

BEHAVIOR OF THE GROUP-PREDATORY ANT
PROATTA BUTTELI (HYMENOPTERA : FORMICIDAE) :
AN OLD WORLD RELATIVE OF THE ATTINE ANTS

M.W. MOFFETT

Museum of Comparative Zoology
Harvard University, Cambridge, Massachusetts 02138 U.S.A.

Reçu le 17 mars 1986

Accepté le 23 septembre 1986

SUMMARY

1. Morphological evidence indicates the Southeast Asian genus *Proatta* is phylogenetically close to the Attini. The gyne of *Proatta* is described for the first time.

2. Colonies of *Proatta butteli* are polygynous, with numerous queens present. There is no evidence for aggression between queens or differential treatment of queens by workers. Also, there is no sign of intraspecific aggression: the ants readily accepted workers transplanted from distant sites.

3. Workers search for food solitarily, foraging only a short distance (invariably less than a meter) from each nest entrance. Within the limited foraging area worker density tends to be high, and clumps of as many as 50 foragers are sometimes present. This foraging pattern allows for rapid exploitation of discovered food. Recruitment occurs along odor trails formed from a pheromone originating in the poison gland.

4. In addition to small prey and scavenged arthropod corpses, the ants capture prey larger than themselves. Such prey are taken by an inchoate form of group predation. The first worker to encounter the prey attempts to restrain it. Because of the high forager density, additional workers soon arrive seemingly by chance and aid in pinning the prey in place. Unlike attine ants, *Proatta butteli* does not feed on fungi.

5. The worker repertoire, temporal division of labor, and emigration behavior are discussed. Although workers vary little in head width (0.51 to 0.70 mm), they show a modest division of labor by size, with smaller individuals being relatively numerous in the brood area.

ZUSAMMENFASSUNG

Verhalten der gruppen-räuberischen Ameise *Proatta butteli*
(Hymenoptera : Formicidae) : Eine Altwelt-Verwandte der Neuwelt-Tribus Attini

1. Morphologische Belege legen den Schluss nahe, dass die südostasiatische Ameisengattung *Proatta phylogenetisch* der Tribus Attini nahe steht. Die Königin von *Proatta* wird erstmals beschrieben.

2. Kolonien von *Proatta butteli* sind polygyn. Aggression zwischen den Königinnen oder unterschiedliches Verhalten der Arbeiterinnen zu bestimmten Königinnen konnte nicht beobachtet werden. Intraspezifische Aggression scheint nicht zu existieren: die Ameisen können leicht zwischen entfernten Nestern ausgetauscht werden.

3. Arbeiter gehen einzeln auf Futtersuche; sie entfernen sich dabei kaum weiter als 1 Meter vom Nesteingang. Innerhalb des begrenzten Fouragierbereiches ist die Arbeiterdichte oft beträchtlich; bisweilen findet man bis zu 50 Futtersucher an einem Fleck. Dieses Fouragierverhalten ermöglicht eine schnelle Ausbeutung von Futterquellen. Mit Hilfe von Spurpheromonen, die aus der Giftdrüse stammen, werden Nestgenossen rekrutiert.

4. Meist erbeuten die Ameisen kleine Beuteobjekte, doch manchmal werden auch Beutetiere, die grösser als die Ameisen sind, gefangen. Dies geschieht durch ein einfaches, kooperatives Beuteverhalten. Anders als Arten der Tribus Attini ernährt sich *Proatta butteli* nicht von Pilzen.

5. Das Verhaltensrepertoire, Arbeitsteilung und Emigrationsverhalten werden diskutiert. Obgleich die Arbeiterinnen nur wenig in der Kopfkapselbreite variieren (0.51 bis 0.70 mm), zeigen sie doch eine gewisse grössenabhängige Arbeitsteilung, wobei die kleineren Individuen häufiger im Brutnest vorkommen.

INTRODUCTION

The genus *Proatta* contains the single species *Proatta butteli* Forel, from the Malay Peninsula, Borneo, and Sumatra. FOREL (1912) noted the morphological similarity between workers of this ant and those of the New World attine ants, and EMERY (1922) placed the genus in the Attini. WEBER (1958) attributed the similarities between *Proatta* and the attine ants to convergence. The evidence that *Proatta* belongs in the Attini is reviewed here, and the queen of *Proatta* is described for the first time. Also reported is the first available information on *Proatta* natural history.

