Foraging Behavior in the Malayan Swarm-Raiding Ant *Pheidologeton silenus* (Hymenoptera: Formicidae: Myrmicinae)

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ABSTRACT Workers of the myrmicine ant *Pheidologeton silenus* (F. Smith) search for food in narrow column raids and in swarm raids up to 3 m wide, much as do army ants (Dorylinae and Ecitoninae) and the closely related species *Pheidologeton diversus* (Jerdon). *P. silenus* lacks the stable trunk routes of *P. diversus.* Media and major workers also perform fewer exterior tasks than do *P. diversus,* and they function outside the nest mainly in clearing trails and killing prey. Swarm raids advance at up to 4.5 m/h, faster than in *P. diversus* but still slower than in most army ants. This species feeds largely on animal material, and, unlike *P. diversus,* apparently never harvests seeds directly from fruiting plants. Despite the relatively rapid raid advance, *P. silenus* is generally less successful at catching massive or agile prey than *P. diversus* and collects mostly larval forms and other readily captured invertebrates. The significance of differences in raid velocity between species of group-hunting ants is discussed.

KEY WORDS Insecta, *Pheidologeton silenus,* group hunting, raid velocity

THE ANT *Pheidologeton silenus* (F. Smith) is common in forest habitats in Malaysia, Sumatra, and Borneo. *P. silenus* is a close relative of *P. diversus* (Jerdon), a more widespread species recently shown to forage by group hunting (Moffett 1984). Group hunting is usually associated with army ants (Dorylinae and Ecitoninae; Gotwald 1982). Ants using this strategy search for food in groups rather than as solitary individuals that recruit assistance from a distance (as do most predatory ants that "raid"; Moffett, in press). I show here that *P. silenus* is also a group hunter, and indeed that this species has in some respects converged further to "true" army ant behavior than *P. diversus.*

Methods

Most of the observations on *P. silenus* were made in forests on Penang Hill (Penang, Malaysia) and at the Field Studies Center of the Universiti Malaya at Gombak (Selangor, Malaysia). Some foraging behavior was also documented at many of the other sites in Peninsular Malaysia, Thailand, Borneo, Sumatra, and Java, where this species was collected.

Foraging was studied by mapping columns and raids daily for selected colonies or study areas, and by photographing and mapping the progression of raids. Samples of food were taken from foraging columns for identification and analysis. Polyethism data were collected primarily from Gombak colony No. 80-83 by sampling all workers carrying out specific tasks, then constructing polyethism curves based on worker size. The results were often similar to those for *P. diversus* and so are presented in less detail here than in my paper on *P. diversus* (Moffett 1987). Voucher specimens are deposited at the Museum of Comparative Zoology, Harvard University.

Results

Raid Structure and Dynamics

Workers of *P. silenus* typically stick close to trails, and indeed show less tendency to travel short distances from other ants than do *P. diversus* workers. As in *P. diversus* (Moffett 1984), workers search for food in column raids and swarm raids. Raids can be initiated by disturbances to a trail. For example, columns often advanced from the point along a trail where I had spent some time collecting food samples from returning ants.

P. diversus ants near the raid front wander considerably and show no clear behavioral pattern on reaching new ground (Moffett 1984). The behavior of *P. silenus* at the front tends to be more distinctive. Many workers crouch down and move forward slowly for variable periods before retreating; thus their behavior somewhat more closely approximates that of army ants (Schneirla 1971).

Column raids can advance at least 3 m without reaching more than about 20 cm in width. However, some raids expand into swarm raids. Judging from the number of *P. silenus* swarm raids observed, this species probably raids in swarms more often than *P. diversus.* The largest *P. silenus* raids measured were 3.0 m in width. Swarm raids of *P. silenus* generally advanced at 3–4.5 m/h, appreciably faster than in *P. diversus* (about 2.0 m/h; Moffett 1984).

