Insectes Sociaux, Paris
1986, Volume 33, n° 1, pp. 85-99

TRAP-JAW PREDATION AND OTHER OBSERVATIONS ON TWO SPECIES OF *MYRMOTERAS* (HYMENOPTERA : FORMICIDAE)

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Reçu le 7 juin 1985 Accepté le 30 décembre 1985

SUMMARY

Field and laboratory studies on a colony of *Myrmoteras toro* collected in Central Sulawesi and a *M. barbouri* colony from Singapore have provided the first ecological and behavioral information on this enigmatic formicine genus. Both species capture prey singly by the trap-jaw method, much as do many dacetine and odontomachine ants. Before striking the ants open their jaws 280°, the greatest degree yet recorded in the ants. Also, the nest area is defended from encroachment by other invertebrates by slapping intruders repeatedly with the mandibles.

M. toro workers catch a variety of small, soft-bodied arthropods. *M. barbouri* preys largely or entirely on springtails. I hypothesize that the trigger hairs characteristic of *M. barbouri* and other species of the subgenus *Myrmoteras* could represent an adaptation to collembolan prey.

Recruitment to food (sugar baits) and during emigrations appears to be absent.

ZUSAMMENFASSUNG

Beutefangen mit Schnappkiefern und andere Beobachtungen an zwei Arten von Myrmoteras **(Hymenoptera : Formicidae)**

Freiland- und Laboratoriumsuntersuchungen einer Kolonie von *Myrmoteras toro,* die im Central Sulawesi gesammelt wurde, und einer *M. barbouri* Kolonie von Singapore, lieferten die ersten ökologischen und verhaltensbiologischen Informationen über diese wenig bekannte Gattung der Unterfamilie Formicinae. Die Arbeiter jagen einzeln und fangen mit ihren langen Schnapp-Kiefern kleine weiche Evertebraten, ähnlich wie es von Arten der Dacetini und Odontomachini bekannt ist. Bevor die Jägerinnen zuschnappen öffnen sie Kiefer um 280°. Das ist der grösste Mandibel-Offnungswinkel, der bisher von Ameisen bekannt ist. Bei der Nestverteidigung werden Eindringlinge häufig mit den Mandibeln gestossen.

M. toro jagt kleine, weiche Arthropoden, während *M. barbouri* nahezu ausschliesslich Springschänze fängt. Ich nehme an, dass die Trigger-Haare, die typisch für *M. barbouri* und andere Arten der Untergattung *Myrmoteras* sind, eine spezielle Anpassung für das Collembolenjagen sind. Rekrutierung zu Futter und Nestplätzen scheint nicht vorzukommen.

INTRODUCTION

Myrmoteras belongs to a loose assemblage of genera which have been considered the most primitive members of the subfamily Formicinae (Wheeler, 1910). These genera, which include *Gesomyrmex, Gigantiops, Myrmecorhynchus, Myrmoteras, Opisthopsis* and *Santschiella,* remain among the least studied ants, in spite of their obvious phylogenetic significance. The only genera for which there is any behavioral and ecological information are *Gesomyrmex* (Wheeler, 1930 ; Cole, 1949) and *Gigantiops* (Wheeler, 1922 ; Wilson, 1984).

Myrmoteras is among the most distinctive of the tropical Asian ant genera, and represents perhaps the most aberrant genus in the subfamily Formicinae worldwide. Workers and gynes are easily recognized by their enormous eyes and elongate mandibles armed with acicular teeth (Moffett, 1985). These remarkable ants are seldom collected, and virtually no observations have been made on living material.

Two subgenera of *Myrmoteras* are recognized (Moffett, 1985). *Myagroteras* workers and gynes lack the long, paired trigger hairs characteristic of the subgenus *Myrmoteras.* I here report observations on one species in each subgenus : *M. toro* Moffett in the subgenus *Myagroteras,* and *M. barbouri* Creighton in *Myrmoteras.* My observations confirm that *Myrmoteras* ants are trap-jaw predators, as Creighton (1930) first proposed.

MATERIALS AND METHODS

I collected a colony of *M. toro* on 15 July 1983 in forest near the village of Toro, 82 km south of Palu in Central Sulawesi. The colony is the type series for the species (Moffett, 1985). The captive colony was housed in a 13.5 × 8.5 cm box with a clear plastic top. The bottom of the box was covered with compacted soil which was kept slightly moist ; a wad of moistened cotton served as a water source. After a month in captivity the ants moved into a test tube with a stoppered water supply.