MATERIALS AND METHODS

The primary study colony was located in the Singapore Botanical Gardens at the base of a small *Flacourtia rukam* tree. Subsamples of this large colony were excavated and kept in plastic boxes, where the ants nested in chambers carved in a plaster-of-Paris floor. Additional field and laboratory observations were made on colonies elsewhere in the Botanical Gardens and other sites in the Malay Peninsula (Penang Hill; the University of Malaya Field Studies Center at Gombak; and Kuala Trenggan in Taman Negara National Park), and the Samunsam Wildlife Sanctuary (Sarawak).

Workers were divided into age classes on the basis of pigmentation for analysis of division of labor: "light" workers were vivid yellow with at most a trace of orange; "medium" workers were slightly duller and had a stronger orange hue; while "dark" workers were dull orange red (gaster and legs distinctly lighter and orange-yellow). The size of the worker behavioral repertoire was estimated by fitting the observed fre-

quency distribution to a lognormal Poisson distribution as described by FAGEN and GOLDMAN (1977), using a computer program supplied by R.M. FAGEN. Size-related division of labor was considered separately, but the data are more limited because of difficulties in accurately distinguishing worker size classes in this monomorphic species.

DESCRIPTION OF GYNE

See *figure 1*. Total length about 6 mm, with little size variation. Head width of three Singaporean gynes 1.05-1.06 mm; head length 1.08-1.10 mm; cephalic index 96-98. Head similar to that of worker, but roughly triangular in full face view; eyes oval, maximum diameter about 20 % of head length; ocelli prominent; mandibles and antennae as in worker. Trunk massive, with full complement of flight sclerites, and only about 25 % longer than high; very similar in shape to that of *Atta* gynes. Metanotum with a single blunt spine medad, as in male. Petiole and postpetiole as in worker. Gaster heavily sclerotized, massive, of a length slightly greater than that of alitrunk. Head and alitrunk areolate-rugose (with alveolate microsculpturing) as in workers but more strongly impressed.

PHYLOGENETIC RELATIONSHIPS

WEBER (1958) removed the genus *Proatta* from the Attini, noting morphological differences between *P. butteli* and attine ants. Yet there are several characters that suggest *P. butteli* is phylogenetically close to the Attini; indeed, this species is most similar to *Myocepurus* and *Myrmicocrypta*. Perhaps most remarkable is the resemblance of the larva to those of attines, as has been confirmed by G.C. and J. WHEELER (1985). Yet in spite of probable evolutionary ties between *Proatta* and the Attini, this genus should be excluded from the Attini for geographic and behavioral reasons, at least until attine phylogeny is better understood.

For female castes, probable synapomorphies include:

1. The blunt spines on the head and alitrunk of workers, which closely resemble those found in many *Myocepurus* and *Myrmicocrypta* species and some other attines.
2. Presence of a projection located somewhat ventrad on the posterior-lateral surface of the head (see *fig. 1*), remarkably similar to projections found in *Myrmicocrypta* (feeble ridges present on the heads of *Myocepurus* workers may be homologous).
3. Presence of a narrow, finger-shaped extension of the clypeus, which is produced back between the antennal carinae, as in *Myocepurus* and *Myrmicocrypta*.

