

Research article

Predation by the army ant *Neivamyrmex rugulosus* on the fungus-growing ant *Trachymyrmex arizonensis*

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Summary. Raids by the army ant *Neivamyrmex rugulosus* (tribe Ecitonini) on a nest aggregation of the fungus-growing ant *Trachymyrmex arizonensis* (tribe Attini) resulted in major brood loss and partial destruction of the fungus-gardens in the attacked nests. *T. arizonensis* workers attempted to rescue their brood by carrying them to *ad-hoc* shelters under rocks above ground, but the army ants pursued the workers to retrieve much of the brood. Raids on single colonies lasted about half an hour, after which the escaped *T. arizonensis* workers returned to their nest with any rescued brood. Raids on single nests occurred repeatedly during the 24-hour period the army ants swept through the *T. arizonensis* nest aggregation. Compared to unraided colonies, raided colonies were left with only about 25% of their brood. Army ant predation thus is an important source of brood loss to *T. arizonensis* and probably also to all attine ant species. The behavioral, morphological, and nest-architectural defenses of fungus-growing ants against army ant predation are discussed.

Key words: Army ants, Attini, *Neivamyrmex*, predation, *Trachymyrmex*.

Introduction

Army ants in the Neotropical tribe Ecitonini are major predators of arthropods (Rettenmeyer, 1963; Schneirla, 1971; Gotwald, 1995). Some conspicuous and widespread army ant species, such as the tropical *Eciton burchelli* or the North American *Neivamyrmex nigrescens*, have received extensive study, and their impact on arthropod communities have been relatively well documented (summarized in Schneirla, 1971, and Gotwald, 1995). Social insects, and ants in particular, are a preferred prey of army ants (Mirenda et al., 1980; Gotwald,

1995). However, surprisingly little is known about the impact of army ant predation on fungus-growing ants (tribe Attini). Despite considerable research on the ecology and behavior of attine ants (Weber, 1972; Hölldobler and Wilson, 1990), only a handful of cases of army ant predation on attine ants have been reported.

The few documented cases of army ant predation on attine ants generally involved opportunistic observations by naturalists when they chanced upon predatory raids in the field. Not surprisingly, conspicuous mass raids of the army ant *Nomamyrmex esenbecki* and *Eciton* species on *Atta* leafcutter ants have been documented repeatedly (Schneirla, 1958; Rettenmeyer, 1963, 1982; Mariconi, 1970; Schade, 1973; Swartz, 1998). In contrast, other reported cases of army ant predation on attine ants are generally singular observations, such as a raid of *Eciton burchelli* on the lower attine *Apterostigma urichi* (Weber, 1945), a *Labidus praedator* raid on *Acromyrmex crassispinus* (Fowler, 1977), and raids by various *Neivamyrmex* species on different *Trachymyrmex* species (Cole, 1939; Schneirla, 1958; Mirenda et al., 1980). Because attacks of army ants on the more inconspicuous primitive (non-leafcutter) attine ants are mostly subterranean, these scant observations probably represent the “tip of the iceberg,” and army ants may well be major predators of fungus-growing ants, as they are for many other ants. To our knowledge, the impact of raids on attine ant nests has yet to be quantified for any attine species. The accumulated evidence indicates that army ant raids result in major brood loss, but not worker loss, because army ants generally raid only brood (and possibly callow workers), but rarely take adult ants as prey (Schneirla, 1971; Gotwald, 1995).

We report here observations of the raid of the army ant *Neivamyrmex rugulosus* on a nest aggregation of the fungus-growing ant *Trachymyrmex arizonensis*, including an estimate of the resulting brood loss. *N. rugulosus* occurs in a

very limited range that includes the Chiricahua Mountains (Arizona) and possibly also Sonoran Mexico (Watkins, 1985) and is rarely collected (Watkins, 1985; R. Johnson, pers. comm.). Nothing is known about the raiding and emigration behavior of *N. rugulosus* (Watkins, 1985; Gotwald, 1995).

