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A SLAVE-MAKING ANT IN FLORIDA: *POLYERGUS LUCIDUS* WITH OBSERVATIONS ON THE NATURAL HISTORY OF ITS HOST *FORMICA ARCHBOLDI* (HYMENOPTERA: FORMICIDAE)

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ABSTRACT

The slave-making ant *Polyergus lucidus* is reported for the 1st time from Florida. *Formica archboldi* is its host species, not previously known to be parasitized in this way. The behavior of these 2 species is described and compared to that of related forms from other regions.

RESUMEN

Se registra por primera vez la hormiga esclavista *Polyergus lucidus* de la Florida. *Formica archboldi* es su hospedero, que no se conocía previamente que era parasitado de esta forma. Se describe el comportamiento de las 2 especies, y se compara con el de hormigas emparentadas de otras regiones.

Dulosis is a form of social parasitism in which the workers of 1 species of ant periodically raid colonies of related species for brood. The plundered brood is reared in the nest of the parasite by workers of the host species which serve as the nurse, forager, defense, and construction force for the mixed colony. Often referred to as slave-making, this type of parasitism is unique to Formicidae, but has arisen several times independently within the family (Wilson 1971).

Talbot (1967, 1968), Harman (1968) and Marlin (1968, 1969, 1971) have reported on the natural history of *Polyergus lucidus* Mayr in Michigan and Illinois, and Kwait and Topoff (1983) have recently published on the species'

behavior on Long Island. This paper reports observations made in 1983 on 3 colonies of the so-called subspecies *P. lucidus longicornis* Smith near Gainesville, Florida and its host, *Formica archboldi* Smith. In the opinion of JCT, the Florida population simply represents the southern end of a spottily distributed and somewhat variable species; *P. lucidus*. In view of the morphological and (as shown below) behavioral indistinctness of the Florida *Polyergus*, we refer to these ants henceforth as *P. lucidus*. This should not be construed as a formal taxonomic change at this time.

This is the 1st record of *F. archboldi* as a slave in *Polyergus* nests. This *Formica* is a member of the *pallidefulva* group, to which most other host records for *P. lucidus* belong (Smith 1979).

Florida *P. lucidus* were observed in a turkey oak-long leaf pine sandhill community with sparse clumps of wire grass and patches of gopher apple as ground cover. Other ants common at the site are *Formica pallidefulva* Latreille, *Camponotus socius* Roger, *C. floridanus* (Buckley), *Paratrechina arenivaga* (Wheeler), *Leptothorax pergandei* Forel, *Solenopsis pergandei* Forel, *S. geminata* (F.), *Pogonomyrmex badius* (Latreille), *Aphaenogaster floridana* M. R. Smith, *Pheidole morrisi* Forel, and *Odontomachus brunneus* (Patton). *Prenolepis imparis* (Say) is conspicuous from November through April, but is inactive on the surface during the warmer months.

OBSERVATIONS

RAIDING AND ASSOCIATED BEHAVIORS

On 22 May CJ discovered a column of *P. lucidus* workers (from Colony I) crossing a path at 1800 h EDT running very rapidly toward their nest at the base of a wire grass clump. Each worker bore a pupa from the raided nest. Upon reaching their own nest, the workers entered it quickly and did not reappear. In subsequent observations, returning *P. lucidus* were always seen to carry stolen *F. archboldi* brood directly into the nest. This differs from JCT's oft-repeated observation of *P. breviceps* Emery in Illinois, Colorado, and New Mexico, in which the returning raiders hesitate at the nest entrance, where they drop off the plundered brood, which is then carried by the *F. fusca* L. slaves into the nest.

Colony I was visited on several occasions in June and early July but it was not until 9 July that a raid was observed. On each previous visit, observations were made from 1600 h or 1700 h until 1900 h, but we saw little or no *P. lucidus* activity. On 9 July, the *P. lucidus* made 4 consecutive raids on a large colony of *F. archboldi*. Beginning about 1730 h, 3 *Polyergus* workers emerged one by one and milled about the nest entrance for a minute or two before leaving the nest in various directions. Shortly before 1800 h, one was seen returning hurriedly. By this time, 10 workers were milling about the entrance. The returning scout entered the nest. After less than one minute a group of 25 workers set off in a compact column in the direction from which the scout had come. In a few minutes, they arrived at and immediately entered the *F. archboldi* nest. Several dozen *F. archboldi*, some bearing brood, scurried out from their nest and took cover under nearby leaves. The *P. lucidus* soon reemerged and headed speedily for home. They entered their nest without hesitation. After 60-90 seconds they reemerged, milled about the entrance for a minute or two, then set off again. On the first raid, 25 workers participated and 21 returned with pupae. (Cor-

responding numbers for the subsequent 3 raids were 31, 25; not counted, 25; and 36, not counted). Thus between 80 and 100 pupae were robbed from a single host colony by a work force of no more than 36 *P. lucidus* workers. This sort of repeated raiding was called a "compound raid" by Marlin (1969).