The *M. barbouri* colony was collected at Bukit Timah Nature Reserve in Singapore on 15 April 1985. The colony was provided a 18 × 13.5 cm clear plastic box with a moistened plaster of Paris bottom. At one end shallow nest chambers were carvel in the plaster of Paris surface and covered with red glass. As in *M. toro,* there was little worker mortality, but there was a gradual attrition of brood. Only eggs and small larvae remained after three weeks.

Behavioral repertories for *M. barbouri* workers and gynes were compiled during 12 hours of observations during daylight hours over a three day period. At one minute intervals all the behaviors observed for the complete colony were recorded. The total number of kinds of behavioral acts was then estimated by the method of FAGEN and GOLDMAN (1977).

RESULTS

Field observations

Myrmoteras toro. The colony was collected at an elevation of about 900 meters in relatively open, secondary forest which extended in a narrow band between the cultivated valley and a wide expanse of primary forest farther in.

I discovered the ants by recognizing one individual just as it disappeared beneath a dead leaf in the litter. Overturning the leaf I found a group of about twelve *Myrmoteras* workers with brood. Apparently the ants had been tightly clustered where two leaves lay in contact. The leaves were slightly moist and were loose within the litter. A cluster of six ants (including one dealate queen) was then located on the exposed surface of a leaf fragment which had most likely fallen to the side when I lifted the first leaf. The ants appeared undisturbed by the exposed situation, but, once disturbed directly with a forceps, the they proved excellent sprinters.

During the next four hours the leaf litter was carefully searched out to about four meters in every direction. Four individuals were collected during the first half hour, all within a meter of the original colony location. One of these workers carried a microlarvae. Altogether 22 workers were collected, as well as 1 queen, 7 pupae, and a number of larvae and eggs. This was apparently the entire colony.

Myrmoteras barbouri. The colony was found at an elevation of about 100 meters in disturbed primary forest. A worker was located in leaf litter. She was capable of startling bursts of speed, rushing to the underside of a leaf every time I moved my hand to within 20 cm. After capturing a springtail, the ant walked 30 cm from her original location to the nest. The nest was in a narrow, centimeter-deep crevice in the soil beneath the litter with a wide (1.0 × 0.3 cm) entrance. It contained a dealate queen, two alate gynes, workers, and brood. Altogether eight workers were collected, including two foragers taken during an hour of observations of the nest entrance. The surrounding ground was searched thoroughly for additional ants, but none were found within a five meter radius of the nest. My assumption is that this was the complete colony.

Behavioral repertories for Myrmoteras barbouri

Behavioral repertories for *M. barbouri* are presented in *table I.* The actual number of behavioral categories was estimated as 26 ± 2 acts for workers and 16 ± 6 for gynes ($\bar{x}$ ± s.e.). Individual behaviors of special interest are discussed elsewhere. Note the following, however :

Table I. — Behavioral Repertories of *Myrmoteras barbouri* workers and gynes. The number of acts observed for each behavior is followed in parentheses by the relative frequency of performance of that behavior for each caste.

Tabelle I. — Verhattensrepertoire der Arbeiterinnen und Königinnen von *Myrmoteras barbouri*. Tabelle gibt die Gesamtzahl der jeweiligen Verhaltensakte an, und in Klammern ihre relative Häufigkeit.

	Workers	Gynes
Self-grooming	482 (.6048)	189 (.8750)
Allogroom worker	41 (.0514)	12 (.0556)
Allogroom gyne	30 (.0376)	5 (.0231)
Carry egg	10 (.0125)	2 (.0093)
Carry larva	11 (.0138)	2 (.0093)
Carry pupa	6 (.0075)	1 (.0046)
Lick egg	4 (.0050)	1 (.0046)
Lick larva	18 (.0226)	2 (.0093)
Lick pupa	3 (.0038)	0
Regurgitate		
with worker	5 (.0063)	0
with gyne	4 (.0050)	0
Lick nest surface	4 (.0050)	0
Manipulate debris	28 (.0351)	0
Carry debris		
within nest	7 (.0088)	0
to outside of nest	6 (.0075)	0
Carry dead nestmate	2 (.0025)	0
Nest defense		
attack intruder	9 (.0113)	0
remove inturder	3 (.0038)	0
Grapple with nestmate	5 (.0063)	0
Forager departing nest	69 (.0866)	2 (.0093)
Lick sugar bait	11 (.0138)	0
Unsuccessfully track potential prey	12 (.0151)	0
Track and capture prey	5 (.0063)	0
Feed on prey		
inside nest	16 (.0201)	0
outside nest	6 (.0075)	0
Total number of acts	797 (1.0000)	216 (1.0001)

