PSYCHE

Vol. 92 1985 No. 2–3

BEHAVIORAL NOTES ON THE ASIATIC HARVESTING ANTS *ACANTHOMYRMEX NOTABILIS* AND *A. FEROX**

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The workers of some ants fall into two size classes, each with a distinctive morphology and without intermediates. This condition, known as complete dimorphism, has arisen independently at least seven times among ants (Wilson, 1971). Perhaps the most dramatic examples of the dimorphic worker condition are found in the myrmicine genus *Acanthomyrmex*. One of the most startling species is *A. notabilis* (fig. 1), in which the trunk and gaster of the major are only fractionally larger than those of the minor caste, while the head is relatively enormous. In life, the head is thrown back over the trunk, and in fact much of the trunk fits conveniently into a cavity in the underside of the head capsule. The trunk is therefore virtually concealed even when the animal is viewed from the side. Moreover the waist and gaster are typically drawn up close to the body and are thus inconspicuous. Indeed, an observer's initial impression of a live *A. notabilis* major will likely be one of a "walking head."

Eleven species of *Acanthomyrmex* ants have been collected (Moffett, in prep.), all endemic to the Oriental region. To date no information pertinent to the behavior and ecology of these rarely collected ants has been reported. I present preliminary findings concerning two species here.

**Manuscript received by the editor May 10, 1985*

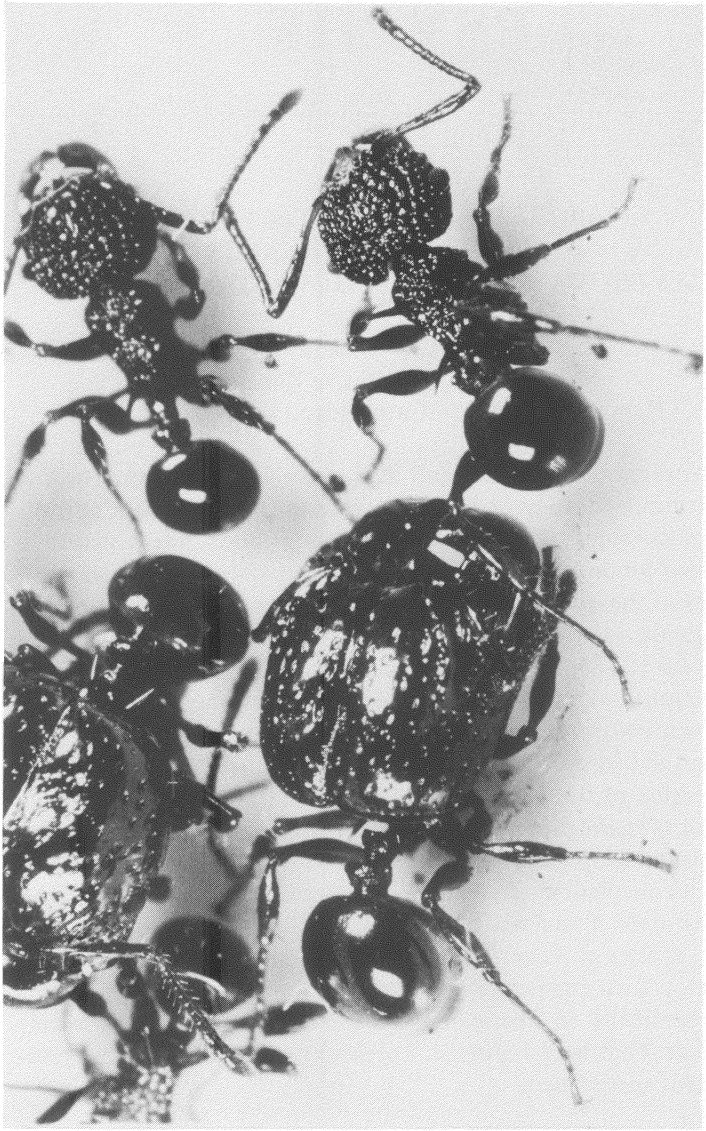

Figure 1. Captive workers of *Acanthomyrmex notabilis*.

