Articles

Mark W. Moffett

Division of Labor and Diet in the Extremely Polymorphic Ant *Pheidologeton diversus*

Pheidologeton diversus *shows the greatest worker size variation recorded for any ant: workers from the same nest vary a full tenfold in head width and over 500-fold in dry weight. This paper documents the complex division of labor in raiding, food harvesting, trail construction, and defensive behaviors associated with this polymorphism. Four physical castes are distinguished: minors, nonreplete medias (which aid minors in the construction of soil covers on trails, excavation, and food transport), nonreplete majors (which "tamp" trail covers and hoist trail obstructions with their heads), repletes (medias and majors with expanded crops, which normally stay in the nest). In addition, three temporal castes of minors occur (as well as wounded individuals); additional temporal castes will probably be discovered. Minor workers are both small and very numerous, and, being relatively expendable, attend to most tasks involving a high risk of mortality (such as pinning down prey). Many tasks (such as tearing up prey) are attended to by a broad range of worker sizes, with the size of the workers varying according to the characteristics of the object attended to. This behavioral flexibility on the part of* P. diversus *workers, along with the flexible foraging pattern in this species, apparently explains the success of* P. diversus *in exploiting diverse foods: common foods include small and large prey, many kinds of seeds (some collected directly from fruiting plants), and massive fruits and carcasses.*

Mark W. Moffett *(Museum of Comparative Zoology, Harvard University, Cambridge, MA 02138), a graduate of Beloit College, is a doctoral candidate researching the evolution of social behavior. He has spent much of the last 10 years traveling extensively in Central America, South America, and Asia in connection with research on various animal groups.*

Figure **1.** *Extremes in size variation among* Pheidologeton diversus *workers. The large major shown here probably has a dry weight 500 times that of each minor worker riding on its body. (~ × 17.5)*

Division of labor is one of the hallmarks of the ants. Within ant colonies labor is often divided between worker age- and size-classes (representing "temporal castes" and "physical castes," respectively). The extent to which physical caste systems are developed appears to be correlated with the complexity of social organization (Oster & Wilson 1978). This suggests that species with the most extreme forms of worker polymorphism could rank among the pinnacles of ant social evolution. Surprisingly, of about 300 ant genera (Snelling 1981) only *Atta, Eciton, Daceton,* and *Pheidologeton* include species with more than two physical castes (Oster & Wilson 1978); in these ants, workers are referred to as minors, medias, and majors on the basis of size. Division of labor has been studied in three genera from this select group (Franks 1985; Silva 1972; Wilson 1962, 1980), all of which are known for their intricate social architectures. This paper describes worker behavior in a species of the fourth genus, *Pheidologeton diversus,* and emphasizes division of labor during foraging. In connection with this, the remarkable diet of this species is considered in detail for the first time.

Mark W. Moffett

NATIONAL GEOGRAPHIC RESEARCH 3(3):282–304 (1987)

P. diversus is a member of the largest of the major taxonomic groups of ants, the subfamily Myrmicinae. *P. diversus* is widespread in tropical Asia (see Moffett 1986). The complexity of social organization in *Pheidologeton* has been borne out by studies of foraging in this species (Moffett 1984). The ants build stable, 5- to 100-m-long routes called trunk trails. Workers search for food in groups, and hence in this respect are convergent with army ants (Dorylinae and Ecitoninae). Columns of ants advance from the nest or out from a trail and then retreat; food is taken during the advance. Some of these "column raids" expand into fan-shaped "swarm raids" typically 2 to 3 m wide, sometimes containing tens of thousands of ants.

Methods

Data were collected in 1500 hours of field observations on *P. diversus* at both disturbed and undisturbed sites in southern Asia (India, Malaysia, Singapore, Thailand, Indonesia, and the Philippines). Polyethism (division of labor) studies centered on colony 65–82 at the Singapore Botanical Gardens, here referred to as the experimental colony.

The size (head width, a widely used measure of ant size) of all nonminors (medias plus majors) was estimated to the nearest 0.2 mm by visually comparing workers with a series of precisely measured ants glued to a card. Tests of the author's accuracy with this method showed that errors as large as 0.4 mm were possible for large majors, but it is clear that all tasks were performed by a much broader range of worker sizes than this. Size was estimated for workers that crossed a point on the trunk trail of the experimental colony over about 14 hours during a four-day period. The resulting sample of 2000 ants was used as an estimate of the relative frequency of different nonminor size classes outside the nest. At the same time and continuing for eight days afterward, nonminors engaging in 11 exterior activities were censused to produce polyethism curves. The relative abundance of minors and nonminors in selected exterior activities was compared with the proportion of ants on the trunk trail that were nonminors (Table 1).

Table 1. Percentage of *P. diversus* Workers Engaged in Various Tasks

Task	n	Nonminors (%)
1. Control sample (walking on trunk trail)	12512	1.81
2. Enter raid	1000	1.50
3. At raid front	350	0.29, $p < 0.05$
4. Attack prey	362	6.08, $p < 0.001$
5. Harvest from grass plants	446	8.07, $p < 0.001$
6. Drink sugar-water bait	500	6.40, $p < 0.001$
7. Drink vegetable-oil bait	378	4.76, $p < 0.001$
8. Gnaw prawn bait	292	3.42, $p < 0.05$
9. Carry solid-food burdens on trunk trail	1994	0.90, $p < 0.01$
10. Attack author's finger on trunk trail	352	0.85

Differences from control sample were evaluated using χ^2 test.

Worker Polymorphism

By at least one criterion — the range of worker sizes found in a colony — *P. diversus* is perhaps the most polymorphic of all ant species. Workers vary a full tenfold in head width (Figure 1), and the largest nonrepletes have dry weights over 500 times greater than the smallest. In comparison, the range in head widths only approaches fourfold in *Daceton armigerum* (Wilson 1962); fivefold in *Eciton burchelli* (Franks 1985, Silva 1972); and about eightfold (with a 100-fold range in dry weights) in *Atta cephalotes* (Wilson 1983; personal communication), to name only the most polymorphic species in each genus.

Worker samples from Singapore nests showed at least a trimodal size-frequency distribution. Minors formed a distinct physical caste. For example, in a sample of 7185 ants from one excavated nest, minors ranged from 0.56 to 0.68 mm in head width, with a gap in the frequency distribution separating the largest minor from the smallest media (head width, 1.14 mm). Nonminors formed 3.9% of the sample, but this probably was an overestimate (e.g., nonminors represented just 0.45% of workers in a more completely collected Thailand colony). The size distribution for nonminors in the Singapore colony is given in Figure 2 (see also Baroni Urbani & Kutter 1979). Peaks in this and other Singapore colony samples occurred at head widths of 1.4 to 1.8 mm and 2.8 to 3.2 mm; ants with head widths of 4.6 to 5.4 mm may represent another peak (as also suggested by samples from some other colonies). Ants with head widths of 2.6 mm or less will be referred to as media workers in the text; larger ants are majors.

Replete workers have grossly enlarged gasters due to considerable distention of the crop with an edible oil; they can readily be distinguished from other workers that have temporarily filled their much smaller crops to repletion after drinking liquids outside the nest. Replete castes occur in certain other ants (Wilson 1971), and their crop contents serve as a reserve food supply. *P. diversus* repletes occur in all media and major size classes (Figure 2), but are not found among minors.

