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Foraging Dynamics in the Group-Hunting Myrmicine Ant, *Pheidologeton diversus*

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Pheidologeton diversus *workers group-hunt (that is, search for food in raiding groups) and are in this way remarkably convergent with army ants (Dorylinae and Ecitoninae). Raids appear usually to take independent courses and are capable of tracking areas of high food density. However, raid advance is not dependent on continual food discovery at the raid front, since raids can advance over areas without food. Most raids extend from trunk trails, which originate when the basal trail of a raid remains in use even after the original raid has ceased. Trunk trails can last at least as long as 10 weeks, with the terrain and the distance to the nest influencing the trail stability. Territories are limited to the trail systems, with rich food items in particular being vigorously defended. Group hunting permits* P. diversus *to quickly harvest booty, usurp foods from competing species, and capture large prey. This strategy is compared with the raiding strategies of other ants. I hypothesize that group hunting originated from an ancestor which hunted solitarily from trunk trails through the acceleration of trail production and reduction in worker autonomy.*

KEY WORDS: *Pheidologeton diversus*; Myrmicinae; army ant; group hunting; swarm raid; column raid; trunk trail; foraging strategy.

INTRODUCTION

The Myrmicinae is the largest of the ant subfamilies (Snelling, 1981). The range of foraging strategies known for the Myrmicinae provides a measure of the diversity of this group, particularly since the strategies adopted by ants relate to the environmental contingencies they face (Hölldobler, 1978). Certain myrmicine species hunt solitarily without the aid of recruitment (e.g., Wilson,

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1962), while others display a variety of recruitment techniques (see Hölldobler, 1978), and some have developed long-lasting routes called trunk trails to foraging areas (e.g., Hölldobler, 1976; Shepherd, 1982). Until recently one of the few ant foraging strategies not documented for a myrmicine species was the group-hunting pattern (see Oster and Wilson, 1978) characteristic of army ants [i.e., ants in the subfamilies Dorylinae and Ecitoninae (Gotwald, 1982; Topoff, 1984)] and a few species in taxa phylogenetically close to these ants (e.g., Maschwitz and Mühlenberg, 1975; Hölldobler *et al.*, 1982). Now group hunting has been demonstrated in the myrmicine ant *Pheidologeton diversus* (Moffett, 1984). Anecdotes regarding the behavior of *Pheidologeton* ants have been presented by early naturalists (Rothney, 1889; Wroughton, 1889, 1892; Bingham, 1903; Jacobson, 1910; Pham, 1924; Karawajew, 1935), but otherwise the genus has essentially been ignored.

P. diversus is a polymorphic ant (Baroni Urbani and Kutter, 1979) common throughout much of Southeast Asia. The species is an extreme trophic generalist (Moffett, 1987). Long considered to be primarily granivorous (Wheeler, 1910; Forel, 1921–1923; Wilson, 1971; but note Moffett, 1985, p. 176), much of its diet is in fact composed of animal matter, including agile invertebrates (many considerably larger than the ants) and, on rare occasions, even small live vertebrates. The ants also consume carcasses, fruits, nuts, bark, and leafy plant material (Moffett, 1987).

P. diversus workers nest in the ground and build trunk trails (as defined by Hölldobler, 1977), foraging from the trails in raids which can advance 20 m or more (Moffett, 1984). The ants move out from trails (or the nest site) in narrow columns. A minority of these column raids expands into fan-shaped swarm raids typically 2–3 m wide. The swarm raids of *diversus* advance slowly (usually about 2.0 m/h); column raids at least initially have a greater velocity (Moffett, 1984).

Here I examine the foraging dynamics of *Pheidologeton diversus* through experiments on and sequential mappings of raids and trails and compare its foraging strategy with those of other ants. How does *diversus* efficiently harvest a spectrum of both uniformly and patchily distributed foods in a competitive environment? The study suggests that the success of *diversus* can be explained in part by its flexible foraging pattern, which integrates features shared by certain other myrmicine ants with group-hunting behaviors commonly associated with army ants. The result ranks among the most complex foraging strategies known.

METHODS

A total of about 1500 h of observations on *P. diversus* was made during fieldwork in eight Asian countries. Disturbed sites were usually chosen for experimental work because of the relative ease of documentation. The bulk of the experiments reported here was on colonies at the Singapore Botanical Gardens and at the Bukit Timah Nature Reserve in Singapore. Extensive additional observations were made at sites near Malacca and Kuala Lumpur in Malaysia, and in Karnataka State in southern India, and are reported where they add to or differ from the Singapore data.