Field Notes

Acanthomyrmex notabilis. A colony of *A. notabilis* (F. Smith) was discovered at an elevation of about 200 m in primary rain forest at the Tangkoko-Batuangus Reserve in Northern Sulawesi. The entrance to the nest was a simple, unadorned opening near one end of a 15 cm diameter log. Minors foraged on the mossy surface of the log and in the leaf litter at its side. All foragers located during two hours of behavioral observations were within 40 cm of the nest; no more than three ants were seen foraging at any one time.

The log was dissected with a machete. The wood was hard and in good condition. The nest entrance led into a single passageway, 6 cm long and 4 mm in diameter with smooth, hard walls. This was apparently a natural channel, modified little if at all by the ants. The colony contained three majors, 37 minors, and numbers of eggs, larvae, and pupae. Unfortunately no queen was found. If the nervous behavior of the *A. ferox* queen described in the next section is typical of the genus, it is likely the *A. notabilis* queen escaped while I chopped free the end of the log with the colony. However, few if any workers probably escaped, as no workers were observed even to approach the entrance during this time.

The captive ants were placed in a 8.5 × 13.5 × 3.5 cm high plastic box with a transparent lid and compacted soil substrate. The ants clustered together on the substrate, with the majors at the periphery of the cluster. Later the ants moved into a test tube with stoppered water supply. Before this emigration occurred, one to four minors usually foraged at any given time, but after the emigration no ants were observed to depart from the tube to forage.

Acanthomyrmex ferox. I collected *A. ferox* Emery workers in rain forest at Pleihari-Martipura Reserve Forest in Central Kalimantan, Indonesia. I found foragers in the same area on two subsequent afternoons. These foragers moved largely on top of leaf litter, perhaps in this way avoiding the many relatively aggressive *Lophomyrmex* and *Pheidologeton* ants on the ground below.

A group of workers and males with a dealate queen was eventually located by following ants that carried sugar grains or sesame seeds from baits I had set out. The ants were clustered together between two small leaf fragments suspended above ground level within loose leaf litter. The ants and males were lined up side by

side; one minor held a larva in its mandibles. Except for the queen, which quickly rushed off into the surrounding litter, none of the ants made any move during my disturbances, even when I carefully picked up one of the fragments in forceps for close examination.

Additional workers (including a major, a minor carrying a larva, and three instances of adult transport of minors) were taken from a 2.5 m route extending along the ground and over leaf litter to the nest site. The ants had apparently been in the process of emigrating to the site of the leaf fragments. Unfortunately I was unable to trace the emigration route back to its origin because of the scarcity of ants along it. Indeed, during over an hour of observations on this route, the frequency of ants declined until none were seen during the last thirty minutes. Altogether I took 47 minors, two majors, seven males, one dealate queen and a small number of brood. Presuming the emigration had been at or very near completion, this would represent nearly the complete colony.

The captive ants were maintained as described for the *A. notabilis* colony. As in *A. notabilis*, the workers congregated together on the exposed surface with the brood massed together among them and with the majors usually at the periphery of the brood area. The location of the cluster often shifted.

Diet

Acanthomyrmex notabilis. A. notabilis apparently has a broad diet, collecting fruits and seeds, capturing tiny invertebrate prey, scavenging for dead invertebrates and probably accepting a variety of sugary materials as well.

Only one returning *A. notabilis* forager carried food, this a tiny (0.5 mm) fragment of a small isopod. In captivity minors promptly carried small arthropod corpses to the nest. There the corpses were surrounded by minors, which licked them and gradually tore them into pieces. Majors were never observed to feed on animal material (or any other food except by regurgitation).

There is some evidence for predation in this species. In the field four live 2–3 mm immature centipedes were placed before foraging ants; these were picked up and carried directly to the nest. A small entomobryid collemolan, which I held before a forager with fine forceps, was also seized and carried off. In the captive colony a tiny

live hemipteran nymph was seized by a minor, carried to the nest, and then torn apart and consumed by several individuals.