Like *P. diversus* (Moffett 1984) and army ants (Schneirla 1971), *P. silenus* swarm raids are fan shaped, the fan area consisting of a column net-

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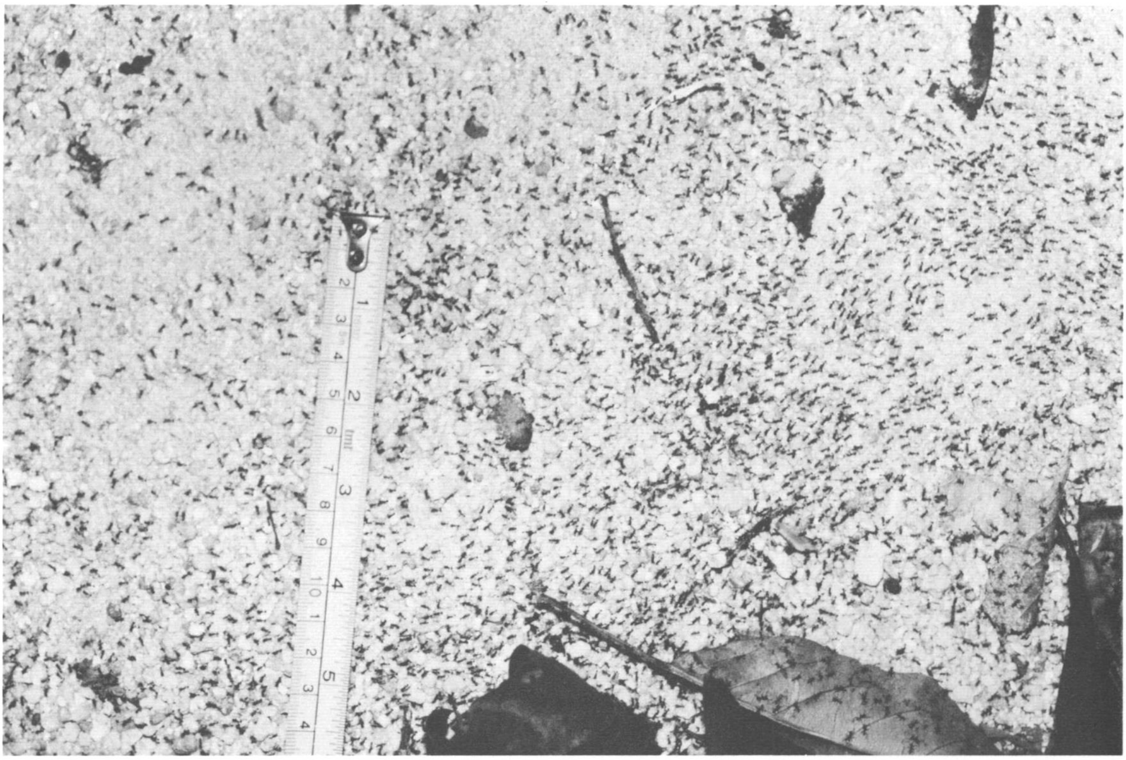

Fig. 1. Part of the fan of a 2.5-m wide swarm raid of *P. silenus* advancing over sand. This raid is estimated to have contained at least 60,000 workers (colony No. 05-83).

work. Raids differ in structural detail, however. Some have a band of mostly independently moving ants (the "swarm") behind the advancing margin at the head of the fan. Other raids are similar, but the swarm is indistinct. In such cases, most ants follow columns all the way forward to a mutual "raid front" defined by the nearly equivalent advance of all columns. The columns are dense at the raid front.

On three occasions I saw raids in which the fan area was a virtually continuous sheet of advancing ants (density throughout the raids about 3–6 ants/cm^2; Fig. 1). Although many ants followed columns within the fan, even most ants between columns advanced toward the raid front (usually ants between columns were fewer and moved in various directions).