1. It was not possible to distinguish the original, dealate queen of the *M. barbouri* colony from the two gynes, which lost their wings soon after collection. One gyne stayed away from the nest for periods of hours : her departures from the nest accounted for two observations of gyne " foraging " in *table I*.

2. " Attack intruder " refers to workers using their mandibles to strike arthropods entering the nest. " Remove intruder " refers to an ant picking up or dragging such an intruder out of the nest (see the section on nest defense). A variety of small soil invertebrates were kept in the observation box.

3. Workers in the nest occasionally held each other's mandibles in a brief tug-of-war, then released their grip and moved apart. This is referred to as " grapple with nestmate " in *table I,* and was observed altogether 11 times.

The repertory of *M. toro* was apparently similar to that of *M. barbouri.* However, the workers were not observed grappling with nestmates or feeding on prey away from the nest. Also, the queen of this colony did not participate in brood care and did not allogroom workers.

Nesting behavior

M. toro ants congregated together in the observation box, preferring sites beneath a leaf fragment or other sheltered location. The nest site often shifted, usually following disturbances. The *M. barbouri* colony preferred the artificial nest chambers, although distrurbances sometimes caused a temporary shift in colony location.

The brood of both species were scattered or laid side by side, except for small clumps of eggs and microlarvae. Even in an undisturbed colony, most *M. toro* larvae and pupae were held in place by workers, gently gripped between the worker's mandibles or immobilized with the forelegs. When the *M. toro* colony was collected, most workers had been holding a larva or pupa, even at the moment the ants had first been exposed. *M. barbouri* workers only occasionally held immatures in place.

The long mandibles present a problem in picking up brood. Smaller immatures were held far from the body, gently gripped between the distal mandibular teeth. Even the small, oblong eggs were carried this way (*fig. 1*). Pupae were gripped by the teeth all along the mandibular borders.

Emigrations

Emigrations, at least over short distances within the plastic nest container, seemed to depend on individual worker initiative ; if recruitment occurred I did not recognize it. In three documented *M. toro* emigrations the queen moved first, running out of the nest area in response to some disturbance (such as tapping the box repeatedly). The workers were not disturbed as readily. However, they showed increased searching behavior within 15 minutes of the queen's departure. After finding the queen, some of the workers began transferring brood to her new location.

The gynes of *M. barbouri* were not as easily disturbed as the *M. toro*

Fig 1. — *Myrmoteras toro* worker holding an egg.

Abb. 1. — Eine *Myrmoteras toro* Arbeiterin hält ein Ei.

queen. However, all of the ants dispersed following a severe disturbance. The ants gradually reclustered without apparent recruitment.

No adult transport was recorded for either species.

Prey capture and diet

Mandible mechanics

The mandibles of *Myrmoteras* workers serve as a trap to capture prey, and thus are highly mobile. At one extreme, they can be directed forward so that the mandibular shafts are approximately parallel and the apical tooth on one slightly overlaps that of the other. However, when fully opened, a portion of the mandibular shafts disappears from view beneath the eyes, so that the angle between the mandibles is an incredible 280° (*fig. 2*). In this position the mandibles are immobile and appear to be locked in place.

Tallies of the *M. barbouri* ants taken at hour intervals indicate over 80 % (100 in 119 observations) of the workers in an undisturbed colony held both mandibles ahead ; the proportion of gynes was similar. In contrast, foraging workers kept their mandibles fully opened most of the time (37 of 42 observations). My observations were similar for *M. toro*.

After the mandibles have been opened, the ant can release one or both from the ' locked ' position and swing them forward again. However, the

Fig. 2. — *Myrmoteras toro* worker with mandibles fully opened.

Abb. 2. — Eine *Myrmoteras toro* Arbeiterin mit voll geöffneten Mandibeln.

mandibles can also be spasmotically closed. The latter behavior is essential to prey capture and nest defense, as shown below.