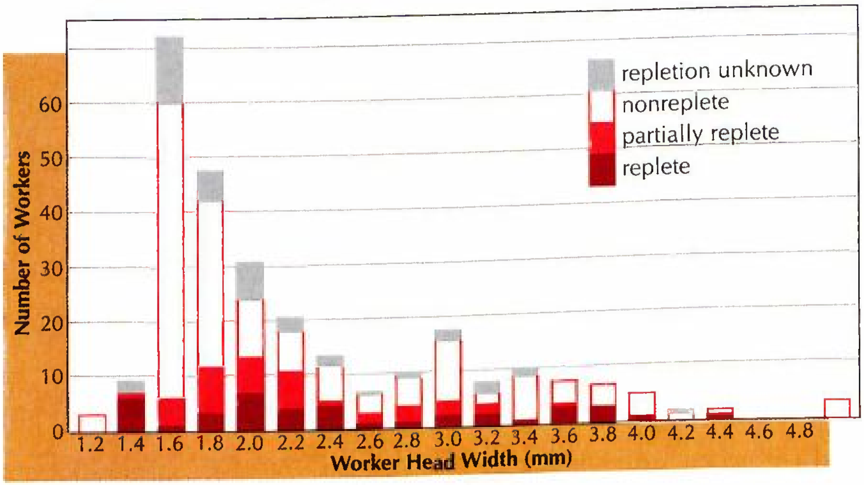
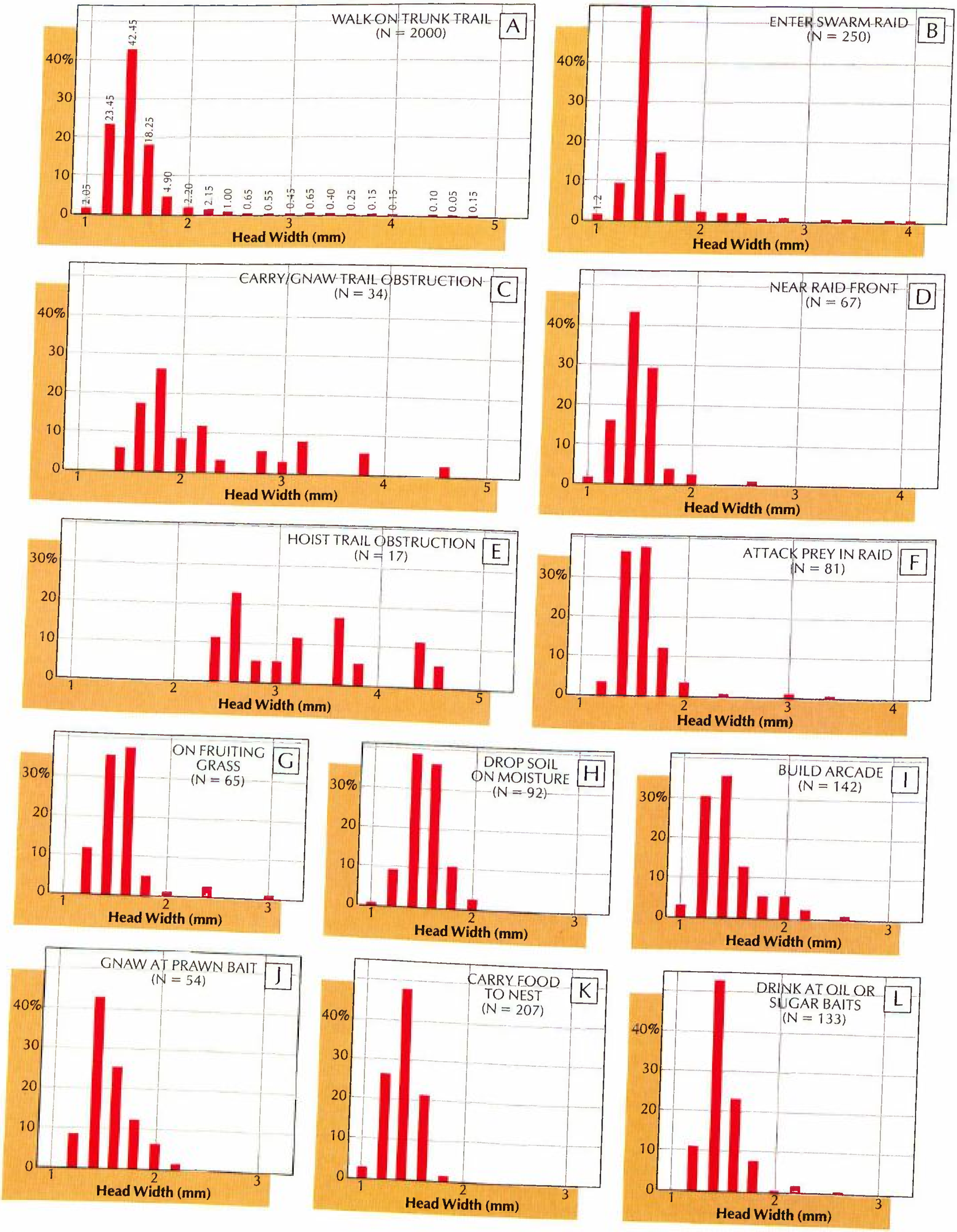


Figure **2.** *Nonminor worker size-distribution in* Pheidologeton diversus *colony no. 50–82, based on a sample of 278 nonminors. Repletes made up 46% of the ants that were collected with intact gasters; here they are categorized as fully replete or partially replete (those with moderately enlarged gasters).*

Worker Location — Trails and Raids

The size distribution of workers on trunk trails differs most notably from the distribution within the nest in the relative rarity of major workers (compare Figure 2 with Figure 3A) and the complete absence of replete workers. The proportion of nonminors on trails that are major workers can vary from about 0.5 to 4%.

P. diversus workers discover food in the course of raid advance (Moffett 1984). Data for ants entering swarm raids indicate that nonminors of all sizes are involved in raids (Figure 3B). The proportion of workers entering raids that are nonminors is likewise no different from that on the trunk trail (Table 1, no. 2). However, while a broad range of nonminor workers is also found within about 5 cm of the advancing raid front (Figure 3D), these ants are relatively rare at raid fronts compared with minor


WALK ON TRUNK TRAIL (N = 2000) A
2.05 23.45 42.45 18.25 4.90 2.20 2.15 1.00 0.65 0.55 0.45 0.65 0.40 0.25 0.15 0.15 0.10 0.05 0.15
40% 30 20 10 0
1 2 3 4 5
Head Width (mm)
ENTER SWARM RAID (N = 250) B
1.2
40% 30 20 10 0
1 2 3 4
Head Width (mm)
CARRY/GNAW TRAIL OBSTRUCTION (N = 34) C
40% 30 20 10 0
1 2 3 4 5
Head Width (mm)
NEAR RAID FRONT (N = 67) D
40% 30 20 10 0
1 2 3 4
Head Width (mm)
HOIST TRAIL OBSTRUCTION (N = 17) E
30% 20 10 0
1 2 3 4 5
Head Width (mm)
ATTACK PREY IN RAID (N = 81) F
30% 20 10 0
1 2 3 4
Head Width (mm)
ON FRUITING GRASS (N = 65) G
30% 20 10 0
1 2 3
Head Width (mm)
DROP SOIL ON MOISTURE (N = 92) H
30% 20 10 0
1 2 3
Head Width (mm)
BUILD ARCADE (N = 142) I
30% 20 10 0
1 2 3
Head Width (mm)
GNAW AT PRAWN BAIT (N = 54) J
40% 30 20 10 0
1 2 3
Head Width (mm)
CARRY FOOD TO NEST (N = 207) K
40% 30 20 10 0
1 2 3
Head Width (mm)
DRINK AT OIL OR SUGAR BAITS (N = 133) L
40% 30 20 10 0
1 2 3
Head Width (mm)

workers (Table 1, no. 3). Apparently many of the larger ants become involved in harvesting foods found farther back within the raid before they can advance to the raid front.

Harvesting Food

Overview of the Diet

A sample of 200 food burdens was collected from the trunk trail of the experimental colony by taking the first food item to be carried past a set point along the trail at the end of five- or 10-minute intervals. (Food was not sampled more often because taking food often evoked a defensive reaction, disrupting food traffic for one or more minutes.) Results indicate that while small items were most numerous, larger burdens formed a very significant part of the biomass collected (Figure 4). Large burdens were more important than these data indicate, since burdens with a dry weight exceeding 75 mg were completely lacking from this limited sample. Indeed, burdens of at least 200 mg, estimated to make up 0.1% of the items carried, could easily have accounted for a quarter of all food biomass. Some items (such as many prey) were dissected by the ants for transport, further biasing the sampled size distribution toward smaller foods than were actually collected at the raid front.