Foraging Dynamics

Raiding occurred around the clock. Subterranean raiding was probably important, given the frequency of raids emerging from the ground at widely separated points away from any apparent nesting site. At the opposite extreme, raids were found on tree trunks at a height of at least 2 m.

Trail stability was documented at Penang by recording the location of *P. silenus* columns in a dry stream bed for 25 d. Columns usually lasted less than 1 d, and the most stable column lasted 3.5 d. The longest any length of trail was continuously used during a 12-d study on Gombak colony 80-83 was 3 d (Fig. 2). In contrast, *P. diversus* colonies usually have one or two stable routes often lasting weeks (Moffett, in press). *P. diversus* sometimes forms stable subterranean routes which can often be detected by the repeated emergence of raids from various holes in the ground along the route. No such pattern was observed in *P. silenus*, where raids often emerged unpredictably from widely scattered sites. It seems likely, therefore,

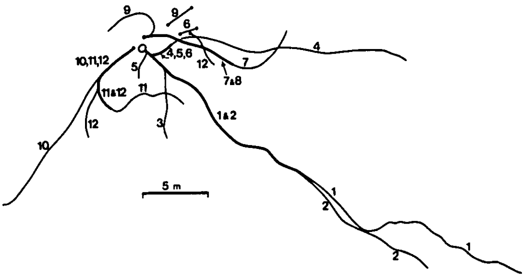

Fig. 2. Maps of the activities of *P. silenus* colony No. 80-83. Twelve maps drawn at 1-d intervals are overlaid; numbers indicate the d(s) on which various trails were in use. The colony nested at the open circle; closed circles indicate where trails went below ground.

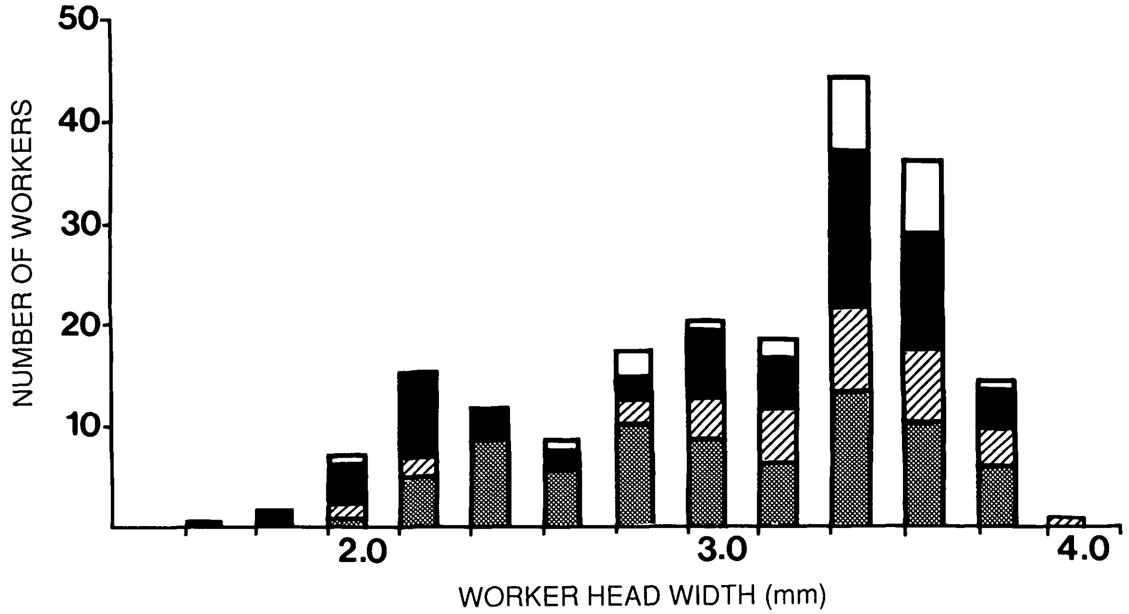

Fig. 3. Nonminor worker size distribution in *P. silenus* colony No. 80-83. Worker head widths were measured to the nearest 0.2 mm. The replete caste is here divided between "fully replete" individuals (stippled bars), and those with less extremely enlarged gasters (hatched bars); the remaining ants are nonrepletes (dark bars) and undetermined individuals (open bars).

that long-lasting foraging routes are completely lacking in *P. silenus*.