A clump of about 35 fig seeds was present within the *A. notabilis* nest (fig. 2). Similar tiny seeds were found in the nests of *A. notabilis* colonies collected from rotten wood by W. L. Brown, Jr. on Mount Klabat, not far from Tangkoko-Batuangus Reserve. A minority of other, unidentified seeds of a size comparable to the fig seeds or slightly larger were also present in these nests. In the field *A. notabilis* minors carried three sesame seeds to their nest from a bait of bird seeds. However, captive *A. notabilis* ants completely ignored all seeds provided, including the fig seeds taken from their own colony.

There are indications that seeds are normally a significant part of the diet. Many of the fig seeds taken from *A. notabilis* nests had their outer layer gnawed away. Moreover, the mandibles of the majors were badly worn, which would be expected if this caste mills seeds. The region of northern Sulawesi that includes Mt. Klabat and the neighboring Tangkoko-Batuangus Reserve is exceptionally rich

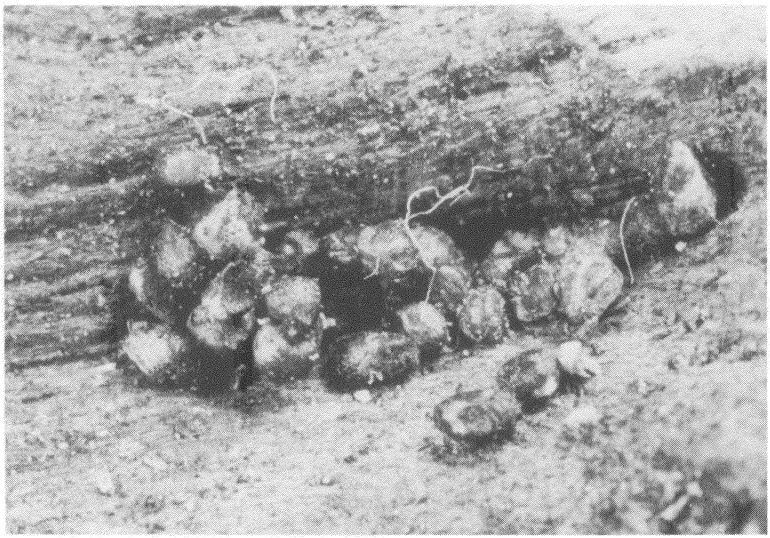

Figure 2. Fig seeds from *Acanthomyrmex notabilis* colony in situ.

in fig trees, which could account for the apparent high density of *A. notabilis* colonies in the area.

The *A. notabilis* minors frequently drank from sugar or honey solutions (while largely ignoring baits of cooking oil). I was unable to find any evidence of recruitment to sugar baits (or any other foods) either in the field or in the laboratory. For example, during a 90 minute period several minors independently found and drank at a sugar bait placed 8 cm from the nest entrance in the field. Although ants that had fed usually returned directly to the nest, their return was not followed by an increased rate of forager exodus. The response of the ants to baits located far from the nest remains to be investigated.

Acanthomyrmex ferox. A. ferox probably has a similar diet breadth to *notabilis*. In the field I provided the foragers with baits of sugar grains, olive oil, and seeds from a canary seed mix with sesame seeds added. Two ants drank from the oil baits and several carried off sugar grains and sesame seeds (but no other seeds). In captivity the minors consumed dead insects and drank sugar water; capture of small prey was not demonstrated. As in *A. notabilis*, no feeding was ever observed on seeds. However, in this case the ants did carry sesame seeds and fig seeds to their current "nest site" on the floor of the plastic box, and when the nest site shifted, the seeds were transferred along with the brood. Most likely this species is also partially granivorous.

A. NOTABILIS BEHAVIORAL REPERTOIRE

A total of 344 behavioral events were recorded during eight hours of observations on the captive *A. notabilis* ants over a 10 day period, during which time 3 majors and 17–18 minors were alive (in addition, about fifteen hours of observations were made before the ethogram data was compiled). The ethogram is presented in table 1.