On 10 July, Colony I raided 2 separate *F. archboldi* colonies (i.e. the "multiple raid" of Marlin 1969). Both *F. archboldi* colonies were small, as only a small number of diminutive *F. archboldi* individuals were flushed when the *P. lucidus* entered their nests, and only about 20 of the *Polyergus* returned laden from each raid, some bearing larvae, rather than the usual pupae. The 1st of the 2 raids occurred between 1735 and 1800 h. The 2nd raid began at 1815 h and went in precisely the opposite direction from the 1st. The 1st raiding party was accompanied by a dealate *P. lucidus* queen, who was frequently at the head of the column, as reported by Marlin (1968). The queen did not return with the laden workers, but remained in the raided nest.

On 14 July, *F. archboldi* slaves from Colony I were observed carrying brood to a new nest site about 4 meters from the original nest. *F. archboldi* slaves carrying brood were followed to the new site. On 15 July, at 1730 h, 24 *P. lucidus* left in the direction of their old nest, apparently on a normal raid. Upon arriving at the old nest, the raiders entered and remained inside for 4 minutes. Over the next 10 minutes, the *P. lucidus* emerged 1 by 1 carrying *F. archboldi* workers held in the characteristic pupoid pose of ants during social carrying. Two *Polyergus* were carried by *Formica* workers in the same way. This rather spectacular mode of aiding in colony emigration was reported recently by Kwait and Topoff (1983), who considered such behavior an adaptive alternative use of the generally implastic raiding behavior of *Polyergus*. It is not surprising that *Polyergus* colonies relocate periodically, as this may help them avoid local depletion of host colonies from which to steal brood.

On 16 July, 33 workers from Colony I emerged at 1807 h and headed in the direction of their old nest. Upon arriving at the old nest, 6 workers entered it, while the others milled around the entrance. Two minutes later, the 6 had resurfaced and the procession continued in the same direction. After 6 minutes, they reached and entered a *F. archboldi* nest. In less than a minute 28 *P. lucidus* bearing pupae, and 1 bearing a larva emerged and ran quickly toward their nest. The unladen workers straggled behind.

On 15 July, CJ discovered a 2nd *P. lucidus* colony (Colony II). The workers were crossing another portion of the same path on which the 1st was found, at 1803 h. At 1820 h they arrived at a large colony of *Formica* whose nest was concealed beneath leaves. Thirty-two *Polyergus* participated in the raid: 28 returned laden. In a 2nd raid on the same host nest, 26 went out, and 25 returned of which 24 carried pupae. The missing worker fell into an antlion pit and was killed on the outward portion of the raid. On 16 July, 30 workers from Colony II left at 1740 h along the same path as the previous day, but never reached a host nest. By 1800 h all *P. lucidus* had straggled back to their nest.

In the summer of 1984, CJ discovered a 3rd *P. lucidus* colony about 100 m WNW of Colony II, in the ecotone between the sandhill community in which Colonies I and II were located and the more mesic woodland to the west. Colony III was a larger colony; counts made during 1 raid observed by CJ

and 1 observed by JCT both yielded about 45 workers. Colony I was not rediscovered in 1984, but Colony II was found nesting beneath a wiregrass clump about 2 m south of its previous nest site. The population of Colony II had increased since 1983 when it contained 25-30 workers. Several highly successful compound raids on large *F. archboldi* colonies by groups of 36-38 *P. lucidus* workers from Colony II were observed in 1984. A raid in which the *P. lucidus* never reached a nest of *F. archboldi* was observed once each in Colonies II and III. Several *P. lucidus* workers from both of these colonies were caught by antlions while conducting raids.

On several occasions, *F. pallidefulva* nests or workers were seen near *P. lucidus* nests or raiding columns. However, *F. pallidefulva* is apparently not enslaved by the *P. lucidus* population under study, as *P. lucidus* were never seen to raid colonies of the former, nor were *F. pallidefulva* ever observed among the slave-force of *P. lucidus* colonies.