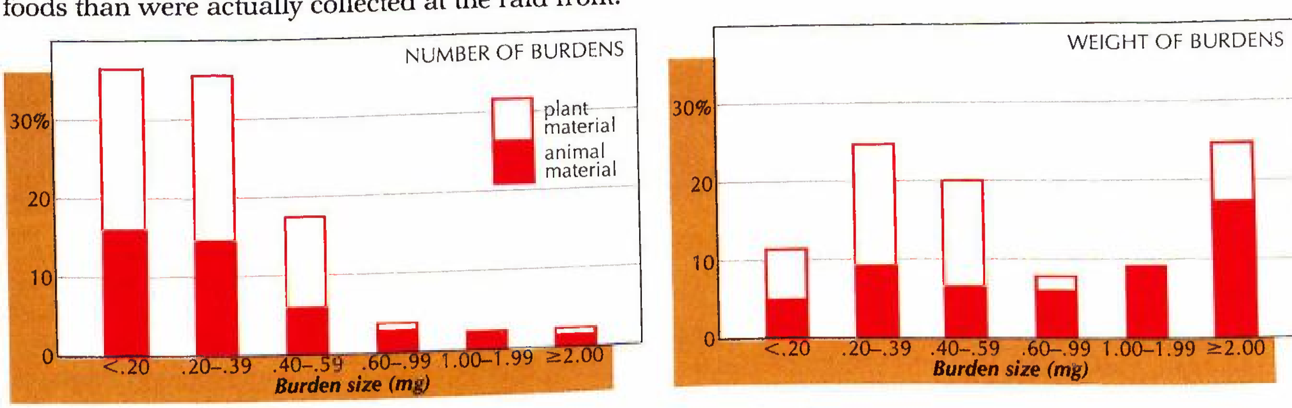


Figure **4.** *Proportions of food burdens in different size-classes, based on a random sample of 200 burdens carried to the nest of colony no. 65–82. For comparison, minors, which carry almost all burdens, have an average dry weight of 0.1 mg.*

In the experimental colony 43.5% of the items carried, and at least 60% of the total dry weight, was animal material. Samples taken from other Southeast Asian localities indicate that animal material can represent anywhere between 10% and 70% of burden weight. Middens usually consist mostly of plant material, and it is likely that a greater proportion of the animal matter collected is actually consumed.

This colony is estimated to have been taking in about 1800 items per hour or about 22 g (dry weight) of food a day; the rate probably can reach at least twice this. Clearly the ants are capable of harvesting far greater quantities of food when conditions permit: a 300-g pile of seeds from a canary food mix can be carried off within eight hours.

Crop contents represent additional food not sampled in these experiments. All ants will imbibe liquids from moist animal and vegetable sources. The amount of food transported in worker crops varies considerably, depending on the foods collected.

Predation

A broad spectrum of terrestrial invertebrates was captured live. Relative abundance of groups represented in food samples from the trunk trails of four Singapore colonies was typical for most localities: insects (30.5%), annelids (22.7%), gastropods (16.2%), isopods (6.4%), inver-

Figure **3.** *Polyethism curves for* Pheidologeton diversus *media and major workers: size-frequency distributions of nonminors engaged in various extranidal activities. Worker sizes estimated to nearest 0.2 mm. Sample sizes (N) are given for each task. The proportion of majors (head width ≥ 2.8 mm) differs significantly from the control sample (A) in graphs C, E, and K ($p < 0.05$, χ^2 test); in addition, majors participate in the tasks shown in H, I, J, and L less frequently than expected by chance.*

Mark W. Moffett

Figure 5. Prey attack in Pheidologeton diversus: ***left,*** *minor workers attempting to pin down a large termite soldier at the raid front (note that the soldier has killed two minors) (~×16);* ***right,*** *a major arrives and crushes the soldier's head (~ × 11).*

tebrate eggs of all kinds (6.2%), chilopods (4.8%), amphipods (3.1%), and arachnids (2.8%); the remaining 7.3% could not be identified or assigned to one of these groups (total, 457 items).

The author has records of *P. diversus* finding and killing representatives of 21 insect orders (including adult forms in all orders listed except Trichoptera): Collembola, Diplura, Thysanura, Ephemeroptera, Odonata, Dermaptera, Mantodea, Orthoptera, Blattodea, Isoptera, Plecoptera, Psocoptera, Zoraptera, Hemiptera, Homoptera, Diptera, Neuroptera, Coleoptera, Trichoptera, Lepidoptera, and Hymenoptera. Most common were the Orthoptera and Blattodea, and larvae and pupae of Diptera and Lepidoptera. Arachnid prey were usually free-roaming spiders such as lycosids, salticids, and mygalomorphs, as well as mites, scorpions, and spider eggs.

Vertebrates were rarely captured. While observing a swarm raid at night in India, frogs (Ranidae) came to a light and often jumped into the raid. One of these (snout-to-vent length, 3 cm) was killed after it became entangled in twigs within the raid. In Sulawesi ants were observed feeding on a frog almost as large, but whether they killed it is not known. On several occasions workers were seen transporting freshly killed geckos (snout-to-vent length, 1.5 to 2.5 cm). Lizard eggs were also taken.

Prey Selection

The prey sample data suggest that workers attack virtually anything within their reach. Observations of prey capture generally support this view. Sometimes workers are kept at bay by invertebrates with chemical defenses (e.g., some Hemiptera, Coleoptera, and Diplopoda, which nonetheless are occasionally captured). Also, ant workers are seldom

Mark W. Moffett

killed during raids. Termite foragers are sometimes taken in numbers, yet nasutes and other soldiers can deter attacks (e.g., Forel 1921–1923). However, intact social insect nests are never raided for booty.

Immobility provides no protection from attack (although active quarry are attacked with increased vigor), in contrast to prey defenses against ecitonine army ants (Schneirla 1971). A potential victim has the best chance of surviving if it quickly rushes out of the raid, since the ants will follow prey only a few centimeters beyond current raid borders. Escape is more likely for column raids than swarm raids because prey can more easily extricate themselves from the smaller raided area. Thus column raids seldom take agile prey like crickets and roaches.

Even in swarm raids the majority of invertebrates avoid capture. For example, roaches and centipedes often rush ahead of the ants each time a raid front reaches them. These insects can be driven ahead of a swarm raid for an hour or longer, before (in some cases) they are eventually captured. Prey that run, leap, or fly greater distances after a disturbance are more likely to escape capture initially and completely avoid the path of the raid thereafter. The most vulnerable prey are slow-moving snails, earthworms, and insect larvae.

Prey Capture

Prey about as large as a minor worker (notably small mites and collembola) can be captured by single minors. Larger prey are invariably taken by groups of workers acting in concert. For example, hundreds of workers can successfully bring down scolopendromorph centipedes or *Pheretima* earthworms as long as 10 cm, even though these prey thrash about wildly during capture.

Mark W. Moffett

Figure 6. Workers tear young from the back of a mother scorpion they have pinned to the ground. (~ × 11)

Agile minor workers rush toward quarry at the raid front. Prey that either move slowly or blunder deeper into the raided area are soon covered with these ants, which pile on until (if successful) their victims are pinned to the ground (Figure 5, *left*). Medias and majors — generally too slow and clumsy to participate in bringing down prey — then reach the victim and bite it repeatedly, often while moving up and down its body (Figures 5, *right* & 6). The ants are particularly attracted to mobile parts of the prey, so that the prey's legs (and other appendages) are soon torn or chopped off. Even geckos and large centipedes often have every limb removed. With their limbs gone most prey are rendered immobile and can be transported out of the raid with ease.

The majority of ant species either kill or paralyze their prey (Maschwitz et al. 1979). However, *P. diversus* workers do not sting, and their prey are incapacitated entirely by damage inflicted with the mandibles. As a result many large or hard-bodied prey remain alive following capture. For example, large earthworms sometimes struggle violently while being carried by worker groups. Also, most cockroach, cricket, and centipede booty continue to show mouthpart activity for one or more days after being removed from trails during transport to the nest.