Workers frequently held immatures in position for long periods, loosely grasping them in their mandibles ("hold eggs, larvae, or pupae" behaviors in table 1). Pupae and large larvae were held while still resting on the ground, and smaller immatures, including clusters of eggs and microlarvae, were often held raised from the ground. A high percentage of workers holding immatures indicated a low level of colony excitement, although one to a few workers

Table 1. *Acanthomyrmex notabilis* ethogram. The actual numbers of acts recorded are followed in parentheses by the relative frequencies of performance of each act. When fitted to a lognormal Poisson probability distribution using a computer program written by R. M. Fagen (see Fagen and Goldman, 1977), the complete repertory of the minor workers is estimated to include 20 behavioral acts, with a 95% confidence interval of [20, 21] acts.

	MINORS	MAJORS
1. Allogroom minor	53 (.1541)	0
2. Allogroom major	17 (.0494)	0
3. Lick eggs	3 (.0087)	0
4. Lick larva	45 (.0131)	0
5. Lick pupa	29 (.0843)	0
6. Hold eggs	11 (.0320)	1 (0.5)
7. Hold larva	30 (.0872)	0
8. Hold pupa	14 (.0407)	0
9. Carry eggs	9 (.0262)	1 (0.5)
10. Carry larva	24 (.0698)	0
11. Carry pupa	14 (.0407)	0
12. Assist ecdysis to pupa	6 (.0174)	0
13. Feed larva	6 (.0174)	0
14. Regurgitate to minor	5 (.0145)	0
15. Regurgitate to major	1 (.0029)	0
16. Lick sugar grain	36 (.1047)	0
17. Eat dead insect	31 (.0901)	0
18. Hold dead minor	2 (.0058)	0
19. Lick dead minor	5 (.0145)	0
20. Carry dead minor	3 (.0087)	0
TOTALS	334 (.9999)	2 (1.0)

commonly held brood even under apparently quiescent conditions. Majors occasionally also held or carried immatures, even when the nest was undisturbed.

Only minors were observed to allogroom and to lick brood. Larvae fed on regurgitated food from minor workers.

Nest Shifts and Emigrations

Acanthomyrmex notabilis. Before the *A. notabilis* colony had moved into the test tube nest, sudden, severe disturbances (such as shaking the box with the ants) caused the ants to rapidly disperse, with many of the workers carrying brood. Following such a disturbance, small groups of two to four ants usually formed within 10

minutes, and often within a half hour virtually all the ants had recongregated at a single site often different from the original site. During four such cases of worker dispersal I recorded one instance in which a major carried a mass of eggs and microlarvae, and three of a major carrying larvae. When majors held immatures in an undisturbed colony they gripped them gently. During disruptions, however, majors squeezed the brood severely, so that the larvae were pinched. Whether this ever resulted in brood death is not known.

If a shaded nest site was made available to the ants after exposing the current site to a moderately strong light, transfer of workers and brood to that site usually began within an hour. The ants which originally held immatures in place were generally not those that carried them to the new site; rather, most or perhaps all of the carrying was accomplished by those often relatively few individuals that had previously been to the new site. If an immature was held by a worker, the approaching ant would antennate the immature, then grasp it in her mandibles and pull gently, her antennae sometimes palpating the other worker. The worker usually released its grip within one to 15 seconds, at which point the first ant promptly carried it away. The ants that had never left the original site gradually appeared to become aroused by the activities of the workers around them, until they, too, sought out and found the new site.

I observed only one instance of adult transport in the course of a shift in colony location, when a normally pigmented minor worker carried a teneral worker. Whether the transfer process also involved some other, more subtle form of recruitment is unclear. However, well defined routes between the old site and the new were lacking. The size of the observation box limited these shifts in nest location to at most a few centimeters; emigrations over greater distances might well be differently organized.

Acanthomyrmex ferox. Shifts in nest location also occurred in captive *A. ferox*. These were initiated by the queen, which often ran out of the brood area following a disturbance; workers and males at the nest site were not so readily disturbed and thus were usually left behind. When one or more workers located her again the colony shifted to her new location. Minor workers carried the brood and males. The males were grasped dorsally at the trunk or waist, with their heads directed either up or down.

