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Pseudomyrmex nigropilosa: A Parasite of a Mutualism

Abstract. Pseudomyrmex nigropilosa *is a parasite of the ant-acacia mutualism in Central America in that it harvests the resources of swollen-thorn acacias but does not protect the acacias. In the process, it also lowers the rate of occupation by the obligate acacia-ants, species of ants that do protect swollen-thorn acacias. Tenancy of an acacia by* P. nigropilosa *must be temporary, since the unoccupied plant is shortly killed by herbivores or competing plants, or is taken over by obligate acacia-ants. As expected of a species of short-lived ant, a* P. nigropilosa *colony produces reproductives earlier in the life of the colony and maintains fewer grams of workers per gram of brood than does a colony of the long-lived obligate acacia-ants.*

In lowland Mexico and Central America there are 11 species of swollen-thorn acacias (*Acacia*). They are occupied by at least ten species of obligate acacia-ants (*Pseudomyrmex*); the worker ants patrol the surface of the acacias to keep off herbivores and vines, and in return the acacias produce food bodies and nesting structures. The ant colony cannot maintain itself away from the acacias, and in most habitats the acacias cannot survive to reproductive maturity without the services of a colony of obligate acacia-ants (*1–3*). Here, I describe a widespread parasite of this mutualism and show how its colony structure is adjusted to a parasitic way of life.

Pseudomyrmex nigropilosa Emery is a yellow-red pseudomyrmecine ant with workers 6 to 8 mm long, a size similar to that of obligate acacia-ants (*4*). The workers cut their own entrance holes and nest exclusively in the thorns of swollen-thorn acacias (*5*), harvest the modified leaflet tips as food bodies and feed them to their larvae just as do obligate acacia-ants, and obtain their sugars from the extrafloral nectaries on the acacia petiole. However, in very striking contrast to the obligate acacia-ants, the workers of *P. nigropilosa* do not protect the acacia against vines, insects, or vertebrates.

Pseudomyrmex nigropilosa neither attacks foreign objects on the acacia nor cleans its foliage of debris. When approached by an animal, the workers run behind the branches and often into a thorn. The workers are not active at night outside the thorns. In short, they behave toward foreign objects as do the workers of the many species of twig-inhabiting *Pseudomyrmex*, except that *P. nigropilosa* does not even scavenge moribund insects or catch small live ones. It is a true parasite of the coevolved system of aggressive obligate acacia-ants and swollen-thorn acacias. By occupying thorns and eating the food produced by the acacia, it lowers the rate of colonization by obligate acacia-ants and slows the growth of young obligate acacia-ant colonies. In turn, this interaction lowers the fitness of the acacia because, without protection from an obligate acacia-ant colony, it is more likely to die before maturity (*2, 3*).

How then does *P. nigropilosa* persist as such an extreme food specialist, since the acacia requires an aggressive, patrolling obligate acacia-ant colony to stay alive? A *P. nigropilosa* colony can survive as such a specialist because of the lag of as much as a year between the time when a swollen-thorn acacia loses its obligate acacia-ant colony and the time when it dies of herbivory or shading, or gains another obligate acacia-ant colony. Swollen-thorn acacias lose their usual occupants through fire, predation by birds, starvation of the colony through deciduousness of the acacia during an exceptional dry season, and unknown causes of queen death. The founding queens and colonies of *P. nigropilosa* sur-

Table 1. Three colonies of obligate acacia-ants (*Pseudomyrmex belti, P. ferruginea*, and *P. nigrocincta*) compared with one of *Pseudomyrmex nigropilosa* (*11*). All weights are oven dry.

	Workers			Alate virgins					Thorns on trees in colony		
Species	Total (g)	Per unit of brood (g/g)	Individual (mg)	Individual queen (mg)	Individual male (mg)	Total queens (g)	Total males (g)	Males/queens (g/g)	Total (*N*)	Percentage with brood	Physogastric queens (*11*) (*N*)
P. nigrocincta	5.67	0.84	0.48	1.06	0.55	0.9113	0.6454	0.708	1019	54	2
P. ferruginea	29.62	0.81	0.73	1.73	1.02	5.5443	1.4644	0.264	3488	46	1
P. belti	20.74	0.75	1.09	2.55	1.36	8.2256	5.4253	0.660	3131	51	1
P. nigropilosa	1.38	0.30	1.04	2.74	1.47	0.3099	0.2934	0.947	537*	59	11

* In addition to these, there were 230 thorns into which the *P. nigropilosa* workers had not bothered to cut entrance holes, which suggests that they are limited by food, not space. All food bodies had been harvested from the leaves of the swollen-thorn acacia occupied by this colony.