Foraging behavior

Both species foraged during the day. Foragers licked sugar grains, but ignored cooked rice, bread, and cooking oil. Both species ignored dead arthropods. However, after a period of worker mortality connected with airplane transport, the *M. toro* ants fed on freshly killed, immobile mosquitos dropped among their brood.

Foragers moved rapidly, often with sudden stops and starts. The ants are capable of pivoting in place, and can also move backwards short distances ; these skills were used in tracking prey.

Myrmoteras toro. Out of a wide range of invertebrates aspirated daily from forest leaf litter, including many larger than the ants, workers of *M. toro* took a variety of prey their size or smaller (workers are 5.2-5.6 mm long). However, the ants only successfully captured soft-bodied arthropods, or teneral individuals of relatively hard-bodied species. The capture and consumption of the following arthropods was recorded : three tiny (2.0-2.5 mm) crickets ; six 2-4 mm termite workers ; four 2-3 mm teneral earwigs ; a 4 mm diplurid ; one 5 mm scolopendromorph centipede ; a 3 mm entomobryid collembolan ; one 3 mm beetle larva ; and several wounded mosquitos.

M. toro workers respond rapidly to movements in their vicinity. The following describes the typical events leading up to prey capture. When a small arthropod approaches within 3 cm of a forager, the ant wheels toward it and moves rapidly forward. The mandibles are cocked back and the funiculi extend toward the quarry. As the worker draws close, its antennae contact the arthropod and the ant halts. Its antennae gently palpate the sides of the target, as if gauging its size (*fig. 3*). Within one second both mandibles snap forward, and, if the strike is successful, the long, sharp mandibular teeth sink deep into the target. The gaster is often shaken briefly before the strike.

If the quarry is in motion, the forager typically follows 0.5-1.0 cm behind, often for 10 cm or more. Workers rarely struck a moving target ; if the quarry stops, the worker trailing it makes a final approach and strikes.

After stabbing the prey, the forager carries it directly to the nest. Prey are typically held far out in the mandibles, gripped in the most distal mandibular teeth, the same teeth that penetrated the prey during the strike.

Myrmoteras barbouri. Apparently *M. barbouri* eats mainly springtails. As with *M. toro*, the ants were provided invertebrates aspirated from litter, including some that would have fallen prey to *M. toro*. The ants came near numerous small, soft-bodied arthropods without attempting to strike them. Among these were geophilemorph and scolopendromorph centipedes, millipedes, mites, spiders, isopods, diplurids, isoptera, and orthoptera. Eleven out of twelve records of prey capture in captivity were of small (1-3 mm long) entomobryomorph collembolans (podurids were rejected). The only exception was a campodeid, which the ants captured and consumed after they were supplied invertebrates at the end of four days of food deprivation. In the field, food had been collected from two foragers returning to the nest : in both cases these were also entomobryomorph collembolans.

M. barbouri workers have long trigger hairs, which *M. toro* lacks. The ants appear to strike their quarry at the instant the tips of the trigger hairs