Diet

Less than 20% of nest-bound *P. silenus* ants usually carried food in their mandibles, and few burdens carried were much larger than the minor workers carrying them. In contrast, commonly 40% or more of inbound *P. diversus* ants carried solid food, including occasional items thousands of times the weight of a minor worker (the largest recorded burden of *P. silenus* had a dry weight <300 times that of one minor worker). The rarity of large items among the booty reflects both the infrequency with which large items were collected and the extent to which items were torn apart before transport. These differences, and the comparatively low frequency and intensity of harvesting activities during *P. silenus* raids, suggest that this species is a less efficient food gatherer than *P. diversus*. However, the possibility remains that *P. silenus* takes a larger proportion of its food as liquid carried within worker crops.

Food burdens sampled from returning *P. silenus* workers consisted mostly of animal material. Most common were insect larvae (such as caterpillars, maggots, and beetle grubs), eggs of invertebrates, isopods, termites, and earthworms. Also represented were adult Coleoptera and Hymenoptera (mostly ants), Orthoptera, Hemiptera, Homoptera, Collembola, and other insects, as well as small spiders, centipedes, and millipedes, and more rarely planaria, harvestmen, snails, and other groups.

Compared with *P. diversus*, very large prey (such as big earthworms and centipedes) were conspicuously absent among the booty, while larval forms tended to be numerous (often representing 50% or more of the burdens carried). Relatively few agile prey were taken; Orthoptera, which sometimes occurred in booty samples, almost invariably escaped when dropped into swarm raids. *P. silenus* was clearly less efficient than *P. diversus* at capturing large, agile prey, in spite of the species' more rapid raid advance.

Unlike *P. diversus* (Moffett 1987), *P. silenus* took little vegetable matter (that is, usually well under 10% of food biomass). At Penang, the ants carved up the seeds of *Elaeocarpus* trees; figs and other fruits were also eaten on the spot. Workers also carried away flower parts (petals, pistols, etc.). At many localities, sundry small seeds were collected entire. However, this species responds much more feebly to seeds than does *P. diversus* (Moffett 1987). For example, the ants often ignored baits of a canary seed mix even when little other food was taken.

Observations at mango, banana, and meat baits suggest *P. silenus* is slower and less persistent than *P. diversus* at tearing down bulk foods. Workers usually abandon baits after 1–2 d regardless of the amounts of food remaining.

Worker Polymorphism

Excavations of colony No. 80-83 indicate that *P. silenus* workers show a trimodal size-frequency