T. arizonensis is a locally abundant species that ranges from Arizona to Texas (Hunt and Snelling, 1975; O'Keefe et al., 2000) and is frequently collected in faunistic and ecological surveys (Wheeler, 1907; Weber, 1966; Eastlake Chew and Chew, 1980). Near the Southwestern Research Station (Portal, Arizona) where our study was conducted, *T. arizonensis* appears to reach exceptionally high abundance (R. Johnson and R. Snelling, pers. comm.). We estimate that the colony density of *T. arizonensis* at our study site in the Chiricahua Mountains may reach several dozens or even hundreds of colonies per hectare. Thus, though *N. rugulosus* is a rare army ant in the Chiricahua Mountains, *T. arizonensis* probably is a frequent prey of *N. rugulosus* and other local army ants. Indeed, nests of several *Trachymyrmex* species, including *T. arizonensis*, are regularly attacked by the abundant sympatric army ant *N. nigrescens* (Cole, 1939; Schneirila, 1958; Miranda, 1980).

Materials and methods

A colony of *N. rugulosus* was discovered on August 10, 2001, at about 1700 hrs in a juniper-oak forest (GPS location 31°53.32'N, 109°12.48'W; 1676 m elevation) just outside the borders of the Southwestern Research Station (approximately 5 miles west of Portal, Arizona). The transport of *N. rugulosus* brood by workers indicated that the colony was in the migratory phase. The new bivouac into which the army ants were moving, apparently an abandoned or raided ant nest underlying a rock, was then excavated. Because of the disturbance of excavation (about 150 workers and brood were collected from the underground chambers), the army ants relocated their bivouac to a new location 21 meters distant from the excavated bivouac. Observations on August 10 continued until 0100 hrs the following morning when the move to the new bivouac was complete, and again intermittently on August 11 at 0830, 1130, and 1630 hrs to monitor army ant activity. Despite the disturbance caused by collecting the night before, the new bivouac appeared as robust and large as previously observed. Disturbance of army ant nests occasionally alters the migratory behavior during subsequent days (H. Topoff, pers. comm.), so the below observations on army ant colony movements have to be interpreted with some caution, though it seems unlikely that the disturbance significantly distorted the predatory impact on the raided *Trachymyrmex* colonies. No above-ground trails were observed during the three daytime checks on August 11. The first active above-ground trails were observed at about 1730 hrs on August 11, and at 1810 hrs the first raids in the *T. arizonensis* colony aggregation were observed. By then the army ant colony had moved, mostly through underground passages, to a steep (about 45°) hillside. At least several dozen *T. arizonensis* colonies nested under boulders in that slope, in addition to several other ant species (*Pheidole* sp., *Camponotus* sp., and *Crematogaster* sp.). The slope was relatively unstable, covered with many rocks, some sparse vegetation (mainly grasses), and some oak-leaf litter. Many underground passages must have existed in the slope because foraging trails surfaced only sporadically. Most foraging activity occurred completely underground, but was apparent whenever army ant trails surfaced for short distances, or when agitated resident ants left their nests to combat the army ant invaders on the surface near their nest entrances. Army ant activity was observed carefully on August 11 between 1730 hrs until 2230 hrs, with a break between 1830–1900 hrs, and on the morning of August 12 from 0900 to 1030 hrs.

At 2100 hrs the army ants were found to have moved out of the hillside and continued their migration into an adjacent forested area, and observations were terminated.

The three *T. arizonensis* nests observed to have been raided, as well as two additional *T. arizonensis* nests believed to have remained unraided, were excavated on August 13 and 14 to collect all fungus-gardens and all brood. Collected garden fragments were examined in the laboratory under a microscope to count all brood. In addition to the five nests excavated at the site of the army ant raid, we also censused the brood of two other colonies that had been excavated with the same methods during the week preceding the raid. These two additional *T. arizonensis* colonies were collected at two different locations, each within about one kilometer of the site of the army ant raid. Contents of these two nests therefore are not fully comparable to the nest contents at the study site, but we present these additional records to provide a more general impression of other colonies in the area.