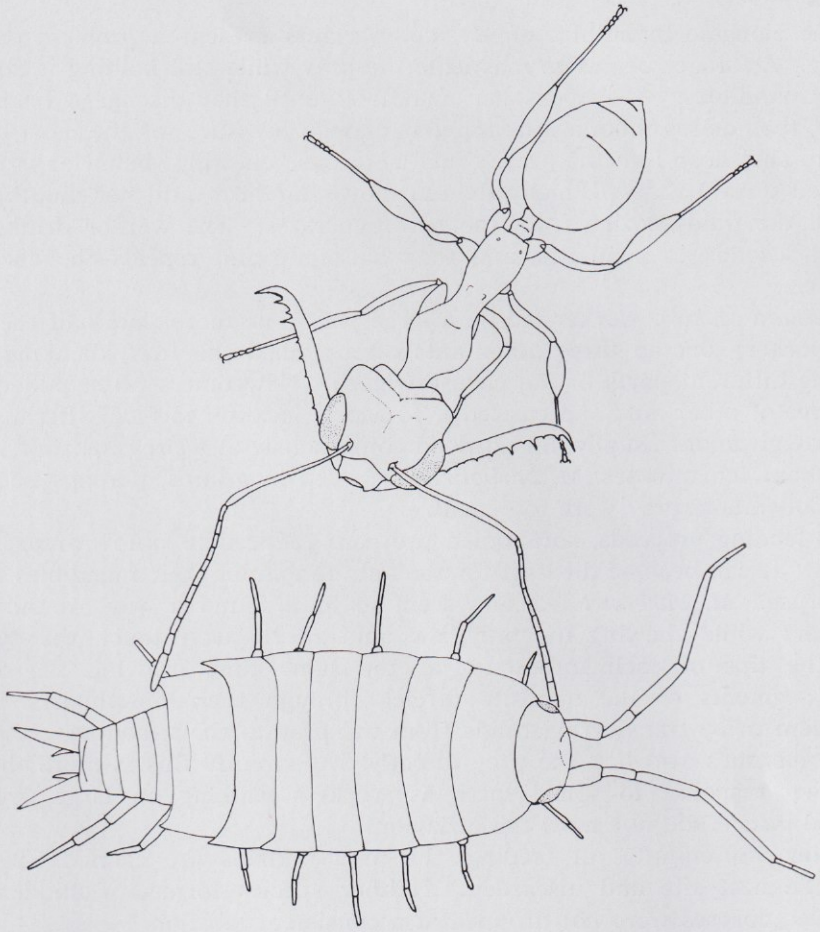

Fig. 3. — *Myrmoteras toro* worker preparing to strike at an isopod (drawn from a photograph). Because the isopod is hard-bodied, the worker's attempt to capture it will fail.

Abb. 3. — Eine *Myrmoteras toro* Arbeiterin ist dabei, einen Isopoden anzugreifen (nach einer Fotografie gezeichnet). Wegen der harten Kutikula gelingt der Beutefang nicht.

contact it, usually without the pause proceeding prey capture typical of *M. toro.* Before the strike the funiculi of the forager tended to be directed almost straight ahead (instead of more laterally, as in *M. toro*). Moving prey were rarely tracked more than 1-2 cm before the ant gave up the chase.

Feeding on prey

The elongate mandibles of *Myrmoteras* ants present a problem during feeding. A forager begins to masticate the prey while still holding it far out in her mandibles. She opens her mandibles until they disengage from the corpse, then closes them again, applying enough pressure for the most distal teeth to sink deep into the prey. This laborious 'chewing' behavior is often repeated several times. Finally the ant moves forward until her mouthparts contact the fluids oozing from the new punctures. The worker drinks for several seconds to a minute, and then backs up and repeats the chewing process.

When a *M. toro* worker fed on a large prey (one more than half the size of a worker), one to three other ants often joined the first, drinking and chewing different parts of the corpse (*fig. 4*). Newcomers often pulled the prey free of other ants and carried it to a new location to feed. Because of this, any given ant usually did not feed continuously at a prey item for more than about ten minutes. *M. barbouri* rarely fed in groups, perhaps because most Collembola prey were too small.

As feeding proceeds, soft-bodied prey are reduced to pulpy, amorphous masses. It can become difficult for the ants to extract their mandibles from the corpse. *M. barbouri* workers seem to have found a way around this problem : while chewing the prey, the ants alternatively touch the corpse with the tips of each foretarsus, at the same time drawing the distal tarsal segments of the opposite foreleg through their mouthparts. The ants seem to be transferring fluids from the prey to their mouths, although they sometimes also lick the prey directly. Apparently this is more than a grooming response to soiled tarsi, as workers walking on large, freshly crushed insects did not show the behavior.

After 5-30 minutes of feeding, the prey remains are carried 5-20 cm from the nest site and discarded. Neither species formed a midden, as discarded corpses were not dropped at a consistent location.

Trophallaxis

A recently fed worker frequently approached another ant and solicited regurgitation. The positions adopted by the ants during trophallaxis varied greatly. Both ants could hold their mandibles in any position. However, most often the donor's mandibles were closed, which forced the other individual to crouch down and twist its head and trunk to the side to reach up at the mouthparts of the donor (*fig. 5*). In other cases both workers leaned to the sides, with their heads tilted as much as 90° so that their mouthparts could make contact. The foretarsi of the receiving ant usually were placed on the head or forebody of the donor, while its antennal tips palpated the donor's head and mandibles. A bout of regurgitation usually lasted 5-30 seconds.