Detailed maps of raids and trails were necessary to document foraging dynamics and were also required for many experiments. Flagged skewer sticks were used to mark the location of trails and raids. Samples of ants were sprayed with differently colored enamel paints to distinguish nests. At 10-day intervals for 100 days, maps were drawn of all *P. diversus* trails within a densely populated 7000-m^2 area within the Botanical Gardens; selected colonies were mapped at shorter intervals. During many experiments care had to be taken to limit disturbances, so as to avoid altering local raiding patterns. Additional experimental methods are given at appropriate points in the text and figure legends.

RESULTS

Trunk Trail Dynamics

Cartographic studies demonstrated that some *Pheidologeton diversus* trails (i.e., "trunk trails") can last weeks or months (Fig. 1). Trail stability is correlated with physical structure. Trails lacking signs of construction are generally transient, while those with a smooth surface free of plants and other obstructions

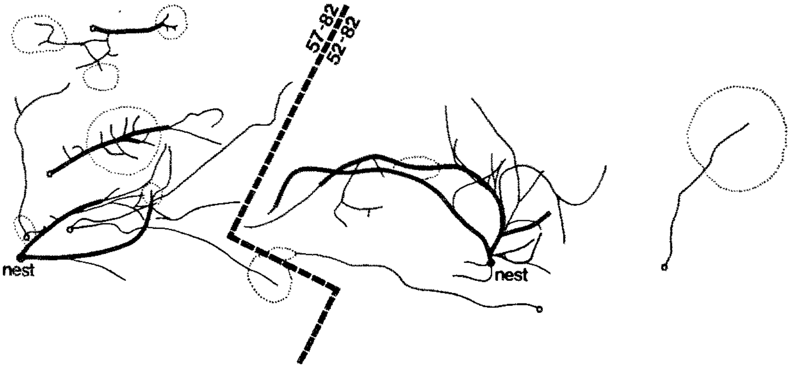

Fig. 1. Maps of the activities for *P. diversus* colonies 52-82 and 57-82, nesting 48 m apart. Eleven maps drawn at 10-day intervals are overlaid. Thick lines: trails in use on more than one mapping day (i.e., "trunk trails"). Thin lines: more transient routes. Dotted lines enclose areas with many trails. Small circles indicate places where trails emerge from the ground away from the nest. The thick dashed line separates the two colonies.

and with conspicuous soil walls or a complete soil cover are apt to be stable (Table I). Thus in *P. diversus* trunk trails on the ground surface are most conveniently defined in terms of the presence of these physical features, to distinguish them from temporary trails such as the basal trails of raids.

By this criterion a *P. diversus* colony typically has one or two trunk trails ranging between 5 and 100 m long (excluding any terminal trail segment lacking a pronounced physical structure); sometimes these have one or two well-constructed branches. Feebly built (transient) trails extend from the trunk trail system to raids or food finds.

P. diversus trails do not often traverse the length of lianas, sticks, or other objects, unlike many epigaeic (surface foraging) army ants (Rettenmeyer, 1963). In the Malay Peninsula trunk trails usually follow the ground surface, but at least parts of some trails lie below ground: in one instance a trunk trail emerged from the ground 25 m from the actual nest site. Also, sections of a surface trail can disappear if the ants discover alternate underground routes. Subterranean trunk trails were common in southern India, at least during my studies there, which were conducted in the dry season (November to March). These trails can be detected by the repeated emergence of raids from various holes in the ground along the route.

A sample of 14 trunk trails ranged in length from 6 to 72 m [mean 26.6 ± 18.6 m ($\bar{X}$ ± SD); median, 28 m]. Thirteen trunk trails checked at 5-day intervals throughout their period of use lasted between about 5 and 75 days (mean, 39.8 ± 23.6 days; median, 30 days); shifts in course occurred within the lifetime of many of these trails. When new trunk trails developed they sometimes

Table I. Stability of Trails in *P. diversus*[a]

		% of trails	
	Number of trails	Within 20 cm of previous location	Within 2 cm of previous location
Worker columns	37	13.5	5.4
Feeble trails	29	65.5	24.1
Trunk trails	15	100.0	60.0
Sunken trunk trails	4	100.0	100.0

[a] Trails with a selected degree of structural complexity were marked at an arbitrary point on the same day, and the deviation from the original location was measured 1 week later. Trails were chosen from several colonies in areas of moderate ground cover. "Worker columns" moved over unaltered ground; "feeble trails" had poorly developed soil walls, "trunk trails" had prominent walls or covers, and in "sunken trunk trails" the trail surface was markedly lower than the surrounding ground. Conceivably some "trails within 20 cm of previous location" were actually new trails that happened to approximate the route of the previous trail. None of the sunken trails shifted more than 5 cm during the subsequent 3 weeks.

took roughly the same course as previous trails, but others went in completely new directions (e.g., Fig. 1).