Results and discussion

Army ant raids on Trachymyrmex arizonensis

Colony # 1

The first observed raid by *N. rugulosus* on a *T. arizonensis* colony took place at 1730 hrs on August 11. *Trachymyrmex arizonensis* workers moved erratically in the near vicinity of their nest entrance, quickly running on the ground and on surrounding stones while holding their mandibles wide open. Some workers carried brood (pupae and larger larvae) or callow workers. The callow workers were curled into a pupal posture with the head and gaster tucked in under the thorax, a posture typical for adult-carrying in attine ants (Weber, 1972). The raided nest was located under a stone approximately 30 cm in length and 10 cm in width. The stone was partly embedded in the ground; the exposed end (facing downslope) covered the nest entrance (about 4 mm diameter), from which a narrow tunnel led to the first empty cavities directly underlying the stone.

A *N. rugulosus* raiding column passed within 60 cm of the *T. arizonensis* nest, and the army ants probably had entered the nest through underground passages. The partially imbedded stone covering the nest and nest entrance provided an overhang where approximately two dozen *T. arizonensis* workers had congregated, some holding brood. The overhang appeared to serve as a temporary shelter for the workers and the rescued brood. Some workers outside the nest were covered with actinomycete bacteria (Currie et al., 1999; Currie, 2001). Such actinomycete-covered workers are generally found only in the gardens and rarely leave the nest (Currie, 2001; U. Mueller, pers. obs.); thus it appears that the army ants had driven actinomycete-covered workers out of the garden chambers. At 1815 hrs some army ants swarming above ground reached the nest entrance and engaged a few *T. arizonensis* workers in a battle. One pair grappled for about one minute; the army ant clamped its mandibles onto a *T. arizonensis* leg and appeared to be trying to sting its opponent. The *T. arizonensis* in return bit the army ant several times. After a minute, the army ant and *T. arizonensis* workers disengaged and separated in different directions. Neither ant appeared injured. Two army ant workers then entered the *T. arizonensis* nest; after approxi-

mately five minutes of observations, the army ants did not reemerge from the nest, though several *T. arizonensis* workers at that point did emerge. Within several minutes the raiding column disappeared. By 1825 hrs, the first *T. arizonensis* worker returned to the nest, some of them carrying rescued brood.

We returned to the site on August 12 at 0900 hrs to find the army ants moving only about 30 cm from the *T. arizonensis* nest entrance that had been raided the previous night, suggesting that this nest had been raided at least twice in less than a 24 hour period. The army ants emanated from a hole near the *T. arizonensis* nest and engaged *T. arizonensis* workers in battle above ground. In one instance a *T. arizonensis* worker was bitten by four or more army ants. The *T. arizonensis* worker lifted its body up so that the gaster could swing underneath the thorax, with the gastral tip pointing forward. As the army ants continued to pull on the *T. arizonensis* worker, she repeatedly stridulated her gaster. After several minutes of repeated stridulation, the army ants released the *T. arizonensis* worker and departed. The *T. arizonensis* worker returned towards the nest entrance, apparently uninjured. In another case a *T. arizonensis* worker grasped a piece of dried grass with its mandibles, while four army ant workers pulled at this worker, without dislodging it. After five minutes, the army ants ceased their attack and left the *T. arizonensis* worker, which in less than a minute started walking, apparently uninjured. Many other *T. arizonensis* workers near the nest entrance appeared highly agitated, walking quickly and changing directions erratically quite unlike typical *Trachymyrmex* worker behavior above ground (Weber, 1972; U. Mueller, pers. obs.). *T. arizonensis* workers moved around the site with mandibles wide open, a clear display of aggression according to Hölldobler and Wilson (1990).

At 0945 hrs the *T. arizonensis* workers hiding under the stone overhang and workers returning from elsewhere moved back into the nest *en masse*. The number of workers returning to their nest suddenly increased significantly for a 5–10 minute period. At 0955 hrs, no more *N. rugulosus* workers were observed at this nest. A few *T. arizonensis* workers were still running about the site, though in general they appeared much less agitated compared to the workers observed at the beginning of the raid.