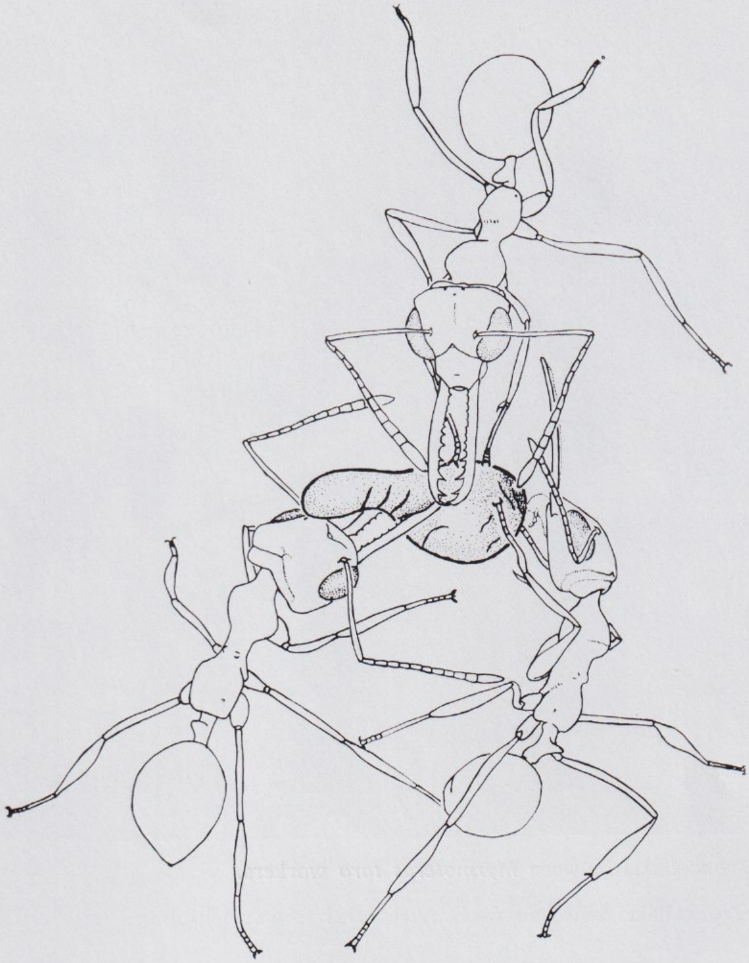

Fig. 4. — Three *Myrmoteras toro* workers feeding on a mosquito (drawn from a photograph).

Abb. 4. — Drei *M. toro* Arbeiterinnen fressen an einem Moskito (nach einer Fotografie gezeichnet).

M. toro workers regurgitated to larvae, as presumably did *M. barbouri* workers. The larvae were never supplied with solid food, and they did not feed on freshly crushed prey I dropped before them. The gynes of both *Myrmoteras* species ignored all food and water placed before them, and apparently fed exclusively by regurgitation with workers.