NATURAL HISTORY OF *F. archboldi*

Schneirla (1944) presented information on the biology of *F. archboldi* at the Archbold Biological Station in Highlands Co., Florida. In the sandhills near Gainesville, Florida, *F. archboldi* nests at the base of grass clumps, or in a nest concealed by leaf litter. On 1 occasion JCT saw them build a small earthen mound about 10 cm in diameter in which they incubated their sexual pupae, but this was in a shady, more mesic site than that in which the other observations reported here were made. Based on several years of collecting in the area, we believe this species prefers scrub or sandhill and other more open vegetation in northern Florida.

F. archboldi colonies are very likely to emigrate after disturbance. All colonies raided by *Polyergus* had moved away by the next time they were observed (usually the next day). Also, unraided colonies from which some of the leaf litter or grass cover was removed, were found to have moved away within a few days. The nest entrances were always cryptic before the colonies were disturbed.

In the sandhill community, *F. archboldi* was a predominant ant observed foraging on vegetation, especially around nectaries, galls, and homopterans. They were much more abundant than the number of nests found would indicate.

Two of the 8 colonies were polygynous; one with 2 dealate females and one with 4. The colony with 4 had only about 25 small workers and almost certainly represented one recently founded pleometrotically.

The prey records of *F. archboldi* are particularly interesting. Foraging activity was especially high in the morning and between 1600 h and 1800 h (especially during the 1st hour of this period). The following records of prey being carried into *F. archboldi* nests were accumulated over several afternoons in late June and July: 8 *Odontomachus*; 1 *Pogonomyrmex*; 2 *S. geminata* females; 1 *S. geminata* male; 1 *S. pergandei* female; 1 tipulid pupa; 2 small cercopids; 2 scarab beetles; 1 subadult *Pictonemobius* cricket; 3 unripe *Stellaria* fruits; 3 *Pinus* "male cones", and 1 grasshopper fecal pellet. All of the ants and most of the other insects brought in were still limp and presumably fresh-killed, though no actual killing was observed. In the case of the cricket, 4 workers cooperated in carrying the prey toward the nest from over 1 m away. Two *F. archboldi* corpses and 1 of *P. lucidus* were carried over 2 m away from the nest and discarded, but CJ excavated

a nest of *F. archboldi* in which subterranean refuse heaps contained remains of numerous *Odontomachus* workers.

DISCUSSION

In these observations, a good portion of the range of behaviors seen in more colonies over a much longer total period of time by earlier authors (see ref. cit.) were seen. The biology of this Florida population of *P. lucidus* is remarkably like that of the northern populations. Marlin (1971) summarized the known biology of *P. lucidus*. To his summary and the data in Smith (1979) may be added the following points, some of which apply specifically to the Florida population:

- (1) The range of *P. lucidus* extends south to at least Alachua County, Florida.
- (2) *P. lucidus* uses *F. archboldi* as host, within the latter's range in Georgia and Florida.
- (3) Raiding occurs in late spring and early summer. No raids have been observed after mid-July, despite repeated visits at the appropriate time of day. It is not known if raids occur before mid-May.
- (4) Alate queens and males were observed emerging on hot, cloudless days in June and early July. No alates were observed after the 1st week of July. Mating was not observed but the dealate queen mentioned above seems likely to have been newly mated.
- (5) Colony populations were small, with from 25 to perhaps 50 workers participating in raids. It is believed that the colonies were mature because they had fully-colored, full-sized workers.
- (6) Only a few, perhaps a dozen, raids are conducted each season, though some or perhaps most are multiple or compound raids, especially the latter. No raids were observed on most days when the colonies were watched.
- (7) *Polyergus* workers aid in relocation of nests by performing an emigration-raid at their old nest and carrying slaves to the new nest site. This was observed independently by Kwait and Topoff (1983).
- (8) On no occasion were the *Polyergus* observed to kill *Formica* or even fight with them. The latter simply fled when their nest was entered by *Polyergus*, then reentered after the *Polyergus* left.

In some of these points, particularly #3, #4, and #5, this southern population of *P. lucidus* resembles the Southern California population of *P. breviceps* Emery (R. R. Snelling, Natural History Museum, Los Angeles Co., pers. comm.). The host of the latter is *Formica occidua* Wheeler, not previously reported as a slave species. *F. occidua*, an abundant *F. fusca*-group species of southern California, is also enslaved by *F. subnuda* Emery in the same region (JCT, unpub. obs.).

Much remains to be known about these and other ants inhabiting the scrubland and sandhills of Florida, which together constitute some of the least studied ant communities in North America. Unfortunately, due to their suitability for development, such habitats are among the most rapidly disappearing in the region. These interesting areas should be studied while they last.

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