During these nest shifts a consistent route often developed between the old site and the new. The emigrating ants observed in the field also followed a distinct route, which in this case could have been at most a few centimeters wide.

Defensive Behavior

Acanthomyrmex notabilis. Foraging minor workers of both *Acanthomyrmex* species were very shy, retreating even after slight disturbances. However, when workers of *Pheidologeton, Aphaenogaster,* and *Pristomyrmex* species common in the vicinity of the nest of *A. notabilis* were held in forceps up to the nest entrance, minors soon emerged to bite at the forager and sometimes grapple with it; the *Pristomyrmex* evoked the strongest response. Following such an experiment, no ants emerged to forage for at least five minutes. After withdrawing each "intruder," I could barely make out the head of a major worker just within the entrance, where no major had been previously. The major bit at a forceps tip that I pushed inside the entrance, holding on so tenaciously I could pull it from the nest.

Captive workers could likewise be provoked to seize a forceps tip, particularly when the worker was in or near the brood area. Biting ants commonly held on so tenaciously that they could be pulled free from the ground. When pulled free, they usually released their grip within a few seconds, unless their tarsi still clung to a piece of substrate, such as a bit of soil—in which case majors in particular would maintain a grip for as long as a minute (fig. 3). Minors gripping a loose object usually rotated that object forward beneath them, while majors did not. Possibly this is explained by a tendency for minor workers to pull backwards when grappling with an intruder.

Captive *A. notabilis* workers fled from *Solenopsis* and *Monomorium* ants, and there was a rapid exodus of the ants and brood if an intruder entered the nest area. However, if the intruders first had their gasters excised, the *A. notabilis* ants behaved much as they did towards single *Pheidologeton diversus* minor workers, which lack the severe stings of *Solenopsis* and *Monomorium*. In this case an *A. notabilis* minor often stood its ground for several seconds, either repeatedly biting at the intruder, or swinging its gaster under its body towards the intruder, or both. A major most commonly first

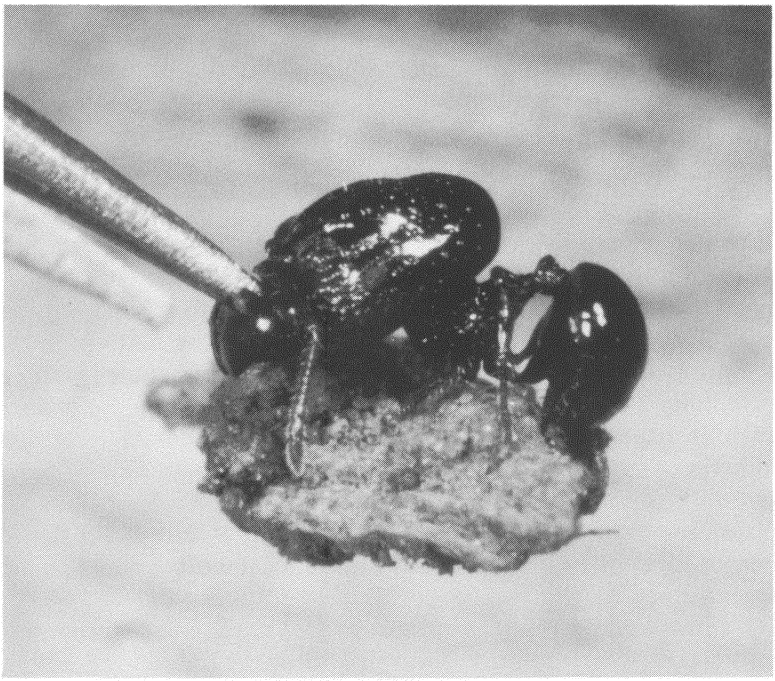

Figure 3. Major worker of *Acanthomyrmex notabilis* biting a forceps tip while clinging to a chunk of soil.

lowered its head so that the intruder was confronted with the broad expanse of the head in full face view, and then brought its gaster under its body, aiming it intermittently at the intruder. Majors sometimes bit and occasionally killed *Pheidologeton* minors, but never *Solenopsis* and *Monomorium* ants, even those with their gasters removed. Workers were most likely to confront an intruder approaching the brood area, and usually fled from workers of other ant species encountered elsewhere.