vive in seedlings or in abandoned large swollen-thorn acacias until the plant dies or an obligate acacia-ant colony moves in and kills or evicts them (*6*). The amount of time a swollen-thorn acacia can survive without an ant colony varies strongly with the amount and kind of competition by other plants, the initial health of the tree, the time of year it lost its obligate acacia-ants, and the density of arthropod herbivores. The time available for occupation by *P. nigropilosa* is also greatly lengthened in habitats that are very unfavorable to obligate acacia-ants, such as frequently burned brushy pastures. *Pseudomyrmex nigropilosa* is probably much more abundant now than before the advent of cattle pastures and roadsides in Central America; in these habitats, it is commonplace for small unoccupied acacias to survive for many months because of the lack of competition and herbivorous insects. Here, *P. nigropilosa* colonies sometimes become quite large (but, I should add, do not attack cattle browsing the swollen-thorn acacias).

On an ephemeral resource such as the unoccupied swollen-thorn acacia, I expect the parasite to display a number of quantitative colony traits that set it aside from the more long-lived acacia-ants (*7*).

1) A new queen of *P. nigropilosa* begins to invest in the production of alate reproductives of both sexes by the time the colony has grown to contain about 20 workers. This requires about 2 months (*8*). For example, the *P. nigropilosa* "colony" in Table 1 had 11 physogastric queens and an average of only 121 workers per queen, yet every thorn contained reproductive brood. In the same habitat, colonies of the obligate acacia-ants *Pseudomyrmex belti, P. ferruginea,* and *P. nigrocincta* all require about 1 1/2 years of growth (a colony size of about 1200 workers) before producing male reproductives and are at least 2 years old before producing reproductives of both sexes (*9*).

2) Since the workers of *P. nigropilosa* are needed only to care for brood and to collect the food so readily available to them, I predicted that there should be a much lower standing crop of workers per unit of brood in a *P. nigropilosa* colony than in the colonies of the three aggressive species mentioned above, since in the aggressive species as many as one-third of the workers in the colony are involved in patrolling the acacia (*10*). This prediction was verified with the large *P. nigropilosa* colony described in Table 1, and I observed similar ratios on numerous occasions when collecting other colonies of *P. nigropilosa* in Central America.

3) I expect that, since relatively fewer resources appear to be going into the maintenance of a worker force, more resources may be going into the production of reproductives in *P. nigropilosa* than in the other species. However, since acacia-ant colonies produce alates throughout the year, it is impossible to determine this from standing crop data such as those in Table 1. The ratio of grams of reproductives to grams of workers in the colony tells us no more about the species-specific rates of production of reproductives than the depth of water in a swimming pool tells us about the rates of input and output.

4) Trivers and Hare (*12*) predict a ratio of 1 male to 3 females in ordinary ant colonies. Accepting their arguments, I would expect totally parasitic ants (species with no workers) to have a sex ratio of exactly 1 : 1 since the queen should have total control of her offspring, but there are no data in the literature on their reproductive broods. I expect the sex ratio of *P. nigropilosa* to deviate in the direction of 1 : 1, which it does (Table 1). However, again I am forced to the conclusion that my data cannot be used as a test of Trivers and Hare's hypothesis because I do not know the sex-specific turnover rates of reproductive male and female tissue.

I have collected *P. nigropilosa* from swollen-thorn acacias all along the Pacific coast, from the vicinity of San Blas, Nayarit, Mexico, to Guanacaste Province, Costa Rica. Over this range, it lives in at least three swollen-thorn acacias (*Acacia hindsii, A. collinsii,* and *A. cornigera*) and is regularly evicted by at least six species of obligate acacia-ants. In all sites, it behaves in the same manner; it exploits a temporarily available resource by harvesting it and moving on rather than investing in the machinery to maintain and possess it in the face of herbivores and competitors.

