

FORMICA WHEELERI: DARWIN'S PREDATORY SLAVE-MAKING ANT?

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INTRODUCTION

Hypotheses concerning the evolution of slavery in ants emphasize the role of excess predation (Darwin, 1859), territorial encounters (Alloway, 1980; Wilson, 1975), or brood transport among polydomous colonies (Buschinger, 1986). Although these views are not mutually exclusive, many investigators have noted the general absence of group predation in dulotic ants (Hölldobler and Wilson, 1990). This has been thought to be true for facultative slave making ants belonging to the genus *Formica*, although most research has been conducted only on the European species *F. sanguinea* (Dobrzanski, 1965), and the related North American species, *F. subintegra* (Talbot and Kennedy, 1940). Relatively little is known about the numerous other species belonging to the *sanguinea* group. For example, although colonies of *Formica wheeleri* are common in western United States, we have but one account of their raiding and nesting activities (Wilson, 1955). In the mountains of southeastern Arizona, colonies of *F. wheeleri* are sympatric with *Polyergus breviceps*, an obligatory slave-making ant with which *F. wheeleri* competes for the same slave species. In this paper, we present the results of a field study revealing that *F. wheeleri* may be the only facultative slave-maker to exhibit the general predatory behavior predicted by Darwin's hypothesis for the evolution of slave-making ants.

MATERIALS AND METHODS

Seven colonies of *Formica wheeleri* were monitored from June 16 to July 16, 1991, during the time period 0730–1700 h (MST). All colonies were located in the Chiricahua Mountains, Cochise County, Arizona. The field site is located 14 km west of Portal,

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Arizona. At an elevation of 2750 m, the habitat is dominated by Ponderosa pine and Douglas fir. Although three species of *Formica* are abundant in this habitat (*F. occulta*, *F. marcida*, and *F. neogagates*), only *F. occulta* is parasitized in this study site.

RESULTS

Raiding Activities: The raiding characteristics of five colonies of *Formica wheeleri* are summarized in Table 1. Prior to the onset of the summer monsoon rains (June 23–July 6), the median time for group raiding was 1405 h. During the rainy season, the median time for group raiding was 4.5 h earlier. It is likely that the earlier onset of raids after July 6 was due to the corresponding drop in daytime temperature when the rainy season began.

The data presented in Table 1 are only for raids in which at least 20 workers simultaneously left the nest area and proceeded in an organized group toward a target nest. But before and after such raids, every gradation of foraging behavior, from individual exploration to group raiding, was observed. Indeed, for most of the day, the distinction between raiding and individual foraging was entirely moot. When individual foragers left the nest, they scavenged for dead arthropods, as do their *F. occulta* slaves. Slave individuals did not participate in group raids on other colonies of *F. occulta*.

Predatory Behavior: During most group raids by *Formica wheeleri*, host workers fled from their nest with brood, fighting between parasite and host was short-lived, and few workers of

Table 1. Summary of *Formica wheeleri* raiding activities

	Range	Median	Sample size
No. of <i>F. wheeleri</i> on raid	21–660	114	42
Time of raid onset (MST)			
June 16–July 06	1215–1612	1405	18
July 07–July 16	0804–1440	0936	29
Distance to target nest (m)	2–31	13	42
No. of brood taken (larvae + pupae)	2–182	25	16

either species were killed. Nevertheless, we observed numerous instances when *F. wheeleri* killed the resident *F. occulta* workers and took the dead ants back to their nest. We also observed predation on other species of ants. Our observations of group predation are summarized as follows:

June 26: During a foray conducted by only 13 raiders from colony 4, one worker of *F. occulta* was killed by three *F. wheeleri*, and dragged back to the nest.

June 27: During a raid by colony 3, two workers of *Camponotus* and one of *Formica marcida* were present near the nest of the target *F. occulta* colony. All three ants were promptly killed and taken back to the *F. wheeleri* nest.

June 28: Workers from colony 3 killed eight *F. occulta* workers at the target nest. Again, all were hauled back to the parasite's nest.

June 28: Raiders of *F. wheeleri* moved out in several bursts. At the target nest, the arriving ants extensively excavated the *F. occulta* nest entrance. As the resident workers came to the surface, they engaged in prolonged fights with the intruders. Fifty-five *F. occulta* workers were killed and immediately carried back to the *F. wheeleri* nest.

June 29: Approximately 1 hour prior to a raid by colony 4, a target nest of *F. occulta* was attacked by a colony of *Polyergus breviceps*, and approximately 45 *F. occulta* workers had been killed (but not removed) by the *Polyergus*. When the *Formica wheeleri* raiders arrived at the site, they promptly retrieved every dead worker.

July 12: A raiding party from colony 2 encountered a column of foragers belonging to the species *Liometopum apiculatum*. Fighting erupted immediately. Although this interaction aborted the slave raid, 28 *Liometopum* foragers were killed and taken back to the *F. wheeleri* nest.