Colonies #2 and #3

At 1000 hrs on August 12 2001, approximately 2 meters from colony #1, another *T. arizonensis* nest was located (colony #2). At this nest site, an army ant raiding column moved directly next to the *T. arizonensis* nest entrance. Several battles between *T. arizonensis* workers and army ants ensued, similar to those observed earlier at colony #1. Again, the *T. arizonensis* workers engaging in battles always appeared uninjured after the army ants ceased their assault. Several army ants at colony #2 were seen to be carrying attine pupae and larvae. The army column at colony #2 disappeared around 1020 hrs.

A third *T. arizonensis* colony under attack was located at around 1010 hrs approximately 1 meter from colony #2. The

raid at this colony (colony #3) appeared to be either a smaller one than the others previously observed or was already diminishing, for only a few army ants were located in the vicinity, and *T. arizonensis* workers were already in the process of returning to their nest. At around 1020 hrs the army ants disappeared at this nest (apparently ending the raid), and, as observed before, many *T. arizonensis* workers returned *en masse* with brood. It is interesting to note that the army ants at both colonies #2 and #3 disappeared from the surface just as the first rays of sunlight reached the hillside. The fact that the *T. arizonensis* workers returned to their nests at this point suggests that the raids ceased underground as well. By 1030 hrs no army ant raiding columns could be seen on the slope, and the agitation of *T. arizonensis* workers at both colonies #2 and #3 subsided.

Impact of the army ant raids on brood and garden productivity

Excavation of the three raided colonies and two unraided colonies from the same site revealed that, compared to unraided colonies, raided colonies were left with about one fourth of their brood after the army ant raid (Table 1). Only two pupae were found in the large colony (colony #1, five garden chambers) that was raided repeatedly (at least twice). Surviving brood appears to be predominantly pupae (Table 1). Compared to unraided colonies, egg and larval brood experienced a $\approx 90\%$ numerical reduction in raided colonies,

Table 1. The number of eggs, larvae (small and large), and pupae present in raided and unraided *Trachymyrmex arizonensis* colonies after the observed *Neivamyrmex rugulosus* raids. For comparison, brood sizes are also given for two *T. arizonensis* colonies that had been excavated at two other sites (within 1 km of the raid site) during the week preceding the army ant raid

	colony size (# gardens)	# eggs	# small larvae	# large larvae	# pupae	total brood
<i>Raided colonies</i>						
Colony #1	large (5)	0	0	0	2	2
Colony #2 ¹	large (>4)	0	0	0	10	10
Colony #3	large (5)	1	4	0	14	19
	Average	0.33	1.33	0	8.67	10.3
<i>Unraided colonies, site of raid</i>						
Colony #4	small (1)	0	12	8	21	41
Colony #5	large (4)	6	5	11	16	38
	Average	3.0	8.5	9.5	18.5	39.5
<i>Unraided colonies, other sites</i>						
Colony #6	intermediate (3)	5	9	15	24	53
Colony #7	large (7)	11	17	22	43	93
	Average	8	13	18.5	33.5	73

¹ No garden and only empty chambers were found in this nest when it was excavated two days after the raid. The ten pupae were found together with approximately 200 workers in an otherwise empty cavity underlying the rock that covered the site where the raid on this nest had been observed. A large fresh refuse pile just outside the nest indicated that much of the garden was dumped very recently. The nest site was carefully excavated, and we therefore believe it is unlikely that any intact fungus garden was missed.

while pupal brood experienced a reduction of about 50% (Table 1). The near absence of small brood in raided colonies suggests that the *T. arizonensis* workers preferentially saved the more valuable larger brood, and that the army ants succeeded at stealing most of the remaining brood. The exact impact of army ant predation on the *T. arizonensis* population at large cannot be estimated from this single study, but the overall predation pressure due to army ants is probably significant given that most raiding observations probably remain unreported (but see Schneirla, 1958; Miranda, 1980). Indeed, H. Topoff (pers. comm.) indicated that army ant colonies can be invariably located in the vicinity of *T. arizonensis* nests whenever finding *Trachymyrmex* workers milling about their nest, holding brood in their mandibles or protecting a brood pile on the surface near their nest. Walking in ever-widening circles outward from such a *T. arizonensis* nest, Topoff “never failed to find a colony of *Neivamyrmex* nearby (5–15 meters)” (H. Topoff, pers. comm.), supporting the view that *Neivamyrmex* ants are important predators of *T. arizonensis*.