Workers of all sizes aid in prey dismemberment (Figure 3F), but nonminors are disproportionately abundant (Table 1, no. 4). Small prey are usually handled with about equal effectiveness by either medias or majors. In contrast, a range of worker sizes appears to be needed to handle most large prey: majors are more successful at removing massive limbs and crushing the trunks of large prey, while medias and minors reach into tight corners and gnaw off smaller or less accessible limbs. Given that majors are rare, this difference in capability suggests that majors

Mark W. Moffett

Figure 7. A media worker of Pheidologeton diversus *extracts a seed from a fruiting grass stalk.* (~ × 16)

should selectively attack larger prey, while medias should not be selective. Yet all ants attack prey irrespective of its size. Nonetheless majors tend to be relatively common at large prey, since the greater time required to dispatch large prey allows majors to accumulate at the prey over a longer period. In contrast, small prey are often subdued by medias before larger workers arrive.

Harvesting Seeds

P. diversus workers collected a variety of seeds, which formed the bulk of the plant material in their diet. For example, within a 0.2-ha study site in the Philippines, Oquias (1982) identified seeds of 29 grassland and secondary forest species from nests and trails of *P. diversus.* These included 29 genera in three monocot and 10 dicot families. However, seeds were not collected indiscriminately. Oquias (1982) found that although aguingay *(Rottboellia exaltata)* seeds were consistently available throughout the rainy season, *P. diversus* switched to other seed species when they became available. Colonies observed in the present study harvested massive seed baits vigorously at first, but after repeated feedings the ants became much slower at removing seeds and they often abandoned the baits.

P. diversus take many seeds from the ground where they fall, but they collect others directly from plants. Commonly harvested Singapore plants include the grasses *Axonopus compressus* and *Paspalum conjugatum* and the sedge *Cyperus kyllingia.* The ants climb up stalks of fruiting grass but rarely ascend adjacent vegetation to the same height; this suggests that the ants recognize these food sources. Minors are the first ants to climb the stalks; but as time passes, medias and small majors

(Figure 3G) join the minors and eventually become disproportionately abundant (Table 1, no. 5). Minors gnaw and pull on seeds but are inefficient at freeing them from the stalks, while nonminors usually succeed in pulling out seeds (or rarely chopping free sections of the spikelet) within a few seconds (Figure 7). Often minor workers intercept medias before the larger ants can leave the stalks with the harvested seeds; as a result medias often remain on stalks for long periods (10 minutes or more) to pull out seeds, which the minors carry away.

Workers of all sizes can mill seeds (i.e., chop open seeds so that the contents can be eaten). For example, in India, workers commonly removed seeds from the composite *Ageratum conyzoides*. Some seeds were carried down the stalks, but most fell from the plants. Groups of workers of all sizes gathered to mill the fallen seeds on the ground below the plants. In contrast, in the Malay Peninsula, seeds were almost invariably milled only after being carried to the nest. However, some seeds, thrown out into the midden entire, can germinate (Oquias 1982). Minor workers can mill only small, delicate seeds; presumably only large majors successfully mill the toughest seeds.

Harvesting Bulky Foods

Massive items such as carcasses and fruits can be harvested over long periods of time. Palm nuts, bananas, figs, potatoes, and cacao pods are among the many items consumed. Minors and medias deposit soil on large moist foods (Figure 3H) and often build soil covers over them (much as described for the construction of soil covers over trails). Covers can be as much as 27 cm in diameter and weigh several hundred grams. Often covers consist of two layers, an inner shell next to the food (which the ants apparently climb on as scaffolding to reach moist food) and an outer shell separated from the first by a narrow gap (which protects the ants from disturbance). Fruits and the softer tissue from corpses can be torn up for transport to the nest, but workers often drink from moist foods on the spot.

Large amounts of bait in the form of sugar water, vegetable cooking oil, and fresh prawns were placed near the trunk trail of the experimental colony to simulate food bonanzas. These attracted a disproportionate number of nonminors (Table 1, no. 6–8), including a broad range of medias that drank from them or (in the case of the prawns) aided in tearing them apart (Figure 3J, L).

Mark W. Moffett

Figure 8. Pheidologeton diversus *workers transport an earthworm back to the nest entire. (~ × 0.8)*

The ants sometimes eat the outer, living layers of tree bark (as first reported by Pham [1924]) or bamboo shoots. When they feed repeatedly on certain trees, the surface of the bark can be scarred. Minors extract bits of these plant materials and rotate them between their mouthparts and foretarsi. Since the pieces shrink during this process the ants are probably extracting their liquid contents. Nonminors of all sizes aid at tearing the plant surfaces. Such plant tissues are usually harvested during periods when relatively little other food is taken. Workers abandon bark when meat or a pile of seeds is provided.

Other Foods

Occasionally minor workers were found tending scale insects located near trunk trails; one sample of Malaysian scales was identified as *Ultracoelostoma* sp. (Margarodidae). Pham (1924) reported from Vietnam that *P. diversus* can tend aphids.

Workers rarely transported bird excrement to the nest. Mammal dung was raided for maggots but was probably not eaten.

The ants sometimes carried parts of small flowers (sepals, petals, and

Mark W. Moffett

Figure **9.** *A major worker hoists an obstruction from a trail (~ × 11). See page 270 for a rare instance of a media hoisting an obstruction by using its forelegs instead of its head.*

pistils) to the nest, and flower parts showed up on middens apparently after the ants gnawed on them.

Food Transport

The percentage of nest-bound ants that transport booty varies from about 1 to 80% (most commonly 10 to 40%), and can fluctuate erratically even in the course of a day (additional food is carried in workers' crops). Medias aid in carrying solid food (Table 1, no. 9); majors very rarely transport burdens (as noted by Wroughton [1892]) (Figure 3K). Items smaller than a minor worker are usually carried by single minors, while bulkier items are carried by groups. The percentage of burdens carried by groups is commonly 5 to 10%, while often about 25% of the ants carrying food participate in group transport (both figures vary widely). Over 100 ants can work together to transport massive booty (Figure 8). Often, besides the ants that actually lift the food, ants (minors) are perched on top of the food. Nonminors never ride on food.

Trunk Trail Construction

Most booty is quickly and efficiently transported from the raid front to the nest, a process aided greatly by the trunk trails. Except for the minority of raids that originate directly from a nest entrance, all food is carried down the basal column of a raid to a trunk trail.

Trunk trails are characterized by a well-developed physical structure, including a 1- to 3-cm-wide, smooth surface bordered with walls of soil or with a complete soil cover. Workers of all sizes participate in the construction and maintenance of trails. Trail building is most intense during moist periods, when large numbers of ants are involved. During dry spells, construction all but ceases, even though ants continue to move along the trails. Under such conditions trails become dilapidated, and debris accumulates on the trail's surface.