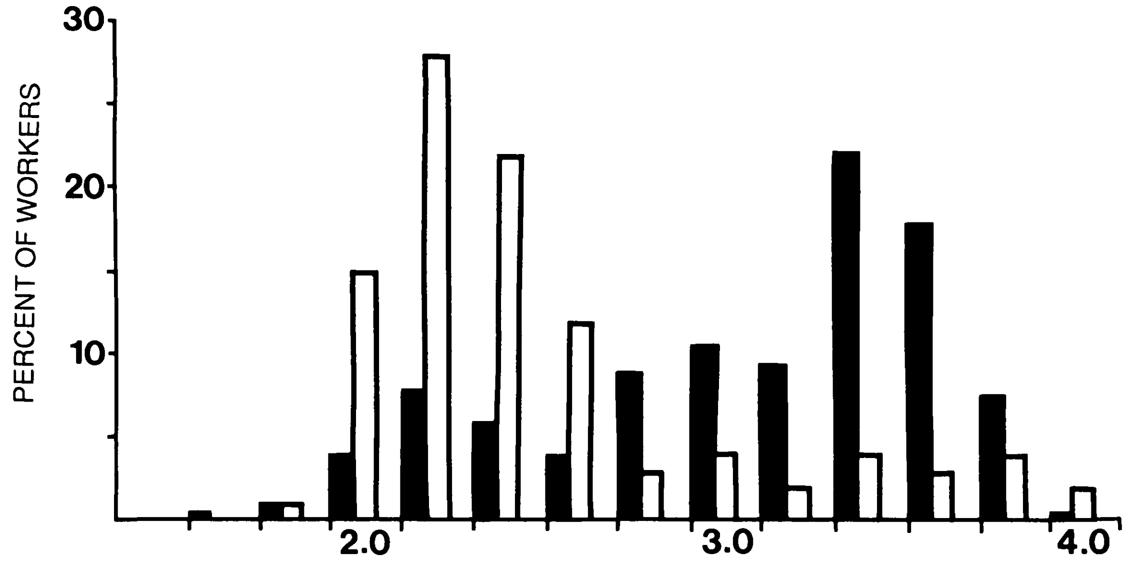

Fig. 4. Polyethism curve for foraging nonminor workers in *P. silenus* colony No. 80-83, compared with the size-frequency distribution of nonreplete media and major workers for the colony as a whole.

distribution, with a discrete minor worker caste and a distinctly bimodal distribution of nonminor (media + major) sizes (Fig. 3). In two excavated colonies, the modes occurred at head widths of 0.7, 2.2, and 3.4 mm. As in *P. diversus*, medias will be defined as nonminors with a head width of 2.6 mm or less.

There were several differences from the *P. diversus* size-frequency distribution—nonminors were even rarer than in *P. diversus*, making up only 0.2–0.3% of the worker population (versus 0.5–1.0%); the size distribution of nonminors was narrower (1.4–4.0 mm versus 1.0–5.6 mm); and major workers were more numerous than medias (making up about 70% of nonminors versus about 25% in *P. diversus*).

Worker Behavior and Division of Labor

Worker Location on Trails and in Raids. As in *P. diversus* (Moffett 1987), replete workers never foraged (repletes are nonminor workers whose crops are greatly distended with oily food that serves as a reserve food supply). Foraging nonminors were greatly outnumbered by minors: in 5 samples totalling 7,733 ants, only 1 ant in 476 was a nonminor. The frequencies of nonminors entering swarm raids and reaching the swarm front were about the same.

The size-frequency distribution of nonminor foragers, however, was virtually a mirror image of that for nonreplete media and major workers in the colony as a whole (Fig. 4), and resembled the distribution of *P. diversus* foragers in the predominance of the media worker subcaste (Moffett 1987).

Harvesting Food. *P. silenus* ants usually responded slowly to prey and accumulated at prey in smaller numbers than did *P. diversus*. This gave prey a better chance of escape. Minors pinned down prey, which were then torn apart by the mandibles of both minors and nonminors (*P. silenus*, like *P. diversus*, cannot sting) (personal observation; C. Kugler, 1978, personal communication). Whereas *P. diversus* tended to carry prey out of raids as soon as its appendages had been removed, *P. silenus* often tore up prey further, even though *P. silenus* ants were slow at dismembering prey. For example, earthworms were often transported entire by large groups of *P. diversus* workers but were usually chopped into pieces by *P. silenus* ants.

I never saw *P. silenus* workers climb plants to obtain seeds; presumably all seeds were taken from the ground. There was also no evidence that media and major workers aided in seed collection, as described for *P. diversus* (Moffett 1987), although seeds were presumably milled by nonminors after arrival in the nest.

Baits of sugar, vegetable oil, and prawns were supplied to colony No. 80-83 to simulate bulk food finds. Workers of all sizes arrived at the baits and behaved much as described for *P. diversus* (Moffett 1987). Yet the ants usually responded weakly and often eventually abandoned the baits. The proportion of nonminors on baits was very low (<1%), corresponding closely to the general foraging population.