In addition to the severe brood reduction, army ant raids probably damage gardens. This is suggested by the apparently higher rate of waste production (discarding of garden fragments on the waste pile just outside the nest) following a raid compared to that of unraided nests. Although we did not specifically measure waste production, waste piles of raided nests appeared to be larger compared to unraided nests on the day following the raid. The freshly discarded waste outside raided colonies consisted of brownish garden fragments that, under the microscope, showed some live mycelial growth, unlike the dead and exhausted waste that is typically discarded by fungus-growing ants.

These observations suggest that the army ants destroyed parts of the fungus-gardens when searching through the *T. arizonensis* colonies for brood (*Trachymyrmex* brood is kept in the gardens), resulting in the increased dumping of damaged garden following a raid. This hypothesis is further supported by the observations that gardens in raided colonies appeared less healthy, with a dark brownish-orange coloration and a matted down appearance. Unraided colonies had gardens that were light brownish-yellow in color, with white mycelium clearly visible and the garden with a fuller appearance. In addition, gardens of raided colonies seemed much more fragile than unraided gardens, as if recently reconstructed from garden fragments by the workers, similar to *Trachymyrmex* gardens in laboratory colonies a day after collection (U. Mueller, pers. obs.). Army ant raids therefore not only reduce brood sizes (colony growth) in *T. arizonensis*, but also appear to damage gardens physically and thus decrease garden productivity.

N. rugulosus bivouac in a *T. arizonensis* nest

At a separate location from our study site (0.4 mi NW of the Southwestern Research Station [GPS location 31°53.32'N, 109°12.23'W; 1737 m elevation]), SC discovered on August 15 2001 an aggregation of approximately 150 *T. arizonensis*

workers under a rock on the ground. The worker aggregation was not in a typical *T. arizonensis* nest chamber, and no garden was present, but most of the workers were carrying larvae and pupae. Within 0.5 m from the worker aggregation, a *T. arizonensis* nest was discovered under a separate rock. Though this rock was too large for complete excavation of the *T. arizonensis* nest, digging around the rock revealed that the nest no longer contained the *T. arizonensis* colony, but rather a bivouac of *N. rugulosus*. Army ant brood was collected from the bivouac, but the army ant queen could not be located. The army ants apparently had usurped the *T. arizonensis* nest for bivouacking.

These observations show that *T. arizonensis* are not only preyed on by army ants, but that they can also be displaced from their nests by bivouacking army ants. Displacement from their nest must have forced the *T. arizonensis* colony to wait in their shelters until the next day's departure of the army ants (if these were in their migratory phase); alternatively, the *T. arizonensis* colony may have been forced to emigrate to a new nest site. Nest emigration has been observed for several attine species, including a *Trachymyrmex* species (Weber, 1941). The causes for these colony migrations are various and include nest flooding (Weber, 1972; Rockwood, 1973), attempted extermination with pesticides or other means (Belt, 1874; Mariconi, 1970; Rockwood, 1973; Fowler, 1981), attempted excavation by anteaters (Autuori, 1941) and humans (Hart, 1897; Autuori, 1941; Weber, 1972), raids by *Megalomyrmex* “agropredator” ants (Adams et al., 2000), colony fission (Mueller and Weislo, 1998), garden infection with virulent fungal parasites (A. Hart and C. Currie, pers. comm.), or unknown factors (Weber, 1941; Porter and Bowers, 1980). Nest usurpation by bivouacking army ants may be an additional cause of attine colony emigrations.