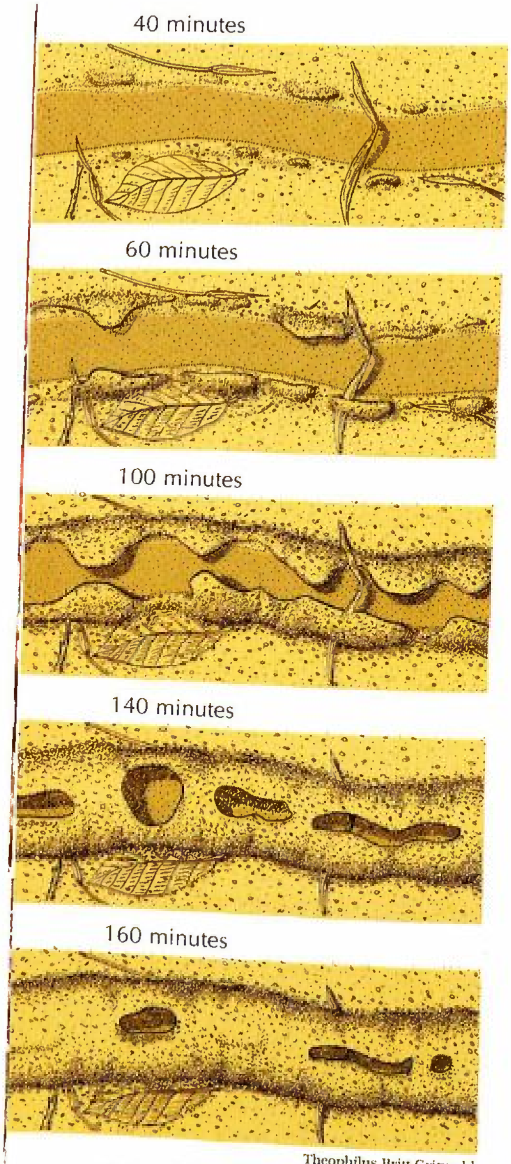


*Figure **10.** Arcade construction. Dark brown indicates the path taken by ants moving along the trail. Minutes are time elapsed since the old cover was torn away by the author. (Based on a series of photographs.)*

Clearing Trails

Medias and majors are constantly involved in trail maintenance. Yet they are particularly active during the initial stages of trunk-trail construction, when traffic flow is frequently impeded by obstructions. Objects lying on a trail are carried or dragged in the mandibles of these larger ants, which drop them at trail borders (very rarely groups of minors carry away objects of similar size). Medias and majors also stop for as long as several minutes to gnaw at obstructions that cannot be moved, such as plants growing in the trail's path, or rootlets crossing the trail surface. Eventually such objects are removed (or at least made level with the surrounding ground) (Figure 3C).

both, Mark W. Moffett

*Figure **11.** Trunk trails: **top,** a trail on the ground surface (~ × 0.3); **bottom,** a sunken trail with periodic exits to the surface (~ × 0.3).*

Sometimes a stick or leaf projecting over a trail lies too near the trail's surface to permit ready passage of booty. Media or major workers passing beneath such an object often raise themselves high on their legs, heaving the object upward with a quick shove of the head (Figure 9). The object usually settles into a position farther from the ground than before, or is knocked partially or entirely off the trail. This "hoisting" behavior is usually accomplished by majors (Figure 3E), and possibly

both, Mark W. Moffett

Figure **12.** *Fighting* Pheidologeton diversus: ***left,*** *area of intense conspecific fighting (~ × 5.5);* ***right,*** *minor at the right is pulling on the neck of one of the original combatants (~ × 15).*

represents the most important role played by large majors (head width > 4.0 mm) outside the nest. Such majors are normally rare on trails (Figure 3A), but it is perhaps only necessary for them to come out as seldom as once every few hours to keep a trail clear.

Covered Ways and Sunken Trails

Minors and medias remove loose debris from trail surfaces and further smooth the trail by prying bits of soil from the ground (Figure 3I). (The same castes are similarly involved in nest excavation.) The soil — as well as sand, leaf fragments, and other debris — is positioned along trail borders. Most of this material originates from the adjacent trail surface, but workers sometimes deposit material collected at distant points along a trail or out from the sides of the trail. In other cases soil is taken from short, blind-ended tunnels excavated by the ants along the trail. These are "mining operations," in that the ants appear to use the tunnels solely as a source of building materials.

The ants preferentially deposit soil and debris onto soil clumps laid down previously. Uninterrupted walls form at trail borders as soil accumulates. When the ground is not too dry these walls often rise and then arch toward each other until a complete cover is formed (Figure 10). The ants are apparently not orienting their building activities solely with respect to the far wall: a wall will continue to arch over a trail even when the opposite wall is never allowed to develop. Vegetation and leaf litter serve as structural supports for cover construction and thus generally aid in the building process.

Medias and majors sometimes push their heads upward against the cover of a trunk trail, which could explain why the interior surface of arcades is much smoother than the exterior. This tamping behavior is most frequently directed at low or sagging covers. Indeed, both in hoisting obstructions and in tamping arcades the workers appear to be responding to pressure against their heads as they pass through cramped spaces. Tamping probably raises sagging covers and conceivably often increases the structural integrity of arcades by binding the soil particles closer together, even though covers can break during this activity.

Tamping is apparently the behavior observed by Rothney (1889), which led Bingham (1903:162) to suggest that majors "may be the trowels and rammers of the Ants' Public Works Department."

The walls and covers are fragile and must be maintained continuously. They are destroyed by rain but are quickly reconstructed afterward. When the ground becomes dry the construction and maintenance of arcades ceases because the bits of soil must be moist to adhere; typically the soil edifices crumble and eventually disappear.

Some trunk trails sink relative to the surrounding ground. This occurs most often in the first few meters of trail out from the nest, and is apparently due to workers' continually removing soil from the trail surface. Some trails become completely submerged, with thick soil roofs lying flush with the ground and periodic exits to the surface (Figure 11). Such trails are relatively impervious to rain and other disturbances.

Defensive Behaviors

Conspecific Fighting

P. diversus territories are spatiotemporal. Conspecific fights break out when a raid front collides with either a raid or a trail of another colony. Small clusters of fighting workers develop, and usually raids soon drain away from the area of conflict. However, the ants do not retreat if food (seeds, for example) is at stake; instead aggression intensifies, and a band of fighting workers demarcates the boundary between the areas controlled by the different colonies. Fighting ceases after one colony drives the other from the site or when the food is depleted. Outbreaks of fighting occur frequently wherever a trail of one colony crosses that of another (via vegetation or the soil cover of the lower trail).

During fights minor workers from different colonies examine each other, often for periods of minutes. Combat begins when two ants grapple (usually interlocking mandibles). Ants often remain locked together for five to 15 minutes or more before disengaging and maneuvering for position again. Most injuries occur after other minors join a fighting pair, pulling on the limbs, neck, or waist of the combatants (Figure 12). Fighting ants often tuck their gasters partially beneath their trunks, making it difficult for other ants to grasp them at the waist. The gasters are waved frequently in apparent stridulation. Workers killed in fights show a variety of wounds (commonly missing appendages), although in some there is little or no sign of external damage.

Medias and majors do not take an active role in conspecific fighting. They are not common in areas of active combat, and usually do not interact with other ants when they enter such areas. The author never found dead media and major workers among the ant corpses following a fight. However, during intense fights at seed bait there were three instances of nonminors' (head widths, 1.4, 3.4, and 4.4 mm) curling into a ball as minor workers pulled on them; the larger ants did not try to defend themselves, but in each case successfully escaped after several attempts.

The slowly unfolding combat behavior characteristic of minor workers contrasts sharply with their behavior during prey capture, when the minors are quick to pin down victims, and media and major workers aid in tearing the prey apart. Most combatants survive (although hundreds of dead can accumulate where fighting continues for days). However, the colony that recruits the largest army to a contested food bait can immobilize its opponent by engaging opponent workers in fights, and it can thereby eventually drive the other colony off the food.

Figure **13.** *Nonminors* (Pheidologeton diversus) *attacking a* Diacamma rugosum *worker that blundered onto a trail.* (~ × 11)

Other Defensive Behaviors

Trail systems of *P. diversus* cut through the home ranges of numerous ant colonies. Loose rows of workers form along trail borders where disturbances from other ant species are frequent. They jab at approaching intruders, keeping them at bay but rarely assaulting them. Most guard ants are minors, but both medias and majors also show this behavior. Often guards are wounded or exceptionally dark-colored (old).

Workers attack when an ant (or other intruder) actually blunders into the midst of the trail. In this case food traffic is often disrupted, since some or all of the ants carrying food usually reverse direction upon reaching the disturbed area. Minors rush at the intruder, which in most cases escapes them by running from the trail. However, if the workers succeed in pinning their adversary to the ground, medias and majors kill it with repeated crushing blows (Figure 13) (illustrated fully in Moffett 1986). These activities resemble prey capture at raid fronts, except that ant corpses are seldom carried to the nest. Common casualties include *Diacamma* and *Odontoponera* workers.

