were positive; G -test, $P = 0.03$), but when we considered only the *Formica* slave-makers the relationship was weak (3/5 were positive; G -test, $P = 0.67$). Thus, the relationship between raid distance and raid number might be unique to *P. breviceps*, but because data were limited to only three *Formica* slave-maker colonies we cannot say with certainty.

DISCUSSION

Our study provides new insight into the raiding activity of one obligate slave-maker, *P. breviceps*, and two facultative slave-makers, *F. puberula* and *F. gynecrates*. This is the first study to report on interactions between *P. breviceps* and the two host species present at our field site (*F. occulta* and *F. sp. cf. argentea*). Moreover, to our knowledge, this is the first analysis of raiding activity of the facultative slave-makers *F. gynecrates* and *F. puberula*.

Polyergus Breviceps Raiding Behavior

In general, our behavioral observations of *P. breviceps* raids are similar to descriptions from other studies (1985a,b), with the exception of one important difference. Topoff (1990) reported that alate queens frequently

Table II. Average Raid Distance and Distance Range for Raids by Slave-Maker Colonies in 2002 and 2003 (Pb, *P. breviceps*; Fp, *F. puberula*; Fg, *F. gynocrates*)

Colony	Host type	Average raid distance 2002 \pm S.E. (meters)	Distance range 2002 (meters)	Average raid distance 2003 \pm S.E. (meters)	Distance range 2003 (meters)
Pb 2	<i>F. sp. cf. argentea</i>	12.1 \pm 2.1	3.7–22	12.2 \pm 1.2	3.6–21.2
Pb 3	<i>F. occulta</i>	14.7 \pm 1.8	8.1–20.1	10.9 \pm 0.7	7.8–15.6
Pb 4	<i>F. sp. cf. argentea</i>	8.1*	—	—	—
Pb 6	<i>F. occulta</i>	8.4 \pm 1.8	1.0–12.6	17.3 \pm 1.7	10.2–38.0
Pb 8	<i>F. sp. cf. argentea</i>	15.0 \pm 2.3	5.2–22.0	10.2 \pm 3.1	3.7–22.0
Pb 10	<i>F. sp. cf. argentea</i>	19.1 \pm 3.4	5.6–29.1	12.6 \pm 2.2	5.4–25.0
Pb 12	<i>F. sp. cf. argentea</i>	—	—	4.0 \pm 1.2	1.0–6.7
Fp 1	<i>F. occulta</i>	—	—	8.7 \pm 1.4	5.9–14.0
Fp 2	<i>F. occulta</i>	24.5 \pm 4.1	4.4–35.5	38.7 \pm 3.7	5.2–54.9
Fg 5	<i>F. sp. cf. argentea</i>	12.9 \pm 1.3	8.9–25.6	13.8 \pm 2.8	6.2–24.0
Fg 12	<i>F. sp. cf. argentea</i>	13.9*	—	—	—

* Colony only conducted one raid

Table III. Pearson Correlation Coefficients for Raid Distance and Raid Number for Each Slave-Maker Colony (Pb, *P. breviceps*; Fp, *F. puberula*; Fg, *F. gynocrates*) During Both Years of Study

Colony	<i>r</i> —2002 (<i>N</i>)	<i>r</i> —2003 (<i>N</i>)	<i>G</i> -test	<i>P</i> -values
Pb 2	0.064 (10)	0.615 (24)	All data	0.04
Pb 3	0.728 (8)	0.054 (11)	<i>P. breviceps</i>	0.03
Pb 6	0.704 (8)	0.324 (17)	<i>Formica</i>	0.67
Pb 8	− 0.117 (6)	0.624 (6)		
Pb 10	0.668 (6)	0.192 (9)		
Pb 12	−	− 0.579 (4)		
Fp 1	−	0.895 (5)		
Fp 2	−0.044 (9)	0.772 (16)		
Fg 5	−0.068 (13)	0.960 (7)		

Note. *G*-tests assumed that 50% of correlation coefficients would be positive. (−) indicates that a colony did not raid during that season

accompanied workers on slave raids and even mated en route to the target colony, which was interpreted as an adaptation for locating and gaining entry to a host colony after mating. Although we did observe one alate queen participate in a slave raid, this was indeed rare, and we never observed queens mating in raiding columns. This suggests that the mating system of *P. breviceps* is diverse and that queens in different populations may have alternative methods of locating and entering host colonies. Clearly, more work is needed in order to fully elucidate the mating system and mechanisms of host nest location for this species.