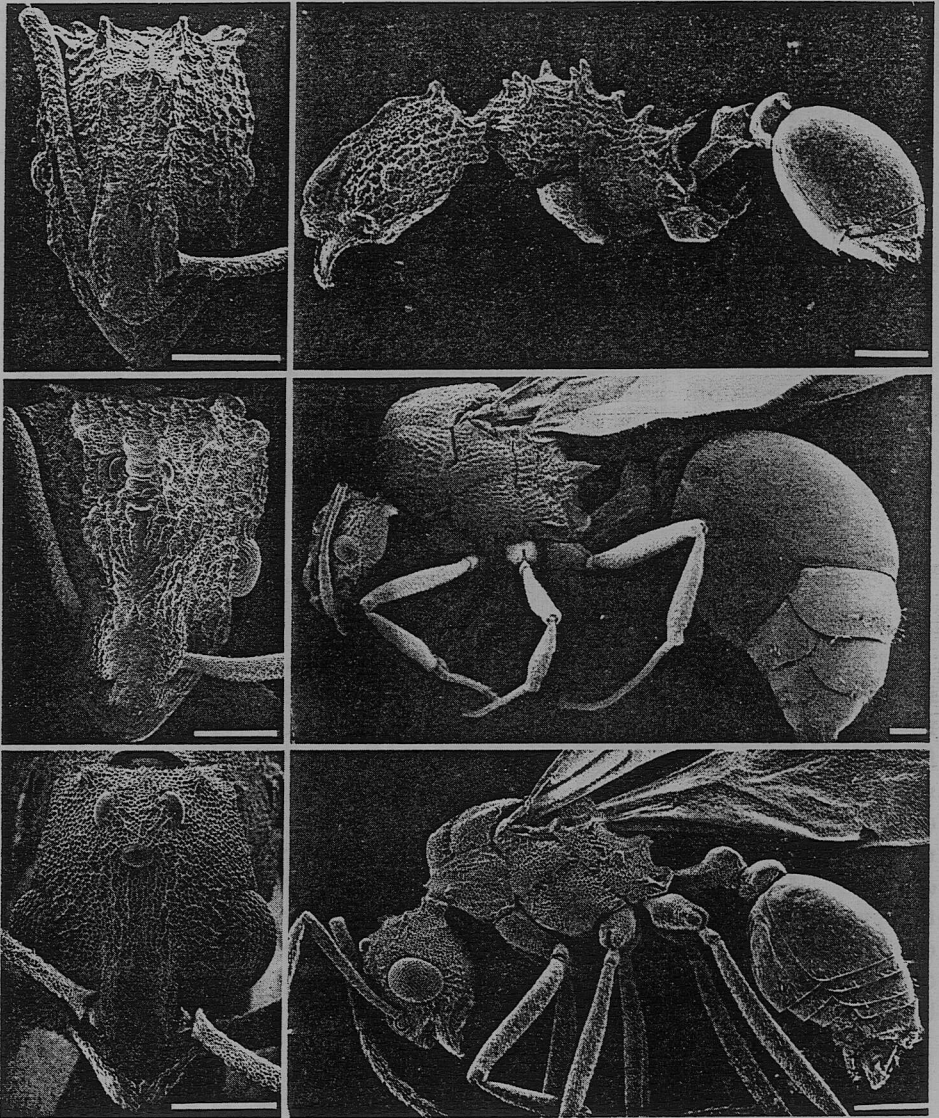


Fig. 1. — *Proatta butteli* from Singapore. Frontal view of heads and side views of entire bodies of worker (upper), queen (middle), and male (lower). Scale bars = 0.25 mm.

Abb. 1. — *Proatta butteli* aus Singapore. Frontalansicht vom Kopf und Seitenansicht des gesamten Körpers von Arbeiter (oben), Königin (Mitte) und Männchen (unten).

4. Shape and position of lateral ridges on the dorsal surface of the petiole node closely resemble most species of *Myrmicocrypta* and *Mycocepurus*. Petiole shape in these genera is very close to that of *Proatta*.
5. Posterior margin of postpetiole indented medad in dorsal view, as in most attines.
6. Queen with two pairs of blunt spines on anterior face of pronotum very similar in size and location to those of *Myrmicocrypta* queens.

Proatta gynes also closely resemble those of attines in wing venation and in trunk shape. *Proatta* males likewise resemble those of attines (fig. 1).

Of the characters distinguishing *Proatta* from the Attini (EMERY, 1922; WEBER, 1958), several (e.g. the number of antennal segments) are apparently plesiomorphies. Contrary to statements by EMERY (1922) and others, the front tarsi of attine ants are not always conspicuously more dilated than in *Proatta*. The front tarsi of *Proatta* and species of *Cyphomyrmex* are particularly similar. The clypeus of *Proatta* is very distinctive; however, this could represent an autapomorphy.