Trail disturbances of a larger scale (for instance stepping on a trail) can set off reactions of even greater intensity. Workers of all sizes attack the source of the disturbance (Table 1, no. 10). The flow of food to the nest completely ceases, while unburdened ants of all sizes rush out from the trail as far as 20 to 60 cm from the point of disturbance. Most ants retreat back to the trail within a few minutes, although occasionally major workers wander away from trails by themselves for as long as 20 minutes. After repeated disturbances a number of majors and large medias are commonly found roaming near a trail. These workers can bite humans. They also drive ants and other insects away from the trail, but are generally too clumsy to successfully attack them while on their own. Anything they do kill is abandoned. They likewise reject any other food, which supports the view that their function is purely defensive.

During the departure of alates, large numbers of nonminors surround the enlarged nest entrances. Otherwise defensive contingents of ants are not present at entrances. However, pounding on the ground above a nest quickly provokes the exodus of numerous aggressive ants, often including repletes when nests are located very close to the ground surface. The proportions of different ant sizes responding to nest disturbances appear to correspond closely to those for the colony as a whole.

Defensive reactions to humans at nests or along trails contrast sharply with the behavior during a raid. Stepping into a raided area often causes a raid to retreat. Documenting a raid's progress can be difficult because of the likelihood of at some point disturbing the raiding ants.

Function of Riders on Food

Minor workers riding on transported booty apparently seldom gnaw on the food. One possible function they serve is to defend booty from *Bengalia* flies (Calliphoridae), which steal food from ants (Bequaert 1922, Maschwitz & Schönegge 1980). Species of *Bengalia* were observed along trails of *P. diversus* in Malaysia, India, and the Philippines during this study; and Jacobson (1910) recorded this in Java. Many attempts at thievery were foiled by riders. In three cases in Malaysia, riders climbed onto the fly before it grasped the food; the fly then hovered, buzzing loudly, in an attempt to force the ants off. Twice one fly stole booty, but instantly dropped it away from the trail. The ants on the booty rushed away, leaving the booty unprotected. The fly (which had alighted on a nearby plant) then flew off with its food.

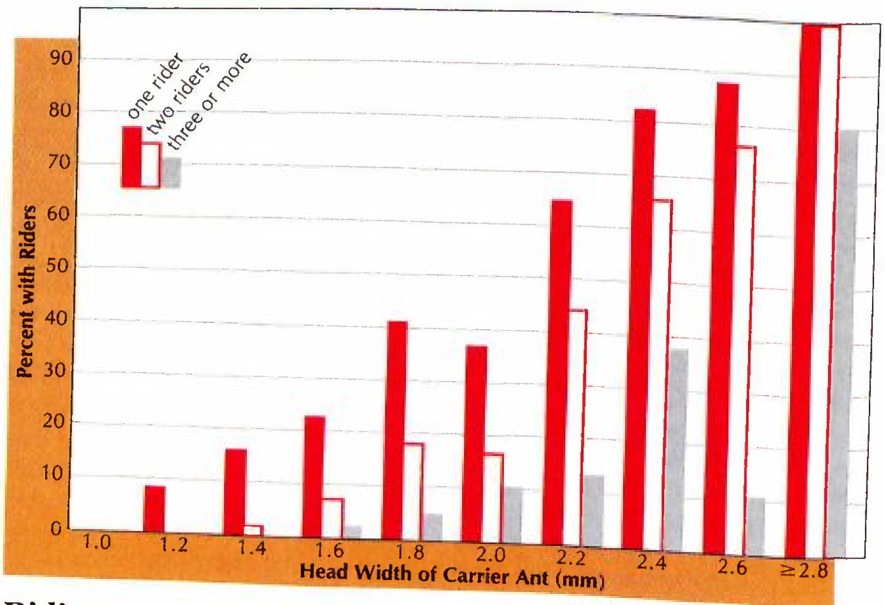


Figure **14.** *Minor workers riding nonminors. The proportion of medias and majors of different sizes carrying given numbers of minors is based on a sample of 2000 nonminors on the trunk trail of the experimental colony.*

Riding Media and Major Workers

Minors ride on top of many of the media and major workers outside the nest. The number of riders is correlated with carrier size (Figure 14), and can reach 20 or more for large majors (Figure 15). Oddly, medias (head width < 2.0 mm) more often have riders when returning to the nest than when leaving the nest ($p < 0.001$, χ^2 test), while the reverse may be true for larger ants (difference not significant with data in Figure 14). Minors climb off (or are knocked from) carriers that run very quick-

Mark W. Moffett

Figure **15.** Pheidologeton diversus *major worker laden with minor worker riders. (~ × 11)*

ly (e.g., in response to a disturbance), or that squeeze through cramped spaces. Riders can accumulate on carriers when the larger ants are immobile (e.g., while a major gnaws on a twig impeding a trail). Specific riders have been observed for up to 20 minutes on the same ant, and probably most riders stay with their carrier for long periods of time.

Riders position themselves with their heads near the body surface and mandibles open, and often with their hind legs flailing in the air. They apparently seldom groom the carrier ant. This is true even for soiled majors, which also have no more riders on average than do relatively clean majors. Riders show no response when their carrier is disturbed by being poked with a stick. However, when riders are disturbed directly they rush off the carrier or attempt to bite the stick.

Division of Labor

Midden Work

Most workers on middens have highly contracted (nonreplete) gasters and are wounded, or are very darkly pigmented (indicating they are older individuals), or both. Both minors and medias carry out the refuse, but majors are sometimes also found on middens.

Division Within the Minor Worker Caste

To document any division of labor within the minor worker caste, samples of minors were collected from the experimental colony while they participated in a number of extranidal activities; a sample of workers leaving the nest served as the control. The results are presented in Table 2. Minors in most behavioral categories more frequently had replete crops than did those leaving the nest. In at least the case of minor workers there was no apparent division of labor between workers returning to the nest with solid food and those carrying liquids (in replete crops), as documented by Gotwald (1974) for *Anomma* army ants. Minors with a slightly lighter pigmentation (presumably relatively young ants) formed about 4% of the minor population outside the nest and were not exceptionally frequent in any of the behavioral categories (Table 2: invariably $p > 0.01$). However, light minors were more often replete than others ($p < 0.01$, χ^2 test; data combined from all samples except drinking from oil or honey baits).

Table 2. Size, Repletion, and Color Differences Between *P. diversus* Minor Workers Engaged in Different Tasks

Task	n	Head Width (mm × 100) ($\bar{x} \pm$ SD)	Replete (%)	Light (%)
1. Control sample (leaving nest)	112	63.1 ± 2.1	6.3	3.6
2. Walk to nest unburdened	52	62.7 ± 2.1	42.3, $p < 0.001$	13.5, $p < 0.05$
3. Solitary food transport	50	61.6 ± 2.0, $p < 0.001$	40.0, $p < 0.001$	4.0
4. Group transport of food	50	61.8 ± 2.2, $p < 0.001$	28.0, $p < 0.001$	2.0
5. Ride food carried by one to four minors	54	61.3 ± 2.2, $p < 0.001$	18.5, $p < 0.01$	5.9
6. Ride food carried by ≥ 10 minors	72	62.5 ± 2.5	18.1, $p < 0.05$	5.4
7. Ride worker away from nest	32	62.1 ± 2.8, $p < 0.05$	28.1, $p < 0.001$	6.3
8. Ride worker toward nest	56	61.8 ± 2.0, $p < 0.001$	20.0, $p < 0.01$	1.8
9. Carry soil	55	62.5 ± 1.7, $p < 0.05$	3.6	12.3, $p < 0.05$
10. Attack author's finger on trail	50	63.1 ± 2.0	2.0	8.0
11. Attack ant on trail	36	62.3 ± 2.0, $p < 0.05$	25.0, $p < 0.01$	0.0
12. Drink sugar-water bait	60	61.5 ± 1.9, $p < 0.001$	93.3, $p < 0.001$	6.7
13. Drink vegetable-oil bait	60	61.5 ± 2.0, $p < 0.001$	90.0, $p < 0.001$	11.7
14. Gnaw prawn bait	60	61.6 ± 2.0, $p < 0.001$	31.6, $p < 0.001$	6.7
15. Put soil on sugar-water bait	40	62.2 ± 2.3, $p < 0.05$	62.5, $p < 0.01$	7.5
16. Put soil on vegetable-oil bait	32	62.6 ± 2.1	34.4, $p < 0.01$	0.0
17. Attack large prey	34	61.4 ± 1.7, $p < 0.001$	23.5, $p < 0.01$	0.0
18. Harvest grass seeds	45	61.6 ± 1.8, $p < 0.001$	15.9	4.4
19. At raid front	44	62.5 ± 2.1	22.7, $p < 0.01$	2.3
20. Guard trail	32	62.6 ± 2.4	0.0	0.0
21. Refuse midden	42	62.2 ± 1.9, $p < 0.05$	0.0	0.0

Differences from control sample were evaluated using z-statistic or χ^2 tests.