Defenses of attine ants against army ant predation

Based on previous attine reports (reviewed above) and the observations of this study, army ants are important predators on fungus-growing ants. The extent of predation is presently unknown for any attine species and probably will be difficult to ascertain because most army ant raids are largely underground and thus remain unnoticed. But even the handful of accidental observations of army ant predation on attines suggests substantial brood loss to army ant predators, particularly those attines that construct nests in the forest litter and superficial soil layers. Because of this predation pressure, attines may have evolved specialized defenses dealing with army ant predation.

As in many social insects (Jeanne, 1975), the architecture of the attine nest probably provides one of the most important defenses against army ants. Many attines locate their garden chambers deep in the ground and connect them with single, narrow passages (Wheeler, 1907; Weber, 1972). These features undoubtedly protect the brood and gardens from the larger, non-burrowing army ant species that hunt near the nest surface (e.g., *Eciton*, *Neivamyrmex*), though this design

may afford little protection against the specialized subterranean army ant hunters (e.g., *Labidus*), and particularly those army ants that burrow laterally through the soil (Gotwald, 1995).

The second line of defense is behavioral. Like other ants, attines attempt to defend their nest entrances (e.g., Swartz, 1998), and, if this is not possible, attempt to escape with some of their brood, as shown here for *T. arizonensis* and previously by McDonald and Topoff (1986) for *Aphaenogaster albisetosus*. The observations on *T. arizonensis* indicate that this species may save about 25% of its brood by temporarily hiding in shelters near the raided nest. Compared to other myrmicine ants, the attine integument is particularly sclerotized and, with a few exceptions (e.g., genera *Cyphomyrmex* and *Mycetophylax*) studded with many spines. These features may afford special protection during combat with army ants. Our observations indicate that *T. arizonensis* workers were not injured by attacks from army ants (see above). The apparently greater investment in integumental armor could indicate strong selection to minimize nest invasion by predators, possibly because attines have to defend not only their brood, but also their vital fungus gardens.

A third possible defense may be chemical protection of the ant brood, either through substances produced by the brood, or by their mutualistic fungi. The brood of many attine species is covered with a mycelial coat of the cultivated fungus (Weber, 1972), and the function of this coat is completely unknown. The coat can be very thick in the case of some *Apterostigma* ants where the brood is virtually integrated and permanently fixed into the walls of the garden (Weber, 1972; Murakami, 1998; U. Mueller, pers. obs.). More often, however, the coating is variable even among brood in the same nest, and of the same developmental stage (U. Mueller, pers. obs.). The mycelial coat of brood might provide chemical camouflage and thus decrease detection by predators that are able to enter a garden. Alternatively, or in addition, the mycelial coat may actually be chemically deterrent. This latter hypothesis was first suggested by observations on tropical *Megalomyrmex* "agropredators" that invade attine nests to consume both attine larvae and fungus (Adams et al., 2000). *Megalomyrmex* workers invariably strip the attine brood of their mycelial coat before consuming the brood while discarding the stripped mycelium. These observations suggest some unpalatability of the mycelial coat to *Megalomyrmex* agropredators, and possibly also to other predators such as army ants (Adams et al., 2000). Interestingly, the mycelial cover appeared to be virtually absent in the *T. arizonensis* brood at our study site in the Chiricahua Mountains, which, under the hypothesis of chemical protection, may have permitted the enormous brood loss of 75% during the observed raids of the army ant *N. rugulosus*. Future study of effects of the mycelial coating on attine larvae survival during an army ant raid may yield important insights into this mysterious integumental brood-fungal association.