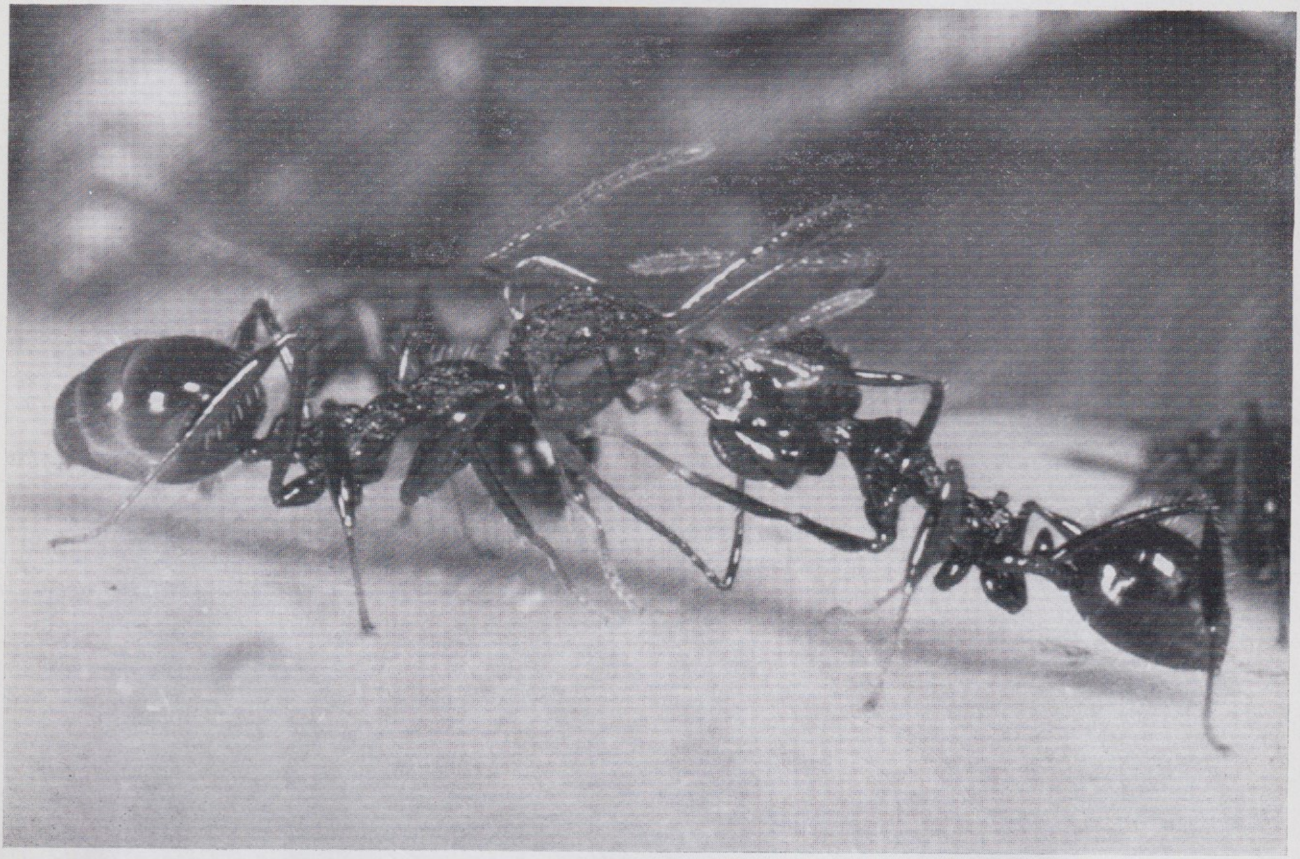

Fig. 5. — Trophallaxis between *Myrmoteras toro* workers.

Abb. 5. — Trophallaxis zwischen zwei *Myrmoteras toro* Arbeiterinnen.

Tests for recruitment

Sugar baits were used to test for recruitment to food in four experiments on each species. In each case the ants were watched for at least 30 minutes. Results for both species were similar. Upon finding a bait, a forager typically drank for 2-10 minutes and then returned directly to the nest, obviously replete. There it engaged in trophallaxis with one to several ants for a few minutes. Particularly in *M. toro,* it would often return to the bait and drink again, and then come back to the nest and once more engage in trophallaxis. A forager could repeat this circuit ten times in an hour, yet there was no evidence of recruitment. No other workers followed the path taken by the forager between the bait and the nest site. Indeed, the forager often did not take the same path on successive trips.

Nest defense

Myrmoteras toro. There were frequent encounters between *M. toro* workers and intruders at the nest site. When an invertebrate approached within 1-2 cm of the brood, one or more of the nearest workers pivoted towards it and opened their mandibles. The ants then advanced and struck the intruder. These blows were generally sufficient to send even a relatively large intruder, such as a centimeter-long cricket, into a hasty retreat. If the intruder moved only slightly, the workers advanced and struck it again. The queen never participated in expelling intruders unless directly disturbed by one. In fact she ran from the nest when an intruder caused a severe disturbance.

The defensive response of the workers was elicited by virtually any small invertebrate approaching the nest site (slow-moving isopods were usually ignored). Although many of the intruders, such as tiny beetles and cockroach nymphs, were most likely innocuous, others, such as ants of a variety of species, represented likely threats.

Most often the intruder was hard-bodied, in which case the ant's mandibles usually ricocheted off the cuticular surface. However, if the mandibles penetrated the integument, the intruder could be captured and eaten. This was observed for a tiny cricket and a termite worker.

Occasionally in escaping the ants, an invertebrate fled directly into the nest. Now larger numbers of workers (commonly up to about six) would immediately turn toward it and begin striking it repeatedly with their mandibles. As a result the invertebrate invariably made a rapid egress. The ants responded similarly to a forceps tip waved among them.