July 12: A colony of *Formica wheeleri* raided a colony of *Polyergus*. Fighting was intense and workers of both species were killed. Although the *Polyergus* did not retrieve any dead *Formica*, the *F. wheeleri* raiders picked up at least 12 dead *Polyergus* workers, and transported them back to their own nest.

Finally, throughout the month-long observation period, raiders of *Formica wheeleri* were observed attacking leaf hoppers, small caterpillars, and spiders that inadvertently wandered into the path of a slave-raid swarm. In all such instances, the arthropods were killed and carried back to the *F. wheeleri* nest.

Brood retrieval: Our observations on predatory behavior suggested that *Formica wheeleri* might be less specialized than *Polyergus* with respect to species diversity of retrieved brood. To document this, 50 pupae of *Camponotus ocreatus* (a non-sympatric species) were placed 0.5 m in front of a *F. wheeleri* raid swarm. The raid halted and all pupae were removed in less than 5 min. When a similar batch of *C. ocreatus* pupae were placed in front of a *Polyergus breviceps* swarm, the raiders ran over the pupae without hesitating and none of the brood was captured. This procedure was repeated on three consecutive days, each with a different colony of *Formica wheeleri* and *Polyergus*. In all cases, every pupa was removed by *F. wheeleri* and none were removed by *Polyergus*.

A similar, and somewhat more natural, test was conducted on June 30. At 1330 h, a colony of *Polyergus* initiated a raid toward a colony of *F. occulta* located 45 m to the south. En route to the target, the *Polyergus* raiders encountered a nest of *Formica neogates*. Resident workers emerged from the nest, and intense fighting broke out as workers of both species grabbed legs and antennae. After approximately 5 min, panic alarm spread through the *F. neogates* nest. The queen emerged, followed by hundreds of workers carrying brood. When most of the adult *Formica* workers had scurried away, the area immediately around the nest entrance was littered with more than one hundred undefended pupae. When fighting ceased, the *Polyergus* workers regrouped, and proceeded another 10 m to the target nest of *F. occulta*. Significantly, not one of the *F. neogates* pupae was retrieved. Eighty-

five of these pupae were aspirated and placed in front of a raid swarm of *Formica wheeleri*. All the pupae were retrieved in less than 5 min.

Emigration: Two emigrations were observed during the field season. The first colony moved 2 m to the east during the period June 23–June 27, and the second colony emigrated 4 m to the east from July 2 to July 6. Throughout the emigrations, both colonies maintained their normal activity schedules. Thus, worker transport commenced at approximately 1300 h, and ceased shortly after 1630 h. In the first colony, workers of *Formica wheeleri* transported all brood, callows (including callow alates of *F. wheeleri*), and adults of both species. Workers of *Formica occulta* were never observed carrying other individuals. Their activities were confined to nest maintenance at the new site. In colony 2, we did observe 1 individual of *F. occulta* carrying an *F. wheeleri* adult. But again, all other brood and adult workers of both species were transferred to the new site by workers of *F. wheeleri*.

DISCUSSION

Facultative slave-making ants, like those in the *sanguinea* complex, represent an intermediate parasitic group, between freelifving species on the one hand, and obligatory dulotic species on the other. In recent laboratory tests by Mori and Le Moli (1988), slaves were removed from colonies of *Formica sanguinea* and *Polyergus rufescens*. Not surprisingly, the behavioral repertory of *F. sanguinea* expanded dramatically within 30 days of slave removal, with workers becoming self sufficient at feeding and brood care. Workers of *Polyergus*, by contrast, were unable to care for their brood, and experienced high mortality. The behavior of both species during emigrations and foraging (summarized in Table 2) also shows that *Formica wheeleri* is less specialized than *Polyergus*.

Most studies on the raiding behavior of species in the *F. sanguinea* complex confirm that slave raiders usually rout their opponents, who typically flee in a state of panic alarm, and that aggressive encounters, when they occur, are brief and do not result in the death of adult individuals from either species (Talbot and Kennedy, 1940). Wheeler (1910) noted, however, that when large

Table 2. Comparison of behavioral characteristics between *Formica wheeleri* and *Polyergus breviceps*.

	<i>F. wheeleri</i>	<i>P. breviceps</i>
Emigrations	<i>F. wheeleri</i> adults carry both brood and adults of both species to new nest	Only slaves transport adults and brood of both species to new nest
Foraging	Workers forage individually and on group raids	No individual foraging
Brood retrieval	Workers retrieve brood even from different ant genera	Only brood from slave or closely related species retrieved
Adult ant capture	Raiders kill and retrieve adults even from different ant genera	Raiders rarely kill, and never retrieve other adults

colonies of slave species offer resistance during raids, prolonged fighting is possible, and many workers of both species can be killed. Despite numerous instances of such fighting, Wheeler did not observe slave-raiders retrieving dead ants of either species. During the period 1955–1960, Marikovskiy (1963) transferred more than 400 colonies of *Formica rufa* into habitats occupied by *F. sanguinea*. The aggressive *F. sanguinea* virtually destroyed all the introduced *F. rufa* colonies. Marikovskiy also reported that *Formica sanguinea* raided five other species of *Formica*, as well as *Camponotus herculeanus*, and *Lasius flavus*. Although adult workers were routinely killed during these forays, only larvae and pupae were transported back to the *Formica sanguinea* nest.