HABITAT AND NESTING BIOLOGY

Proatta gynes also closely resemble those of attines in wing venation in secondary rain forests. Most nests are near tree bases. Colonies infiltrate rotten roots, abandoned termite nests, and other cavities near the surface, forming within them a labyrinth of chambers and galleries. The ants apparently make use of available spaces, with little additional excavation. The chamber surfaces are lined with detritus such as woody frass and prey remains (fig. 2). Dealate queens are numerous, with roughly one queen for every 100-500 workers throughout the nest. Nest entrances are scattered on the ground above the chambers, and are unornamented except for strewn debris. The primary study colony is one of the largest I have seen, probably containing several thousand ants, and possibly 10,000 or more. The nest site has been occupied for at least 3 years.

DIVISION OF LABOR

The behavioral repertoire of *Proatta butteli* within a captive nest is presented in table I; worker foraging behavior is considered separately (see below). These data were compiled during 10 hrs within a five day period. The total repertoire size for workers was estimated to be between 29 and 31 (95 % confidence intervals). Queens showed a limited repertoire, self-groom-



Fig. 2. — *Proatta butteLI* ants. Upper, close-up of two workers. Lower, a nest chamber of one colony in the field (with debris around the perimeter, and a *Pheidologeton diversus* worker head capsule visible near center).

Abb. 2. — Arbeiterinnen von *Proatta butteLI*. Oben, Nahaufnahme von zwei Arbeiterinnen. Unten, Nestkammer einer Kolonie im Freiland (mit Abfall im Umkreis, und dem Kopf einer *Pheidologeton diversus* Arbeiterin nahe der Mitte).

ing themselves and less frequently licking, holding, or carrying egg masses or larvae; 8 behavioral acts were recorded for five queens during ethogram compilation.

The proportion of different worker age classes (light : medium : dark) was 0.35 : 0.46 : 0.19 for workers sampled from within the nest of an intact colony, but 0.09 : 0.34 : 0.57 for ants coming to a bait near an entrance of the same colony (in each case $n = 100$). Light workers were virtually absent within the foraging area away from baits. These data and the ethogram in *table I* indicate a pattern of age polyethism typical of ants (WILSON, 1971),

Table I. — Behavioral repertoire of *Proatta butteli* workers. The relative frequency of performance of each behavior is given for each caste.

Tabelle I. — Verhaltensrepertoire von *Proatta butteli* - Arbeiterinnen. Tabelle gibt die relative Häufigkeit der jeweiligen Verhaltensakte an.

	Light worker	Medium worker	Dark worker	All workers
Self groom	0.3380	0.2383	0.2134	0.2805
Allogroom :				
light worker	0.0298	0.0352	0.0061	0.0242
medium worker	0.0070	0.0195	0.0031	0.0087
dark worker	0.0053	0.0078	0.0031	0.0052
queen	0.0035	0.0039	0	0.0026
Lick eggs	0.0385	0.0078	0.0031	0.0217
Lick small larva	0.0193	0.0078	0.0092	0.0139
Lick large larva	0.1296	0.1133	0.0823	0.1126
Lick pupa	0.0333	0.0352	0.0152	0.0286
Carry worker	0.0053	0.0352	0.0061	0.0121
Carry eggs	0.0385	0.0391	0.0244	0.0346
Carry small larva	0.0158	0.0156	0.0457	0.0242
Carry large larva	0.0280	0.1055	0.2439	0.1065
Carry pupa	0.0210	0.0586	0.0884	0.0485
Assist in :				
larval ecdysis	0.0455	0.0430	0.0061	0.0338
pupal ecdysis	0.0455	0.0508	0.0061	0.0355
adult eclosion	0.0298	0.0234	0	0.0199
Carry meconium	0.0105	0.0156	0.0152	0.0130
Carry dead worker	0.0018	0	0.0061	0.0026
Eat dead worker	0.0053	0.0039	0.0031	0.0043
Bite at brood	0.0736	0.0859	0.0945	0.0823
Eat damaged brood	0.0088	0	0.0092	0.0069
Eat solid food	0.0035	0.0078	0.0031	0.0043
Regurgitate to :				
larva	0.0053	0.0078	0.0061	0.0061
light worker	0.0193	0.0078	0.0396	0.0225
medium worker	0.0035	0.0117	0.0152	0.0087
dark worker	0.0053	0.0078	0.0366	0.0147
queen	0	0	0.0031	0.0009
Handle trash	0.0298	0.0117	0.0122	0.0208
No. acts observed	571	256	328	1155
No. behaviors observed	28	26	27	29