Intruders were usually ejecting from the nest site before they did any damage. However, in one case a *Solenopsis geminata* ant bit the leg of a *Myrmoteras* worker. The *Myrmoteras* swung its gaster under its body, possibly spraying its adversary with defensive secretions. Workers gripped by a leg with a forceps showed similar behavior, as did *M. barbouri* workers attacked by *Pheidologeton diversus* minors. This represents a typical formicine response to enemy attack. Apparently the prey of *Myrmoteras* are never spreyed in this way.

The defensive response of the workers was sometimes brought into play in reaction to prey that struggled after capture. Struggling prey were lifted from the ground and carried to the nest. There workers responded as if the prey was not being carried by a nestmate : the nearest workers converged on the prey and struck it with their mandibles. In the three cases where this was observed (involving two tiny crickets and a termite worker), the prey was literally beaten to death (or at least to quiescence) within 20 seconds.

M. barbouri. The reaction of *M. barbouri* to disturbances at the nest was less dramatic than in *M. toro.* Ants often turned to face an intruder without striking, or moved aside to avoid the intruder. In some cases, a worker gripped the intruder in her mandibles, and then carried or dragged it from the nest. Two small scolopendromorph chilipods, a dipluran, and an unidentified fly larva were given this treatment.

Although intruders (such as centipedes, cockroaches and large springtails) were struck by the mandibles of one or two ants, I never observed mass assaults like those described for *M. toro.* As a result the *M. barbouri* ants were slow at driving many intruders from the nest. Unlike *M. toro,* gynes also struck intruders.

DISCUSSION

Information on the nesting and foraging habits of *Myrmoteras* ants is scarce. FOREL (1893) and WHEELER (1910) assumed that *Myrmoteras* ants are arboreal because of their exceptionally well-developed eyes. F.X. WILLIAMS (in WHEELER, 1922) indicated that *M. williamsi* (subgenus *Myrmoteras*) from the Philippines nests in soil. The observations given here support the view that workers nest and forage on the ground. The ants forage solitarily, using a trap-jaw technique convergent with that of odontomachine and long-mandibulate dacetine ants (MOFFETT, 1985).

W.L. BROWN, Jr. (pers. comm.) collected *M. iriodum* workers (subgenus *Myagroteras*) in S.E. Kalimantan. The ants were in small clusters with brood inside hollow twigs and between leaves in a single 20 m^2 area on the rain forest floor. A single dealate queen along with a few workers and brood were present in one hollow stick. Brown suggests that the colonies could be diffuse, consisting of widely separated groups of workers and brood. However, the *M. toro* and *M. barbouri* colonies I collected apparently had a single nest site. In any case, the limited available evidence suggests that *Myrmoteras* colonies have small worker populations, and that the ants accept a variety of ephemeral nesting sites at ground level.

Disturbances from small arthropods would presumably be frequent for species nesting in relatively exposed sites. When colonies are small, the removal of these intruders must be accomplished so as to minimize the danger to the workers. The defensive strategy of *Myrmoteras* ants (particularly as described for *M. toro*), in which workers ejected intruders from the nest with blows from the mandibles, insures that potentially dangerous intruders are removed without workers having to grapple with them.

Species of *Myrmoteras* in the subgenus *Myagroteras,* such as *M. toro,* lack trigger hairs. This condition is considered ancestral for the genus (MOFFETT, 1985). As demonstrated in the laboratory, *M. toro* ants have a broad diet of small soft-bodied invertebrates. However, *M. toro* workers have little success capturing Collembola. Several times I observed springtails escape during the brief pause in which the *M. toro* ants palpated them, seemingly to judge the distance to the prey before striking. Workers of *M. barbouri* (in the subgenus *Myrmoteras*) were quicker at striking springtails, and such strikes were often successful. Moreover, *M. barbouri* workers largely ignored other potential prey. If the diets of these species are typical of ants in their respective subgenera, the evolution of trigger hairs in subgenus *Myrmoteras* could be related to a specialization on springtails. The trigger hairs may allow for a more rapid response, reducing the possibility that easily startled collembolans will escape.

ACKNOWLEDGEMENTS. — I thank Deborah FLETCHER and Pak ALISI for field assistance, Rolex LAMIANDA, John MACKINNON and Yoga MULYANA for assistance in Indonesia, and Bert HÖLLDOBLER, Edward O. WILSON and two anonymous reviewers for comments on the manuscript. Supported by grants from the National Geographic Society, the National Academy of Sciences and Harvard University (the Richmond Fund).

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