Minors vary little in size: head widths ranged from 0.56 to 0.69 mm in a sample of 1200 minors from the experimental colony. Yet the mean sizes of minors engaged in a variety of tasks did differ from the control sample (Table 2). In many cases this could be attributable to competition for space: smaller workers may have less trouble insinuating themselves at food or on majors. This would explain, for example, why minors riding on small burdens were smaller on average than those on large burdens ($p < 0.01$, comparing tasks 5 and 6 in Table 2). However, it is unclear why smaller minors predominated among the ants carrying food unassisted or minors harvesting grass seeds.

Discussion

Division of Labor

This research has confirmed that a very complex division of labor a - companies the extreme worker polymorphism of *P. diversus*. Polyethism occurs in all stages of foraging and food harvesting, in construction activities and defensive interactions, and during within-nest activities.

Four physical castes can be distinguished among *P. diversus* workers based on task performance: minors (head widths < 0.8 mm: conspecific fighting, pinning down prey); nonreplete medias (head widths 1.0 to 2.6 mm: food carrying, excavating, building arcades — roles shared with minors); nonreplete majors (head widths > 2.6 mm: hoisting obstructions and "tamping" soil covers on trails); and repletes (nonminors serving as food reservoirs). In addition, there are three temporal castes, at least for minor workers. Callows (very young workers) stay inside nests, and at least minor worker-callows aid in tending brood. Also, exceptionally dark (presumably old) minor and media workers (as well as wounded individuals of these sizes) are unusually common among the ants on middens and those that "guard" trails.

Media and (especially) major workers generally specialize in Herculean labors that smaller ants could not possibly perform. However, unlike species of *Atta* (Wilson 1980), workers cannot be divided into numerous narrow size-categories on the basis of tasks they always perform (except for certain roles specific to the minor worker caste). For example, medias and majors of all sizes dismember prey or dissect large fruits. Yet even here a form of polyethism does exist. Larger ants more successfully attack less tractable parts of food, such as the tougher fibers of fruit or more massive prey limbs, while minors and medias reach areas not accessible to ants larger than themselves. Similarly, tough seeds most likely are milled only by majors, and only majors successfully remove the bulkiest obstructions on the trail. In each case there is a correlation between some characteristic of a given task and the size of the workers that perform it; these then can be called "flexible tasks" (Wilson 1980). Presumably the varied diet of *P. diversus* has set limits on the development of specialized castes.

Minor workers carry out most tasks that involve a high risk of mortality. Thus only minors participate in conspecific fights, and usually only minors pile onto struggling prey in raids (or onto intruders on trails) and pin them to the ground. Nonminors generally arrive at prey only after it is secure. Minors, most likely, being both extremely numerous and presumably very cheap to replace, represent a "disposable caste" (Porter & Jorgensen 1981), so that high-risk tasks can be carried out with minimal cost to the colony. However, nonminor workers (and even repletes) commonly become involved in more dangerous defensive activities when the stakes are high; for instance, they are commonly at the scene during severe disturbances to the nest or trails.

Early naturalists have often noted the minor workers that ride on the medias and majors of *P. diversus* (e.g., Bingham 1903, Pham 1924). A similar behavior occurs in some *Atta* species, where minors ride on the leaf burdens carried by larger ants: these "parasol ants" appear to defend their carriers from parasitic flies (Eibl-Eibesfeldt & Eibl-Eibesfeldt 1967). Similarly, *diversus* minors riding on food burdens can defend the food from thieving *Bengalia* flies. However, *Bengalia* flies apparently distinguish food items from ants and so never attack media or major workers. Still, riders on these workers could have a defensive function, since on rare occasions a tiny flying insect (possibly a moth or fly) has been observed to alight on majors without rider ants. Whether this was a parasite is not known. Riding on nonminors could also represent a net energy savings to the colony, because the cost of transport declines with increasing size in ants (Jensen & Holm-Jensen 1980).

A conspicuous feature of *P. diversus* behavior is the intensity of activities relating to trunk-trail construction and maintenance, and the polyethism associated with these activities. The value of medias and (especially) majors in clearing trails of large obstructions is obvious from the traffic jams that result when obstructions are not removed. The significance of cover construction on trails is less apparent. In some ants, such as species of *Anomma* (Gotwald 1982), covered trails are thought to protect workers from desiccation. However, the covers of *diversus* trails break apart during dry weather (as in *Anomma;* Cohic 1948), even though the ants continue to forage on the surface. The investment made by *diversus* ants in arcade construction is probably paid off largely by protection from disturbance. Covered trails do not attract *Bengalia* flies. Also, disturbances from other insects are reduced when trails are covered. Ants of *P. diversus* or other species can cross trunk trails where covers occur, usually without disturbing the activity on the trail.

Convergences with Army Ants

One similarity between *P. diversus* and driver ants (tribe Dorylini) is the inability to sting (Gotwald 1978; Kugler 1978, 1979). Loss of sting function is probably a result of total dependence on coordinated group attacks in the capture of difficult prey. Worker mandibles among the Dorylini are adapted for efficiently cutting and piercing prey during such attacks. In contrast, the mandibles of *diversus* minors are little changed from the generalized form typical of *Solenopsis* and many other myrmicine groups. Such mandibles are adequate for pinning prey to the ground but are incapable of inflicting serious damage to most prey. *P. diversus* relies primarily on the massive mandibles of nonminors to crush and tear prey. These mandibles function equally well in other roles such as milling seeds, and indeed are very similar to the mandibles of specialized miller castes in certain myrmicine ants such as *Pheidole.*

There are some other behaviors that are convergent with those of army ants. For example, along trails both the defensive "guard ants" and the soil arcades have strikingly similar counterparts in *Anomma* (Gotwald 1982:fig. 12). Generally, to the extent that *P. diversus* shows army ant characteristics, this species approximates the Old World driver ants (*Anomma* spp.) more closely than the New World army ants (Ecitoninae), which have been the focus of most of the army ant research. However, other *diversus* characteristics, such as seed milling and the replete caste, are at variance with the behaviors of army ants and clearly reveal this species' myrmicine affinities.

Raiding Behavior and Diet Breadth

The diet of swarm-raiding army ants tends to be broader than that of column-raiding ants. Indeed there are records of certain swarm-raiding species (especially *Anomma*) that collect many foods other than prey (Gotwald 1982). *P. diversus* (which raids both in swarms and columns) is likewise a tropic generalist. This species could in fact represent a more extreme generalist than any doryline or ecitonine species, at least to the extent that a greater variety of food categories (such as seeds, prey, and massive or bulky food items like fruit) form a significant portion of the diet and they are regularly included among the booty. For example, no plant material was found by Gotwald (1974) among the 1357 pieces of booty that he collected from 19 colonies of three *Anomma* species, while a similarly sized sample of *P. diversus* booty would usually contain a diversity of vegetable matter.