Polyergus breviceps apparently raids less often than other *Polyergus* species, as our observations are in line with other studies of *P. breviceps* (Topoff *et al.*, 1985a,b), but far below raiding frequencies reported for *P. lucidus* (50 raids by one colony in one season, Coolkwait and Topoff, 1984), and *P. samurai* (32–63 raids during one season, Hasegawa and Yamaguchi, 1995). Separate studies of single *P. rufescens* colonies yielded 19–27 successful raids in a season (Mori *et al.*, 1991; Lemoli *et al.*, 1994). The reduced raiding frequency of *Polyergus breviceps* may reflect differences in host colony size. A comparison between *P. breviceps* and *P. lucidus* of the number of pupae retrieved per raid suggests that this is the case as *P. breviceps* typically retrieved far more pupae in a single raid than *P. lucidus* (Coolkwait and Topoff, 1984; Topoff *et al.*, 1985a,b). Thus, fewer raids might be necessary for a colony of *P. breviceps* to maintain an adequate slave pool than its congeners.

We found strong differences among *P. breviceps* colonies in the average distance to target host colonies. Hasegawa and Yamaguchi (1995) also reported intercolonial differences for average raid distance in *P. samurai*. Average distance traveled to target nests over the two seasons in our

study was 12.3 m, which is similar to that found for *P. samurai* (11.4 m, Hasegawa and Yamaguchi, 1995) but much lower than averages of 34 and 49 m found for *P. breviceps* in two other locations (Topoff *et al.*, 1985a,b). Such differences could reflect differences in host nest densities at different locations. We also found that raiding distance increased as the raiding season progressed. Thus, colonies that raided only a few times were likely to raid closer to their home nest, while colonies that raided more often began near their home nest but moved outward as the season progressed, probably when local resources were depleted. Finally, it is worth noting that the minimum distance traveled by *P. breviceps* to a host colony was only 1 m (Table II). Czechowski (2005) reported that slaves of large *P. rufescens* colonies commonly formed nearly-independent satellite nests that were raided on several occasions, with slave-makers carrying adult slaves back to the slave-maker nest. Despite the close proximity of the aforementioned host nest to the *P. breviceps* nest that raided it, this raid seemed characteristic of a normal slave raid rather than of the integration raids described by Czechowski (2005).

Formica Raiding Behavior

Our observations of *F. puberula* and *F. gynocrates* are similar to other reports on *F. sanguinea* group slave-makers in the literature (Czechowski, 1977; Topoff and Zimmerli, 1991; Czechowski and Rotkiewicz, 1997; Mori *et al.*, 2000, 2001). Raids were less organized than those for *P. breviceps* as raiders gradually left the home nest rather than en masse. Moreover, raids were characterized by digging and slow entry into the target host nest (sometimes it took hours for raiders to emerge with brood). On several occasions we observed raiders carrying reproductive pupae and even alates on one occasion. Presumably their fates were to be eaten in the slave-maker nest as Mori *et al.* (2000) have reported for *F. sanguinea*.

To our knowledge, there are no published data with which we can compare our data on average raid distances for *F. puberula* and *F. gynocrates*. One *F. puberula* colony conducted longer raids than any other colony of any species at our site, but our sample sizes are too small to make generalizations. There was also a suggestion that *F. puberula* and *F. gynocrates* do not go on longer raids as the raiding season progresses, but again, this might be an artifact of low sample sizes. In fact, the two strongest positive correlations between raid distance and raid number were for colonies Fp 1 and Fg 5 (2003), suggesting that, at least in some years, raid distance increased as the season progressed for these colonies.