with lightly pigmented (younger) workers spending more time at within-nest activities such as licking brood, and seldom leaving the nest.

Proatta butteli workers vary little in size (worker head widths range from 0.51 to 0.70 mm). Yet there is allometry between pronotal width and head width (slope = 0.48 on a double log plot, $r = 0.92$; $n = 25$), and workers of different sizes do show behavioral differences. Workers with a head width of 0.56 mm or less made up 38-90 % ($\bar{X} = 62$ %) of the workers standing on brood piles (based on 13 measurements taken at hourly intervals). These small ants were significantly more common on the brood than they were in the colony as a whole ($p < 0.01$, one sample sign test) (29 % of the captive ant population was small), and commonly groomed brood and fed larvae. Yet small workers did forage, and formed the same proportion of the forager population as they did for the worker population within the nest (in each case about 11 % of a sample of 150 individuals in the field).

Some of the most darkly pigmented individuals have an irregular, encrusting layer of very fine whitish material on their heads and trunks. This material comes free when the ants are placed in alcohol, and is composed of tiny, apparently siliceous grains. There is no evidence to suggest the material functions in camouflaging the ants from predators, as may be the case for the dense debris which accumulates on workers of certain basicerotine and stegomyrmicine ants (HÖLDOBLER and WILSON, 1986).

QUEEN INTERACTIONS

Queens did not show overtly aggressive behavior. Queens tended to be dispersed within nests in the field, although I have taken two or three within a single chamber. Captive queens were often in physical contact with each other. They did occasionally stand partially on top of each other, but there was no clear pattern to this activity that would suggest a dominance function. There was also no evidence for differential treatment of queens by workers. For example, in one small colony sample, all three of the queens present received food frequently by regurgitation. Queen mortality was high in captivity, but most deaths occurred within two weeks after collection and were probably unrelated to social interactions. It is not known whether all queens are inseminated.

INTRASPECIFIC INTERACTIONS

Intraspecific aggression has not been observed. When ants from distant *Proatta* colonies were dropped near the nest entrances of the primary study colony, the intruders were ignored by workers. They walked into the nest

or moved freely around the nest entrances for at least 15 minutes. When eleven workers from a colony from Penang (Malaysia) were added to a captive fragment from a Singaporean colony, they were accepted by the workers, and all eleven were alive two weeks later. In a similar experiment involving different colonies, mortality of the foreign ants was high during the two week period, but was similar to that for marked controls from the same colony. Transplanted workers participated in brood care and foraging.

FORAGING PATTERN

Proatta butteli ants forage without an apparent circadian pattern. Workers do not travel far from nest entrances. In a detailed survey of forager locations for the primary study colony, only six ants (less than 1 % of the worker population outside the nest) were more than 50 cm from a nest entrance, and the greatest distance was 65 cm; all my observations indicate foraging was restricted to within about 1 m of colony entrances. Worker density was highest within a circle 50 cm in radius at the tree base (several hundred ants/m²), lower in a ring 0.5 - 1.0 m out from the tree base (82 ants/m²), and very rapidly declined in more distant 50 cm wide rings because of the paucity of nest entrances farther from the tree.

Furthermore, many foragers were in clumps, with seven clumps of five or more individuals accounting for about two-thirds of all ants more than 10 cm from a nest entrance. At other times clumps of as many as 50 workers occurred beneath leaf litter or on open ground. Most of these ants showed very little activity, and there was usually no evidence of food at their location. The groups were temporary, inconsistent in location, and variable in number. They were not seen in smaller colonies, where foragers also did not reach the densities typical of larger colonies.