More recently, Talbot (1985) studied raids by *Formica gynocrates* (another facultative parasite belonging to the *Raptiformica* group), which pillages colonies of *Formica vinculans*. When attacked, resident workers pick up brood and evacuate their nest, and seek protection at the top of plant stems. Nevertheless, *F. vinculans* workers from large colonies can stage a counterattack, and may be killed in the melee. In one such vigorous raid observed by Talbot, 230 pupae and 89 larvae were captured. Near the end of the raid, when pupa transport dwindled, a few *Formica gynocrates* workers picked up dead *Formica vinculans* individuals and carried them home.

Given the scant evidence for predation by facultative formicine slave-making ants, it is not surprising that researchers have consistently rejected Darwin's claim that dulosis evolved from predatory raiding. It is true that many *F. wheeleri* raids are similar to those reported for other *sanguinea* group species, in that brood is retrieved after driving resident adults from their nest, and that killing of adults typically only occurs when resident workers actively defend their nest. Nevertheless, it is clear from our observations that *Formica wheeleri* is the most predatory *sanguinea* species known to date: (1) it takes adult ants as well as brood, and often just adults of other genera; and (2) this behavior is common.

The discovery of significant predation by *Formica wheeleri* clearly does not call for a major shift in our ideas about the origin of dulotic behavior. First, it could still be argued that predatory behavior of *F. wheeleri* evolved from intraspecific, territorial raids. Although we observed no such interaction during this field season, we do have one past record of such a territorial encounter. Second, although an evolutionary hypothesis of dulosis based on predation can account for brood capture and the rearing of excess pupae, the important issue of non-independent colony foundation must also be addressed.

We have recently shown (Topoff et al., 1990) that newly mated queens of *Formica wheeleri* usurp colonies of *F. occulta* by driving out the resident queen and workers, gathering the pupal brood into a pile, and rearing the pupae through eclosion. We have also argued that the ability to usurp the pupal brood of incipient nests belonging to closely related species would be of tremendous selective advantage to a colony-founding queen (Topoff, 1990a, b). Through olfactory conditioning, rearing of raided brood in the nest of the queen's origin could specify the host species colony to be invaded, and could even provide the queen with some degree of host-species olfactory resemblance, similar to that hypothesized for *Polyergus* (Goodloe and Sanwald, 1985). Such host colony invasions would only be successful, however, if the invading queen usurped pupae from colonies of closely related species, thus ensuring similar ecological requirements. The role of predation in such an evolutionary process would be to facilitate the subsequent capture of additional pupae, with some being used as food, and others reared to become slaves. Although we observed raiders of

F. wheeleri capturing adult workers of *Liometopum*, *Camponotus*, and *Formica marcida* during slave raids, no nest of these species was invaded. To date, such raids on nests have only been directed toward other colonies of *F. wheeleri*, *F. occulta*, and *Polyergus breviceps*. If the species to be raided by *F. wheeleri* is influenced by olfactory experience from their own slaves, raids on these three species may be biased, because all contain workers of *F. occulta*. Since we have found no nests of *F. wheeleri* without slaves, we plan to create such homospecific colonies by providing a newly-mated queen with several hundred pupae. Our goal is to determine whether such homospecific colonies of *F. wheeleri* will exhibit even greater predation, by expanding the range of species whose nests are raided.

SUMMARY

In southeastern Arizona, at an elevation of 2750 m, the facultative slave-making ant *Formica wheeleri* is sympatric with *Polyergus breviceps*. Although three additional species of *Formica* are common in this habitat, only colonies of *F. occulta* are raided for slaves. Like other species in the *Formica sanguinea* complex, every gradation of foraging behavior, from individual exploration to group raiding, was common. Unlike other dulotic species of *Formica*, however, slave raids often resulted in the killing and retrieval of adult ants (in addition to brood) from the invaded colony. We also observed a raid on a colony of *Polyergus*, an obligatory slave maker in direct competition with *F. wheeleri*, because it uses the same host species. In this raid, *Polyergus* adults were also killed and taken back to the *F. wheeleri* nest. Workers of *Formica marcida*, *Camponotus*, and *Liometopum apiculatum* who were foraging in the path of slave-raid swarms were similarly killed and retrieved. These field observations depict a slave-making ant far more predatory than other species in the *Formica sanguinea* complex.

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