Furthermore, the specialized behaviors shown by *P. diversus* workers in harvesting seeds, which they often collect directly from fruiting plants, clearly demonstrate that seeds are not simply an incidental part of the diet. Seed specialists are common in the Myrmicinae (for example, *Messor, Pogonomyremex,* and *Veromessor,* although most species also accept dead insects). At least some harvesting species climb plants to collect seeds, for example, *Messor galla* (Lévieux & Diomande 1978).

Schneirla (1971:77) states that "the main body of a swarm raid, in contrast [to a column raid], acts as a dragnet, flushing out a far greater variety of prey along a much broader front." Yet the greater prey diversity taken by swarm raids cannot be explained by differences in the rates at which different foods are discovered ("flushed out"). Consider, for example, that most column-raiding army ants form a branching network of narrow raids. Presumably one swarm raid as wide as the combined widths of all the advancing termini of this network would uncover various foods at rates no different from the column network. Yet in one sense swarm raids do act as a dragnet: prey that rush about within the swarm while trying to escape become more and more entangled within attacking ants until they can no longer move. At least in *P. diversus,* fewer (and less diverse) prey are successfully captured in column raids, in large part because it is easier for struggling prey to break free of the narrow raided area before they can be overwhelmed.

Acknowledgments

For generous aid in connection with this study I thank Angel Alcala, Musthak Ali, Rauf Ali, S. Appanah, Peter S. Ashton, Clare R. Baltazar, Warren Y. Brockelman, William L. Brown Jr., P. Bhat, K. M. Chinnappa, R. Corlett, R. Dengodi, Deborah A. Fletcher, Neva L. Folk, Raghavendra Gadagkar, Madhav Gadgil, Hisar Gultom, Kumar D. Gorpode, W. H. Gotwald Jr., Krishna M. Hegde, Bert K. Hölldobler, Kathy Horton, Su S. Lee, T. J. Lam, John MacKinnon, D. H. ("Paddy") Murphy, H. Napitupulu, Siew Yin Ng, R. Rumianda, Yellapa Reddy, C. W. Rettenmeyer, M. Shukor, M. Singh, Mary G. Smith, Peter F. Stevens, S. Sottibandu, P. Tantichodok, Yo P. Tho, David R. Wells, and Edward O. Wilson. Research was supported by the National Geographic Society, the National Academy of Sciences, and Harvard University (the Richmond Fund).

Bibliography

Baroni Urbani, C.; & Kutter, N.
1979. Première analyse biométrique du polymorphisme de la caste ouvrière chez les fourmis du genre *Pheidologeton* (Hymenoptera: Aculeata). *Bulletin de la Société Entomologique Suisse* 52:377–389.

Bequaert, J.
1922. The predaceous enemies of ants. *Bulletin of the American Museum of Natural History* 45:271–332.

Bingham, C. T.
1903. Ants and cuckoo-wasps. Blanford, W. T., editor: *Hymenoptera,* vol. 2: *Fauna of British India, Including Ceylon and Burma.* Taylor & Francis, London.

Cohic, F.
1948. Observations morphologiques et ecologiques sur *Dorylus (Anomma) nigricans* Ill. (Hym. Dorylinae). *Revue Française d'Entomologie* 14:229–276.

Eibl-Eibesfeldt, I.; & Eibl-Eibesfeldt, E.
1967. Das Parasitenabwehren der Minima-Arbeiterinnen der Blattschneider-Ameise *(Atta cephalotes). Zeitschrift für Tierpsychologie* 24:278–281.

Forel, A.
1921–1923. *Le Monde Social des Fourmis du Globe Comparée à Celui de l'Homme,* vol. 1–5. Libraire Kundig, Geneva.

Franks, N.
1985. Reproduction, foraging efficiency, and worker polymorphism in army ants. Hölldobler, B. & Lindauer, M., editors: *Experimental Behavioral Ecology and Sociobiology.* Gustav Fischer Verlag, Stuttgart, 91–107.

Gotwald, W. H.
1974. Predatory behavior and food preferences of driver ants in selected African habitats. *Annals of the Entomological Society of America* 67:877–886.
1978. Trophic ecology and adaptation in tropical Old World ants of the subfamily Dorylinae (Hymenoptera: Formicidae). *Biotropica* 10:161–169.
1982. Army ants. Hermann, H. R., editor: *Social Insects,* vol. 4. Academic Press, New York, 57–254.

Jacobson, E.
1910. *Pheidologeton diversus* Jerdon und eine myrmecophile Fliegennart. *Tijdschrift voor Entomologie* 53:328–335.
Jenson, T. F.; & Holm-Jensen, I.
1980. Energetic cost of running in workers of three ant species, *Formica fusca* L., *Formica rufa* L., and *Camponotus herculeanus* L. (Hymenoptera: Formicidae). *Journal of Comparative Physiology* 137:151–156.
Kugler, C.
1978. A comparative study of the myrmicine sting apparatus (Hymenoptera, Formicidae). *Studia Entomologica* 20:413–548.
1979. Evolution of the sting apparatus in the myrmicine ants. *Evolution* 33: 117–130.
Lévieux, J.; & Diomande, T.
1978. La nutrition des fourmis granivores. I. Cycle d'activité et régime alimentaire de *Messor galla* et de *Messor (= Cratomyrmex) regalis* (Hymenoptera: Formicidae). *Insectes Sociaux* 25:127–139.
Maschwitz, U.; Hahn, M.; & Schönegge, P.
1979. Paralysis of prey in ponerine ants. *Naturwissenschaften* 66:213.
Maschwitz, U.; & Schönegge, P.
1980. Fliegen als Beute und Bruträuber bei Ameisen. *Insectes Sociaux* 27:1–4.
Moffett, M. W.
1984. Swarm raiding in a myrmicine ant. *Naturwissenschaften* 71:588–590.
1986. Marauders of the jungle floor. *National Geographic* 170:272–286.
Oquias, E. A.
1982. Foraging ecology of seed feeding ants on secondary forest and grassland ecosystems in Mt. Makiling. M.S. dissertation, University of the Philippines, Los Baños.
Oster, G. C.; & Wilson, E. O.
1978. *Caste and Ecology in the Social Insects.* Princeton University Press, Princeton.
Pham, T.
1924. Sur le régime alimentaire d'une espèce de fourmis Indochinoises *(Pheidologeton diversus)* Ierdon. *Annales des Sciences Naturelles, Zoologie* 10:131–135.
Porter, S. D.; & Jorgensen, C. D.
1981. Foragers of the harvester ant, *Pogonomyrmex owyheei:* a disposable caste? *Behavioral Ecology and Sociobiology* 9:247–256.
Rothney, G.A.J.
1889. Notes on Indian ants. *Transactions of the Entomological Society of London* 36:347–374.
Schneirla, T. C.
1971. *Army Ants: a Study in Social Organization.* Freeman, San Francisco.
Silva, M.M.T.G. da
1972. Contribuição ao estudo da biologia de *Eciton burchelli* Westwood (Hymenoptera: Formicidae). Ph.D. dissertation, Universidade de São Paulo, São Paulo, Brazil.
Snelling, R. R.
1981. Systematics of social hymenoptera. Hermann, H. R., editor: *Social Insects*, vol. 2. Academic Press, New York, 369–453.
Wilson, E. O.
1962. Behavior of *Dacton armigerum* (Latreille), with a classification of self-grooming movements in ants. *Bulletin of the Museum of Comparative Zoology, Harvard* 127:403–422.
1971. *The Insect Societies.* Belknap Press of Harvard University Press, Cambridge.
1980. Caste and division of labor in leaf-cutting ants (Hymenoptera: Formicidae: *Atta*). I. The overall pattern in *A. sexdens. Behavioral Ecology and Sociobiology* 7:143–156.
1983. Caste and division of labor in leaf-cutting ants (Hymenoptera: Formicidae: *Atta*). III. Ergonomic resiliency in foraging by *A. cephalotes. Behavioral Ecology and Sociobiology* 14:47–54.
Wroughton, R. C.
1892. Our ants, pt. II. *Journal of the Bombay Natural History Society* 7:175–203.

Accepted 9 January 1987.