DIET

Proatta butteli workers scavenge for invertebrate remains and prey on live arthropods. The ants also collect bits of fresh or dried vegetation, wood, and other plant material, and recruit to piles of sesame seeds provided near nest entrances. Apparently none of these plant materials are eaten, however, although they are added to the debris the ants let accumulate inside the nest.

Small isopods are generally the most common prey. Prey also included termite foragers (the primary study colony often took *Odontotermes*), workers of other ant species, centipedes, cockroaches, homopterans, and lepidopteran and dipteran larvae. Some prey were larger than the *Proatta* :

the largest prey recorded was a 7 mm long *Rhopalidia* wasp weighing 27 times as much as a *Proatta* worker. Foragers only detected prey very close to them, and would rush at the prey and try to grip it with their mandibles. Attempts to sting the prey sometimes followed, but were often poorly executed.

Arthropods larger than *Proatta* workers were captured by group predation. However, even prey vulnerable to predation by single foragers were often more quickly subdued if one or more workers aided the first.

When a worker succeeded in gripping onto a large arthropod it would attempt to hold the prey in place. Sometimes the worker was dragged along or bitten by the quarry until it released its grip. Yet solitary workers were occasionally successful at restraining relatively huge prey for up to 15 min. The workers accomplished little on their own: large, active prey were never successfully captured by single ants. However, the first ant was often joined within minutes by others, which helped to pin the prey in place. The arrival of aid seemed to be fortuitous, at least initially: foragers sometimes passed within 1 cm of ants struggling with prey without orienting toward them. Recruitment trails were often formed to large prey after several workers had arrived at the prey.

The importance of myrmecophagy to *P. butteli* is reflected in the abundance of ant remains in and around nests. *Proatta* will feed on freshly killed ants. Predation of live ants also occurs, although it is difficult to distinguish predation from defense. In the field I have seen workers capture *Oecophylla longinoda*, *Odontoponera transversa* and sundry *Camponotus*. These ants weigh 10-15 times as much as a *Proatta* worker. Only a small proportion of capture attempts succeed, since the larger ants usually move too quickly for the *Proatta* to respond to their presence.

The most common formicid prey for the Singapore colonies was *Pheidologeton diversus*. In this species the workers group hunt. (MOFFETT, 1984). *Proatta* occasionally captured raiding *P. diversus* ants, but the majority of *P. diversus* taken were stragglers from raids, in most cases wounded ants. Curiously, colonies in Singapore often had a few live *P. diversus* minors and medias in or near their nest entrances. These ants moved as if drugged. The *Proatta* sometimes dragged these ants about, but mostly ignored them; whether they were eventually consumed is unknown.

Large prey were transported to the nest by groups of workers (group transport was poorly developed, however, because workers tended to pull in conflicting directions). These prey slowly pulled apart inside the nest. Ant prey were often difficult to dismember: 1 hr after the *Proatta* had dragged several *Camponotus* and *Oecophylla* ants inside their captive nest, some of the prey were still capable of moving about feebly. Within another hour, however, most of the ants had been torn to pieces and were being consumed.

RECRUITMENT

Proatta foragers recruited workers to baits of sugar water or olive oil, and large pieces of freshly killed crickets or earthworms. Recruitment most commonly occurred for baits placed within 30 cm of a nest entrance. Ants locating baits farther from an entrance often fed at the bait but then did not recruit, or attempted without success to pull or drag the bait. In addition to the baits I provided, workers recruited to decaying fruits, such as those of *Flacourtia rukam*.

Recruitment responses were difficult to document. Typically a network of trails was quickly formed leading to different nest entrances. In one experiment in which the bait was unusually far from the nearest entrance (98 cm), the number of ants reaching the bait each minute climbed steadily to 45-50 per minute within 45 minutes. Because of the high density of foragers, ants began finding the recruitment trail and accumulating at the bait even before the recruiting worker had reached a nest entrance. Some of these ants originated from a cluster of workers on the ground. This greatly speeded the initial build-up of ants at the bait.