Neivamyrmex rugulosus migratory behavior

Because *N. rugulosus* has been collected only four times so far, and its natural history is completely unknown, we report here also a few observations on this rarely encountered army ant. The approximate distances between successive army ant bivouacs was 31 meters on August 10–11 (11 meters between original to excavated bivouacs, and an additional 20 meters to the final bivouac that day), and 24 meters on August 11–12. During the three-day period of this study, colony migrations occurred during the evenings between 1800 and 2200 hrs. The migration on August 10 may have been unnaturally prolonged past midnight because of the attempted nest excavation during the early evening. Towards the end of the colony migration, when fewer workers were on the trail, two species of phorid flies (*Xanionotum hystrix* Brues and *Ecitoptera watkinsi* Disney; det. B. Brown, Natural History Museum, Los Angeles County) and staphilinid beetles (2 *Microdonia* spp.; det. D. Kistner, California State University- Chico) were observed to follow the ants on their trail to the new bivouac; it is possible that these inquilines were present on the trail throughout the migration, but were missed underneath the mass of the migrating ant column. One male *N. rugulosus* was collected as it flew to a headlamp when observing the emigration trail at about 2115 hrs on August 10, indicating that sexuals were present at this time of year.

Like other army ants (Schneirla, 1971; Gotwald, 1995), *N. rugulosus* workers foraged also during the migratory phase, canvassing the general area at the colony front with reticulating foraging trails (i.e., the reticulating fronts of the foraging columns eventually retracted or gradually consolidated into the main migratory column). Foraging raids were observed during the evening (August 10 and 11) and also during early morning (August 12); thus raiding probably continues throughout the night and occurs even after the colony has migrated to a new bivouac. Because bivouacs were subterranean, we cannot rule out the possibility that raiding also continues underground throughout the day, as has been documented for the sympatric army ant *N. nigrescens* (Schneirla, 1971). However, no above-ground activity was observed in our study during the generally sunny, hotter parts of the day.

Two previous, unpublished records of *N. rugulosus* in Arizona were collected by Robert Johnson and Stefan Cover in the Chiricahua Mountains. RJ collected *N. rugulosus* on 22.XI.1996, 3.5 miles northwest of Portal (GPS location 31°55.54'N, 109°12.28'W; 1661 m elevation). SC collected *N. rugulosus* on 08.VIII.1992 at Paradise Cemetery at Forest Service Road 42D, 4.0 miles NW of the junction with Forest Service Road 42 (GPS location 31°55.93'N, 109°15.84'W; 1692 m elevation). In both cases, *N. rugulosus* was found raiding a nest of *Pheidole desertorum*. The very narrow elevational range of the two previous *N. rugulosus* collections (1661 and 1692 m elevation) and the two additional collections made in the present study (1676 and 1737 m elevation) suggest that *N. rugulosus* is an exclusively mid-elevational species that occurs in relatively mesic habitat.