In two cases I observed an *A. notabilis* major bite and kill insects other than ants; these were a 3 mm embiopteran and a termite worker. Both insects had approached the brood area, at which time the major had responded rapidly and effectively, while minors

ignored the intruders or moved away. Thus the majors were apparently responding to nest intrusion. After a period in which the corpse was ignored, the minors found and began feeding on the embiopteran.

Acanthomyrmex ferox. Defensive behaviors of workers of *Acanthomyrmex ferox* confronted with *Lophomyrmex* were similar to those described for *A. notabilis*: both majors and minors antennated the intruder rapidly and then attempted to bite it, or to swing their gasters beneath their bodies in the direction of the intruder, or both. As in *A. notabilis*, the gaster tip was usually brought into contact with the intruder, at least intermittently: examination of photographs indicates that the ants were extruding their stings. *Acanthomyrmex notabilis* workers have the sting apparatus greatly reduced relative to the size of the ant (Kugler 1978), and this is also true of *A. ferox*; however, this appears not to preclude a defensive function.

Discussion

Colony size. *Acanthomyrmex* colonies appear to be small: the *A. notabilis* and *A. ferox* colonies apparently both consisted of less than fifty individuals. In the *A. notabilis* colony, 7.5% (or three out of 40) of the workers were majors, while this figure is 4.1% (two out of 49) in the *ferox* colony. Colonies of *A. notabilis* from Mt. Klabat collected by William L. Brown, Jr. (pers. comm.) also contained about 40–50 workers, including 1–3 majors.

In both *Acanthomyrmex notabilis* and *A. ferox*, workers frequently held immatures passively in their mandibles for long periods, even during intervals of colony quiescence. Similar behavior has been observed for workers of the trap-jawed formicine ant *Myrmoteras toro* (Moffett, in press). The brood holding behavior in both cases seems to represent a means of insuring that workers can rapidly disperse with brood whenever the colony is disturbed. This is a particularly useful strategy for ants nesting in exposed sites where disturbances are common. As in the *A. ferox* colony described here, the *Myrmoteras* colony, which consisted of 22 workers and one queen, had been nesting between leaves lying loose within leaf litter on the forest floor.

Another common trait of *Acanthomyrmex, Myrmoteras toro*, and many other ants with small colonies (including colonies of

many ants at an early stage of growth after the first brood has been raised by the queen, E.O. Wilson: pers. comm.) is the tendency for the queen to be very sensitive to disturbances. While the workers of *Acanthomyrmex* ants are usually timid, the queen of *A. ferox* (and presumably also *A. notabilis*) is exceptionally shy: she often rushed out of the nest at the slightest sign of trouble, leaving her workers, as yet undisturbed, behind her.

HARVESTING ANTS. Nests of the species *A. notabilis* have seed stores, and therefore at least this *Acanthomyrmex* clearly joins the select group of species commonly referred to as "harvesting ants." Harvesting ants are most diverse and abundant in xeric situations. The cosmopolitan genus *Pheidole*, however, includes numerous harvesting ant species found in mesic habitats (W. L. Brown, Jr., pers. comm.). On the other hand, species of the tropical Asian genus *Pheidologeton* have been considered harvesting ants, but while these ants harvest large quantities of seeds, apparently none store seeds (pers. obs.).

The majors of all *Acanthomyrmex* species have traits characteristic of seed millers, including greatly enlarged heads and heavy mandibles with the masticatory borders often severely worn. It is therefore reasonable to infer that the diet of all these species consists at least in part of seeds, but whether all are harvestor ants remains to be ascertained.