Recruiting *Proatta butteli* workers walked to the nearest nest entrance with their gasters touching the ground, at least intermittently. This implicated the gaster as the source of the trail pheromone. Single whole poison glands, Dufour's glands, and hindguts were dissected from workers and crushed on the tip of a sharpened applicator stick, then drawn on a 30 cm trail out from a nest entrance of a captive colony sample of 200 workers. The ants responded only to poison gland trails. The number of ants following the trail at least 10 cm during the first 5 min averaged 18.7 ± 8.8 for poison glands, 0.17 ± 0.41 for hindguts, and was consistently zero for Dufour's glands and controls ($\bar{X} \pm S.E.$; six replicates of each experiment).

EMIGRATIONS

Several emigrations were documented for captive colonies by allowing a colony's water source to dry. The ants used well-formed odor routes. Pupae tended to be transported first, and egg clusters and larvae last. For example, in one case an emigration was divided into three periods in such a way that equal numbers of brood (i.e., one-third of the total of 117 burdens) were carried during each period. The proportion of different immature stages carried (pupae : larvae : eggs) was 0.77 : 0.23 : 0.00 during both the initial third and middle third of the emigration, and 0.20 : 0.63 : 0.17 during the concluding third. Queens emigrate after most of the brood has been transferred.

Light-colored workers carried a higher proportion of egg clusters than did medium—or dark—colored workers ($p < 0.01$, test for differences between proportions, Zar 1984), but the proportions of small larvae, large larvae, and pupae carried did not vary significantly ($p > 0.05$) between worker color (age) classes. Other emigration experiments in which size classes were distinguished showed that small workers (head width 0.56 mm or less), regardless of their coloration, carried egg clusters more often than larger ants ($p < 0.05$). Adult transport usually involved darkly pigmented workers transporting light (callow) individuals.

DISCUSSION

Because of the absence of information on *Proatta*, there has been uncertainty as to whether these ants, like the attines (WEBER, 1972), might raise fungus for food. My observations indicate they do not. Captive ants did not feed on fungi, and even ignored pieces of fungus garden from an *Atta sexdens* colony dropped into their nest chambers.

Proatta, with its predatory behavior, polygyny, and lack of worker discrimination between colonies, seems to have little behavior in common with the attines. Yet *Proatta* accumulate prey remains and other inedible refuse within nest chambers, and fungus commonly grew on this refuse (at least in the nests of captive colonies). This suggests a hypothesis much like that of Von IHERING (1894): if the ancestor of the attines had a similar tendency to keep refuse in the nest, perhaps fungus gardening arose when the ants began to feed on fungus growing on the refuse (other hypotheses on the origin of gardening are reviewed by GARLING 1979). Indeed, most "primitive" attines (such as *Mycocepurus* and *Myrmicocrypta*) raise fungi on bits of insect and plant matter (see WILSON, 1971). GARLING (1979) proposed that the first attines fed on fungi growing on roots; this remains a possibility, but *Proatta* nests are much more often associated with dead roots than living rootlet systems.

A striking feature of the *Proatta* foraging strategy at least in my disturbed study sites, was the limited foraging area used by the ants, and the high density of foragers within much of this area. This strategy requires a dependable influx of arthropods and other food from surrounding regions. An important advantage of the foraging pattern is the rapid exploitation of any large food finds. Whenever an ant discovered an intractable food item, a nest entrance or a cluster of workers on the ground surface was usually close by. Clusters of ants represent an easily accessible reservoir of workers that could rapidly reach nearby food finds. The presence of clustered inactive foragers has also been reported for *Eurhopalothrix heliscata* (WILSON and BROWN, 1984), where they apparently serve a similar function. Small *Proatta* colonies, which lacked

the high forager densities and clusters of workers typical of larger colonies, did not locate baits as quickly, and were unable to catch large, active prey by group predation.