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References

- Adams R.M.M., U.G. Mueller, T.R. Schultz and B. Norden, 2000. Agropredation: usurpation of attine fungus gardens by *Megalomyrmex* ants. *Naturwissenschaften* 87: 549–554.
- Autuori, M., 1941. Contribuição para o conhecimento da saúva (*Atta* spp. – Hymenoptera - Formicidae) I. Evolução do saúvero (*Atta sexdens rubropilosa* Forel, 1908). *Arq. Instit. Biol. (Sao Paulo)* 12: 197–228.
- Belt, T., 1874. *The Naturalist in Nicaragua*. John Murray, London. 403 pp.
- Cole, A.C., 1939. The life history of a fungus-growing ant of the Mississippi Gulf Coast. *Lloydia* 2: 153–160.
- Currie, C.R., J.A. Scott, R.C. Summerbell and D. Malloch, 1999. Fungus-growing ants use antibiotic-producing bacteria to control garden parasites. *Nature* 398: 701–704.
- Currie, C.R., 2001. A community of ants, fungi, and bacteria: A multi-lateral approach to studying symbiosis. *Ann. Rev. Microbiol.* 55: 357–380.
- Eastlake Chew, E. and R.M. Chew, 1980. Body size as a determinant of small-scale distribution of ants in evergreen woodland southeastern Arizona. *Insectes soc.* 27: 189–202.
- Fowler, H.G., 1977. Field response of *Acromyrmex crassispinus* (Forel) to aggression by *Atta sexdens* (Linn.) and predation by *Labidus praedator* (Fr. Smith) (Hymenoptera: Formicidae). *Aggressive Behav.* 3: 385–391.
- Fowler, H.G., 1981. On the emigration of leaf-cutting ant colonies. *Biotropica* 13: 316.
- Gotwald, W.H., 1995. *Army Ants. The Biology of Social Predation*. Cornell University Press, Ithaca, New York. 302 pp.
- Jeanne, R.L., 1975. The adaptiveness of social wasp nest architecture. *Q. Rev. Biol.* 50: 267–287.
- Hart, J.H., 1897. Life history of the parasol ant. *Bull. Trinidad Bot. Garden* 2: 166–178.
- Hölldobler, B. and E.O. Wilson, 1990. *The Ants*. Harvard University Press, Cambridge, Mass. 732 pp.
- Mariconi, F.A.M., 1970. *As Saúvas*. Sao Paulo: Ed. Agronomica Ceres, 167 pp.
- McDonald, P. and H. Topoff, 1986. The development of defensive behavior against predation by army ants. *Dev. Psychobiol.* 19: 351–367.
- Mirenda, J.T., D.G. Eakins, K. Gravelle and H. Topoff, 1980. Predatory behavior and prey selection by army ants in a desert-grassland habitat. *Behav. Ecol. Sociobiol.* 7: 119–127.
- Murakami, T., 1998. *Sociobiological studies of fungus-growing ants Attini: effects of insemination frequency on the social evolution*. PhD thesis, Hokkaido University, Hokkaido, Japan.
- Mueller, U.G. and W.T. Wcislo, 1998. Nesting biology of the fungus-growing ant *Cyphomyrmex longiscapus* Weber (Attini, Formicidae). *Insectes soc.* 45: 181–189.
- O'Keefe, S.T., J.L. Cook, T. Dudek, D.F. Wunneburger, M.D. Guzman, R.N. Coulson and S.B. Vinson, 2000. The distribution of Texas ants. *Southwest. Entomol. Supplement* 22.
- Porter, S.D. and M.A. Bowers, 1980. Emigration of an *Atta* colony. *Biotropica* 12: 232–233.
- Rettenmeyer, C.W., 1963. Behavioral studies of army ants. *Univ. Kansas Sci. Bull.* 44: 281–465.
- Rettenmeyer, C.W., R. Chadab-Crepet, M.G. Naumann and L. Morales, 1982. Comparative foraging by Neotropical army ants. In: *Social Insects in the Tropics* (P. Jaisson, Ed.), Université Paris-Nord, Paris. Volume 2, pp. 59–73.
- Rockwood, L., 1973. Distribution, density, and dispersion of two species of *Atta* (Hymenoptera: Formicidae) in Guanacaste Province, Costa Rica. *J. Anim. Ecol.* 42: 803–817.
- Schade, F.H. 1973. The ecology and control of the leaf-cutting ants of Paraguay. In: *Paraguay Ecological Essays* (J.R. Gorham, Ed.), Academy of the Arts and Sciences of the Americas, Miami, Florida. pp. 77–95.
- Schneirla, T.C., 1971. *Army Ants. A Study in Social Organization*. Freeman, San Francisco. 349 pp.
- Swartz, M.B., 1998. Predation on an *Atta cephalotes* colony by an army ant, *Nomamyrmex esenbecki*. *Biotropica* 30: 682–684.
- Weber, N.A., 1941. The biology of the fungus-growing ants. Part VII. The Trinidad, B.W.I., species. *Rev. Entomol.* 16: 1–88.
- Weber, N.A., 1945. The biology of the fungus-growing ants. Part VIII. The Barro Colorado Island, Canal Zone, species. *Rev. Entomol.* 12: 93–130.
- Weber, N.A., 1966. The fungus-growing ants. *Science* 153: 587–604
- Weber, N.A., 1972. *Gardening Ants: The Attines*. American Philosophical Society, Philadelphia, Pa. 146 pp.
- Wheeler, W.M., 1907. The fungus-growing ants of North America. *Bull. Am. Mus. Nat. Hist.* 23: 271–277.