In conclusion, it is of interest to note that *P. nigropilosa* is a member of a distinct subgroup of the genus *Pseudomyrmex* (*13*). This subgroup contains no members that protect plants, but contains two undescribed species that are extremely similar to *P. nigropilosa* in their reaction to swollen-thorn acacias, and one species, *Pseudomyrmex gracilis,* that facultatively lives in swollen-thorn acacias and treats them as does *P. nigropilosa.*

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References and Notes

1. Obligate acacia-ant is here defined as one of the species that is restricted to swollen-thorn acacia and protects it [see Janzen (*2, 3*) and included references]. *Pseudomyrmex nigropilosa* is thus not an obligate acacia-ant.
2. D. H. Janzen, *J. Anim. Ecol.* **42**, 727 (1973).
3. ——, *Smithson. Contrib. Bot. No. 13* (1974).
4. *Pseudomyrmex nigropilosa* may be morphologically distinguished from all obligate acacia-ants in the study area (*11*) by the fact that the length of the eye of a worker *P. nigropilosa* is greater than the sum of the distance from the anterior margin of the eye to the mandible base and the distance from the posterior margin of the eye to the back of the head in lateral view. Obligate acacia-ants have eyes much shorter than this sum. A worker *P. nigropilosa* can be distinguished from all other *Pseudomyrmex* in the study area by having the combination of (i) length greater than 6 mm, (ii) yellow-red alitrunk and petiolar segments, (iii) scattered stout black erect long hairs on the dorsal side of the first petiolar segment and on the posterior-dorsal surface of the epinotum, (iv) gaster always held straight out behind rather than curled under, and (v) gaster and head never black but rarely darkened to rusty brown. I have compared *P. nigropilosa* from the study area with Emery's type specimen, and there is no doubt that they are conspecific.
5. W. M. Wheeler [*Bull. Mus. Comp. Zool. Harv. Coll.* **90**, 1 (1942)] makes a passing reference to *P. nigropilosa* nesting in hollow twigs, but in 10 years of collecting thousands of twig-inhabiting *Pseudomyrmex* in *P. nigropilosa* habitat, I have never found *P. nigropilosa* nesting anywhere but in swollen-thorn acacia thorns.
6. I have seen obligate acacia-ant colonies discover an acacia containing a *P. nigropilosa* colony growing nearby and kill or chase out all the workers in 1 to 3 hours. A similar event occurs if an occupied swollen-thorn acacia is cut and placed at the base of one containing a *P. nigropilosa* colony.
7. Obligate acacia-ant colonies normally occupy their tree for at least 10 to 20 years and, in some cases, for much longer (*2, 3*).
8. This is based on numerous dissections of unoccupied swollen-thorn acacias for which the dates of abandonment by obligate acacia-ants were known.
9. This is based on numerous dissections of colonies of known age and on results reported in D. H. Janzen, *Univ. Kans. Sci. Bull.* **47**, 315 (1967). A similar reduction of age at first reproduction is observed in multiple-queen obligate acacia-ants of western Mexico; here, it appears that the early production of reproductives is associated with a mechanism of acacia ownership through reestablishment of daughter queens in the acacia (*2*).
10. As an extreme case, when the three obligate acacia-ant colonies listed in Table 1 were being collected, 85, 58, and 74 percent, respectively, of the workers were aspirated off the trunk of the acacia while they were defending the molested acacia and colony. It is virtually impossible to aspirate the *P. nigropilosa* workers off a tree they occupy, because most of them are in the thorns and the remainder are too eager to flee.
11. All four colonies were collected from mature and healthy *Acacia collinsii* growing within 500 m of the Organization for Tropical Studies field station at Hacienda Palo Verde, COMELCO, Bagaces, Guanacaste Province, Costa Rica, between 6 and 15 August 1974. All members of each colony were collected and all were representative in health and behavior. All colonies except that of *P. nigrocincta* were at the upper end of the size range for their species. While the *P. ferruginea* "colony" was functioning as though it were one, in fact, it was based on two physogastric queens, each appearing to control about half of the shoots occupied by the colony as a whole. The *P. nigropilosa* colony is a mix of the brood and adults from 11 physogastric queens scattered through four adjacent acacia shoots. The thorns "owned" by each queen are intermingled on the acacias, and only the ants know which belongs to which. While the sex ratio for an ant species usually cannot be determined from a single colony, mature acacia-ant colonies have the peculiar attribute of producing about the same ratio of males to females in each healthy colony (based on numerous colony dissections).
12. R. L. Trivers and H. Hare, in preparation.
13. While bearing no formal name, this subgroup contains the largest members of the genus, and its members have exceptionally large eyes and long petiolate first petiolar segments. Many of its species have been described as subspecies of *Pseudomyrmex gracilis,* but this is an error inasmuch as I have caught as many as five of them in the same acre of Central American forest.
14. Supported by NSF grant GB35032X and by the teaching program of the Organization for Tropical Studies. Fieldwork was aided by L. Green, J. Pickering, S. Fitzgerald, J. Karr, R. Tim, G. Galbraith, S. Farkus, and D. Janzen. R. Trivers, W. Freeland, J. Pickering, C. Pond, R. Carroll, and B. Bentley offered constructive criticism of the manuscript.

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