Group predation has arisen repeatedly in the ants. The most efficient group predators are the army ants (ecitonine and doryline ants; see GOTWALD, 1982), as well as the few other ant species that have been shown to group hunt (e.g. MOFFETT, 1984). Other predaceous ants forage solitarily, but have been shown to recruit workers from a distance to mobile prey (e.g., *Aphaenogaster* (= *Novomessor*): HÖLLDOBLER *et al.*, 1978; and *Oecophylla*: HÖLLDOBLER, 1983, and HÖLLDOBLER and WILSON, 1978). I found no evidence that recruitment plays a role during the initial phases in capturing large prey in *Proatta* (although recruitment trails can form after several workers have arrived at the prey). Rather, a *Proatta* worker finding a large arthropod seems to depend on other workers arriving at the same site by chance. This would appear to be a far less effective strategy than those involving recruitment. However, because of the high forager densities, assistance usually does show up within minutes.

ACKNOWLEDGMENTS. — I thank D.A. FLETCHER for assistance in the field, and S.S. LEE, D.H. MURPHY, and Y.P. THO for aid in course of research in Malaysia and Singapore, and W.L. BROWN, Jr., B. HÖLLDOBLER, E.O. WILSON and an anonymous reviewer for comments on the manuscript. The research was supported by grants 2397-81, 2588-82, and 3021-85 from the National Geographic Society, and grants from the National Academy of Sciences and Harvard University (the Richmond Fund).

References

- EMERY C., 1922. — Hymenoptera. Family Formicidae, subfamily Myrmicinae. In, P. Wytzman (ed.), *Genera Insectorum*, Fasc. 174, V. Verteneuil and L. Desmet, Brussels, 397 pp., 7 pl.
- FAGEN R.M., GOLDMAN R.N., 1977. — Behavioral catalogue analysis methods. *Anim. Behav.*, 25, 261-274.
- FOREL A., 1912. — Descriptions provisoires de genres, sous-genres et espèces de Formicides des Indes orientales. *Rev. Suisse Zool.*, 20, 761-774.
- GARLING L., 1979. — Origin of ant-fungus mutualism: a new hypothesis. *Biotropica*, 11, 284-291.
- GOTWALD W.H., 1982. — Army ants, pp. 157-254. In Hermann H.R. (Ed.), *Social Insects*, Vol. IV. Academic Press, New York.
- HÖLLDOBLER B., 1983. — Territorial behavior in the green tree ant (*Oecophylla smaragdina*). *Biotropica*, 15, 241-250.
- HÖLLDOBLER B., STANTON R.C., MARK H., 1978. — Recruitment and food-retrieving behavior in *Novomessor* (Formicidae, Hymenoptera). *Behav. Ecol. Sociobiol.*, 4, 163-181.
- HÖLLDOBLER B., WILSON E.O., 1978. — The multiple recruitment systems of the African weaver ant *Oecophylla longinoda* (Latreille) (Hymenoptera: Formicidae). *Behav. Ecol. Sociobiol.*, 3, 19-60.
- HÖLLDOBLER B., WILSON E.O., 1986. — Soil-binding pilosity and camouflage in ants of the tribes Basicerotini and Stegomyrmecini (Hymenoptera: Formicidae). *Zoomorphol.*, 106, 12-20.

- IHERING H. VON, 1894. — Die Ameisen von Rio Grande do Sul. *Berlin Entomol. Ztschrift*, 39, 321-446.
- MOFFETT M.W., 1984. — Swarm raiding in a myrmicine ant *Naturwissenschaften*, 71, 588-590.
- WEBER N.A., 1958. — Nomenclatural notes *Proatta* and *Atta* (Hym.: Formicidae). *Entomol. News*, 69, 7-13.
- WEBER N.A., 1972. — *Gardening ants, the Attines*. Memoir no. 92, American Philosophical Society, Philadelphia, 146 pp.
- WHEELER G.C., WHEELER J., 1985. — The larva of *Proatta* (Hymenoptera: Formicidae). *Psyche*, 92, 447-450.
- WILSON E.O., 1971. — *The Insect Societies*. Belknap Press of Harvard University Press, Cambridge, 548 pp.
- WILSON E.O., BROWN W.L., 1984. — Behavior of the cryptobiotic predaceous ant *Eurhopalothrix heliscata*, n.sp. (Hymenoptera: Formicidae: Basicerotini). *Insect. Soc.*, 31, 408-428.
- ZAR J.H., 1984. — *Biostatistical Analysis*. Prentice-Hall, New Jersey, 718 pp.
-