BEHAVIOR OF THE MAJORS. In the course of this study various roles have been implicated for majors of *A. notabilis*:

(1) Majors presumably mill seeds.
(2) Majors play an important role in colony defense, guarding the entrance when there is a disturbance there, and often biting intruders that attempt to enter the nest.
(3) Majors sometimes carried immatures following severe nest disturbances that led to worker dispersal with brood.
(4) Majors occasionally held or carried immatures in an quiescent colony.
(5) I have one observation of a major holding and carrying a piece of prey.

As in other *Acanthomyrmex* species, the gaster of *A. notabilis* is small, contracted and beadlike; there is apparently no tendancy for majors to take on a replete condition.

Majors of *A. ferox* are involved in attacks on intruding ants, and, as in *A. notabilis*, a role as seed millers is probable. During my limited observations on this species majors were not observed holding or carrying brood.

Majors probably never forage. In the captive colonies, majors of both species were invariably at the nest unless there was a disturbance serious enough to cause the ants to disperse. The only major seen away from the nest site in the field was an emigrating *A. ferox* individual.

Although seed milling has yet to be confirmed by direct observation, this activity very likely represents a primary function of the major caste. Oster and Wilson (1978) point out that seed specialists tend to be monomorphic or at most weakly polymorphic, while ants that have a broad diet consisting only partially of seeds are most likely to be polymorphic, with an extreme miller caste. Strongly dimorphic *Acanthomyrmex* ants have diets composed of small prey and scavenged material as well as seeds, and thus adhere to this rule.

In *Acanthomyrmex* only a very few individuals of the major caste are present in any one colony. Indeed, majors form only a small fraction (less than 10%) of the total worker population, even though the colonies as a whole are very small. This is as would be predicted on the basis of ergonomic theory (Wilson 1968, Oster and Wilson 1978). Because the morphology of *Acanthomyrmex* majors is so specialized, they would be expected to be very efficient at those specialized behavioral acts which they do perform. Therefore, relative to a species in which majors are anatomically less deviant from the minors, fewer individuals are necessary to perform the specialized tasks.

Ergonomic theory also predicts that the more specialized the anatomy of the major, the more specialized its behavior, and the more limited should be its behavioral repertoire (Wilsor 1968, Oster and Wilson 1978). It is therefore somewhat surprising to find that *A. notabilis* majors, perhaps anatomically the most extreme majors of any dimorphic ant, perform at least five social behaviors, among them holding and carrying brood.

Wilson (1984) has shown that in *Pheidole*, majors normally perform a more or less restricted set of behavioral acts. However, they can expand their repertoire to nearly equal that of the minor workers if the ratio of majors to minors is increased experimentally to beyond a set threshold value. This occurred within an hour of the

reduction of minor worker numbers to below the threshold. Wilson suggests that *Pheidole* majors serve as an "emergency stand-by caste" following periods of high minor worker mortality.

One possibility is that the apparent behavioral flexibility of *A. notabilis* majors could be a result of the small size of *Acanthomyrmex* colonies. In small colonies it is likely that the number of minor workers available at any given time will often drop below some minimum necessary to carry out the normal affairs of a colony; as a result frequent temporary crises can be expected to occur. For example, a single rich food find could divert much of the limited population of minors to food harvesting activities, so that for a time an insufficient number of minors are available to care for brood; a larger colony will probably be able to draw upon a reserve force of minor workers to handle such situations. If such labor crises are indeed common, it may be most effective to lower the thresholds beyond which majors perform the behavioral acts typical of minors, so that the threshold is closer to the normal ratio of majors to minors than Wilson (1984) found for *Pheidole*. Perhaps the death of about half of the original minor worker population prior to the start of my observations on the captive *A. notabilis* colony had been sufficient to elicit an expansion of the major behavioral repertoire. If so, further studies may show that under most conditions the repertoire of majors is restricted to defense and seed milling.

Acknowledgements

I am very grateful to John MacKinnon for assistance in Indonesia and Deborah A. Fletcher for field assistance, as well as Peter F. Stevens for identifying the seeds, and William L. Brown, Jr. and Edward O. Wilson for comments on a draft of the manuscript.

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