Spatial Distribution of Slave Raids and Interactions Between Slave-Makers

The spatial distribution of slave raids seems to suggest that slave-maker colonies avoid raiding in areas used by other colonies (Fig. 1). Despite the fact that colonies were in close proximity relative to their average raiding distances, raiding overlaps were rare. Where raiding overlaps occurred, they were either segregated temporally (as for Pb 6 and Pb 8), or they occurred at the edges of colonies' raiding ranges. This coupled with the fact that colonies were aggressive when they encountered one another suggests the possibility that slave-maker colonies defend raiding territories. If this is the case, however, it is difficult to understand how such raiding territories could be established and maintained, at least for *P. breviceps*. The *Formica* slave-makers probably forage, so territories could be established and enforced by foragers. However, since *P. breviceps* workers do not forage, territories are probably established by scouts and may involve olfactory cues. Scouts might avoid areas contaminated by trail pheromones from other colonies, or areas in which previous encounters with other raiding columns occurred.

As few studies have detailed the spatial distribution of slave raids in large slave-maker communities, it is difficult to determine whether spatial segregation of slave raids is indeed common in these systems. We do note, however, that two studies have suggested that slave-maker colonies raid in non random compass directions (Coolkwait and Topoff, 1984; Topoff *et al.*, 1985a). Moreover, one study showed that two *F. sanguinea* colonies appeared to avoid raiding near each other when both were active, but when one colony stopped raiding for the season, the other colony began raiding in its general direction (Mori *et al.*, 2000). These considerations imply that slave-makers may commonly adjust raiding ranges depending on the activity of neighboring colonies, but more studies are needed to verify this possibility. Clearly, this is an exciting area of future research in slave-making ant systems.

Slave-makers clearly acted in an aggressive, territorial manner when they encountered each other in raiding space. In addition, we observed three occasions when slave-maker colonies attacked each other directly at the nest (one intraspecific and two interspecific). Intraspecific raiding has been reported by others, and has been interpreted as territorial behavior (Mori *et al.*, 2001). However, it is also possible that these instances represent simple mistakes (scouts mistaking a mixed species slave-maker colony for a host colony). It is thus interesting to note that in our study all three raids against other slave-maker colonies were between slave-makers that enslaved the same host species.

One final interesting result from our study was that the two host species differed in the proportion of colonies that were raided multiple times during a raiding season. *Formica occulta* host colonies were raided more than once three times as often as *F. sp. cf. argentea* colonies. Because *P. breviceps* raided both host species (individual colonies specialized on one host), this pattern appears to be driven by attributes of hosts rather than slave-makers. These differences could reflect the fact that *F. occulta* nests were less common at this site than *F. sp. cf. argentea* nests. This, coupled with the fact that *F. occulta* colonies were more likely to survive slave raids (Bono *et al.*, [in press](#)), means that nests of this species were probably at higher risk of being raided more than one time during a raiding season.

Recent studies on coevolution between slave-makers and their hosts have indicated that variation in the intensity of arms races is best explained by the geographic mosaic theory of coevolution (Thompson, 1999; Gomulkiewicz *et al.*, 2000). Thus, in order to fully understand how slave-makers and their hosts coevolve, it is essential to characterize their interactions in alternative locations that differ in ecological context. In this study, we provide basic information such as raiding frequency and host usage for three slave-makers in associations with two different host species. Data for *P. breviceps* complements the findings of earlier studies on this species in a different location where it is associated with another host species (Topoff *et al.*, 1985a,b), while these are the first data on the slave raiding activity of *F. puberula* and *F. gynocrates*. Our results also suggest that competition among slave-makers themselves may influence the outcome of interactions between slave-makers and hosts in communities with multiple parasite and host species. Clearly, these complex slave-maker/host communities are valuable systems for future studies on coevolution between parasites and hosts.

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