Minors and medias of *P. diversus* covered large, moist foods with soil and in some cases built soil covers over them (Moffett 1987). Similar responses in *P. silenus* were feeble, and in my experience covers were never constructed. Also, *P. silenus* medias did not deposit soil on food.

Food Transport. All booty was transported by minor workers. This habit differs from *P. diversus*, in which medias carried some burdens (Moffett 1987). However, *P. silenus* ants of all sizes drank at moist foods, and thus aided in transporting liquids.

Because of the infrequency of large burdens, group transport was rare in *P. silenus* (commonly 1% of items were carried in groups, compared with typically 5–10% in *P. diversus* [Moffett 1987]) and tended to involve at most small worker groups (usually fewer than four ants and apparently never more than 12, compared with a maximum of over 100 ants in *P. diversus*; Moffett 1987). Also, minors seldom rode on top of the booty being transported to the nest; such riders were common in *P. diversus*.

Trail Construction and Maintenance. Clearing trails of large obstructions represents an important function of nonminors in both *P. diversus* and *P. silenus*. Majors (and less often large medias) hoisted leaves, twigs, and other obstructions with a quick upward shove of their heads (Moffett 1987). Both media and major workers also dragged obstructions from trails with their mandibles and gnawed at immobile obstructions.

P. silenus trails were sometimes bordered with soil walls or had a complete soil cover, but these structures were more common and usually better developed in the long-lived trunk trails of *P. diversus*. *P. silenus* media workers did not aid the minors in building the walls and covers, unlike *P. diversus* (Moffett 1987).

Defensive Behavior. Conflicts between *P. silenus* colonies have not been documented. Minor workers in an aggressive posture were found along trail borders wherever disturbances from other ant species were frequent, as described for *P. diversus* (Moffett 1987). In contrast to *P. diversus*, nonminors were not observed 'guarding' trails in this way. Workers of the ants *Polyrachis* spp. and *Odontoponera transversa* (F. Smith) were attacked by minors after they stumbled onto trails. Nonminors helped kill such intruders much less often than in *P. diversus* (Moffett 1987).

Minors swarmed out onto the ground in response to a pencil poked into an entrance of colony No. 80-83. Majors and medias (including repletes) quickly accumulated at the entrance and occasionally came out short distances from the entrance. Majors outnumbered medias in this defensive task, as they do in the nest as a whole. These ants bit a twig thrust at them but retreated after a few minutes when left undisturbed. Nonminors of *P. diversus* were less cautious after nest disturbances, rushing from entrances to patrol the surrounding ground alongside minors.

Riding Media and Major Workers. Minors ride on top of nonminors, with the number of riders correlating with carrier size as in *P. diversus* (Moffett 1987).

Midden Work. Refuse disposal was not observed. *P. silenus* lacks the prominent middens found in *P. diversus*.

Discussion

P. silenus is even more reminiscent of army ants than *P. diversus*, given the former's higher swarm raid velocity, worker behavior at raid fronts, greater trail instability, reduced dependence on plant foods, absence of seed collection from fruiting plants, and lack of the long-term harvesting of bulk foods. On the other hand, *P. silenus* takes fewer large prey than *P. diversus* and is slower at tearing down prey and other foods.

The similarities of *P. silenus* to army ants extend even to its myrmecophiles. The staphylinid genus *Pheigetoxenus*, recorded thus far only from foraging columns of *P. silenus*, contains beetles that mimic worker morphology (Kistner 1983). Staphylinids are among the most numerous and diverse myrmecophiles and termitophiles, but mimicry of host morphology is rare outside of army ants (Wilson 1971).

Nonminors are more specialized in *P. silenus* than in *P. diversus*. This is correlated with a reduction in the frequency of nonminors among exterior ants. Medias of *P. silenus* were not observed to transport booty, cover moisture with soil, construct soil covers on trails, or guard trail borders as they do in *P. diversus* (Moffett 1987); these roles are apparently restricted entirely to minor workers.

The most conspicuous difference between the foraging strategies of *P. diversus* and *P. silenus* is the lack of stable trails in the latter. Whereas *P. diversus* colonies typically have one or two trunk routes lasting for weeks or months (Moffett in press), no trails of similar stability were recorded in *P. silenus*. The trunk trails of *P. diversus* permit the ants access to regions distant from the nest and allow rapid worker flow to and from such regions, two of several possible advantages of stable trails (Moffett in press) lost to *P. silenus*.

The high maximal rates of raid advance of *Eciton burchelli* (Westwood), *E. hamatum* (F.), *Labidus praedator* (F. Smith), and some *Anomma* spp. (that is, 15–20 m/h) are commonly quoted in discussions of raiding activity (e.g., Gotwald 1982), but, clearly, many army ants raid more slowly. Indeed, the raid velocity of about 4 m/h in *P. silenus* probably approaches that of some army ants. Unfortunately, raid velocities for most species have not been reported. For example, Schneirla and Reyes (1966) do not state the swarm raid velocity in *Aenictus laeviceps* (F. Smith), but judging from data they give on raid distance and duration, raids probably advance on average at <4 m/h (their figures for raid duration could include intervals of raid retreat, but even so, raid velocities during periods of advance would probably not be much higher than in *P. silenus*).

Monomorphic *A. laeviceps* workers are similar in size to *P. silenus* minor workers, whereas workers at raid fronts in species with a faster raid advance (for example, *E. burchelli* and *Anomma* spp.) are often larger. The possibility of a relationship between worker size (or running speed) and velocity of raid advance in various group-hunting species is worthy of investigation. Although *P. silenus* minor workers average about 15% larger in head width than *P. diversus* minors (and about 50% larger in dry weight), these ants tend to move more slowly than minors of *P. diversus* (on average usually about 0.8 m/min, compared with about 1.0 m/min). This suggests that the greater swarm raid velocity of *P. silenus* is attributable more to a greater efficiency in the process of raid progression than to size differences in workers.

What is the value of high raid velocity to a group-hunting ant? Clearly any increase in velocity would accelerate the discovery of food. Raid velocity may represent a compromise between increasing the rate of food encounter and limitations in the time, energy, and number of workers available to handle food. Certainly raids should not advance so quickly that workers encounter desirable foods faster than they can deal with them.

Army ants have increased the efficiency with which they handle foods to keep up with the high flux of foods into raids. For example, the ants work in groups to transport large booty out of raids rapidly, instead of taking the time to first tear up the food into pieces transportable by single workers. Also, much food is quickly deposited in protected caches along trails, where it is stored temporarily. Similar caches have occasionally been observed for Indian *P. diversus* (Moffett in press), and group transport occurs in both *P. diversus* and *P. silenus*.

The rate of food encounter during a raid is dependent on diet breadth, the densities of the various acceptable foods, and the velocities of these foods, as well as on the raid's width and velocity. For example, if the foods taken are highly mobile prey, and if these prey are found at sufficiently high densities, it may be necessary only for a foraging group to advance very slowly (if at all) to take all the prey it can handle. I have seen networks of *Solenopsis geminata* (F.) columns on the ground below street lights; flying insects were killed by the *S. geminata* as they fell from the lights. It is probable that this behavior does not represent a regular part of the *S. geminata* foraging pattern. Nevertheless, such activity could be viewed as a crude form of raiding—a kind of social sit-and-wait foraging strategy. Indeed, similar column networks have been observed for prolonged periods under lights for *P. diversus* (Moffett in press) and certain army ants (Rettenmeyer 1963).

Further attention to relationships between food encounter rates, food harvesting efficiencies, and raid structure, size, and velocity should provide important insights into variations in foraging strategies shown by group-hunting species.

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