Stretches of trunk trails near to the nest tend to be more stable than distant parts of the trail, and this corresponds with the progressively more elaborate trail construction generally found when proceeding along a trunk trail in the direction of the nest. For example, in extreme cases the first several meters of a trail are sunken relative to the surrounding ground. This structural feature confers exceptional trail stability (Table I).

The stability of a trunk trail is influenced by the terrain through which it passes. Views of subterranean trunk trails through crevices indicate that such trails can be very stable. Trunk trails in dense ground cover are likely to be more stable and better constructed than those on bare ground, as is clearly shown for trails passing through both vegetated and bare areas. One trunk trail in dense vegetation crossed a 2.3-m-wide bare region about midway along its length. Shifts in trail location from one week to the next measured 5, 3, 28, 17, 30, 4, and 21 cm in the middle of the bare region, whereas the trail shifted at most 0.5 cm during the same 7 weeks at an arbitrary marked point in the vegetation on each side of the bare region.

The ants do not appear to be using vegetation as landmarks for orienting along trails [as has been documented for some myrmicine species (Hölldobler, 1976; Hölldobler and Möglich, 1980)]. Thus trails in bare areas are no more stable where they pass near to prominent but well-separated plants. Rather, dense vegetation (and to some extent roots, leaf litter, and other objects) confers trail stability by physically constraining the course the ants can take. In addition, such objects can reduce the severity of disturbances to trails. Downpours, which can obliterate all physical evidence of a trail's existence, are often followed by shifts in course or even trail abandonment; trails protected by vegetation or litter are less often affected. Other severe disturbances can cause shifts in trail course. For example, 30 min after 3 h of repeatedly slapping given points along trunk trails with a ruler at 15- to 20-min intervals, the ants had shifted course locally in four of nine trails to avoid the disturbed areas. No shifts occurred during this interval in any of the same trails at marked points away from these disturbed areas.

Significance of Solitary Ants to Foraging Dynamics

Pheidologeton diversus workers rarely travel on their own more than about 5 cm from a trail. Sometimes single ants are found 10–30 cm from any other ants. Workers that initially appear to be hunting alone occur in the following situations: they may be stragglers from a retreating raid (in which case there are usually other ants taking the same course back toward a trunk trail), they may be in the vanguard of a raid, they may be lost (wandering about and not returning to a trail even if given food), or they may have rushed out from a trail following a severe disturbance [majors can go 1 m or more from trails after disturbances but do not recruit to food (Moffett, 1987)]. Some ants travel out from trails to collect materials for trail construction, and occasionally these ants repeatedly follow set routes (apparently feeble trails) up to about 20 cm from an active trail. Such ants can recruit to foods they find, which can in turn initiate raiding (see below). However, it is clear that virtually all food is taken during raids and that "solitary" ants have, at most, a very slight influence on the overall foraging pattern.

Origin of Raids

Raids apparently can originate from any point along a trunk trail or transient trail or from the nest entrance. Disturbances often start raiding activity. When I stepped on a trail there was an outpouring of ants onto the surrounding ground; the ants usually soon retreated, but sometimes raiding columns developed from the point of disturbance. I also saw raids form after tree limbs or large fruits had fallen onto a trail or after trail activities had been disrupted by other ants. Even gently breathing on a trail could start raiding activity on moist days.

The discovery of food can also stimulate raiding. When a line of seeds from a canary food mix was laid out from the side of a trail, ants advanced rapidly in a column along the line. Column raids often expanded onto the surrounding ground, and in one experiment three swarm raids quickly developed (Fig. 2).

Even the location of single sesame seeds by solitary ants near a trail can initiate raids. In 28 cases of 50 (using colony 57-82) the ant ignored the seed after contacting it, in 11 cases the ant dragged the seed without recruitment, in 4 cases recruitment to the seed by trail-laying apparently occurred but did not lead to raiding and in 7 cases some raiding ensued.

Raids also begin spontaneously, such that a column of ants advances steadily from a trail without apparent provocation. This occurs rarely for any given short section of trail but probably is important when the trail system is considered as a whole. For example, I saw two examples of apparently spontaneous raid origin during exactly 50 h of watching a 2.7-m section of trunk trail from a distance great enough not to disturb the ants. Given a total trail system of 50 m and (hypothetically) an equal rate of raid formation throughout the system, this would account for the occurrence of about 1 raid every 45 min.

Raid Dynamics

Activity on *Pheidologeton diversus* trunk trails continues around the clock, without an apparent daily pattern (Fig. 3). The ants can also forage out from trunk trails at any time, as indicated by the continuous flow of food to the nest (Fig. 3) and the documentation of raiding at night.

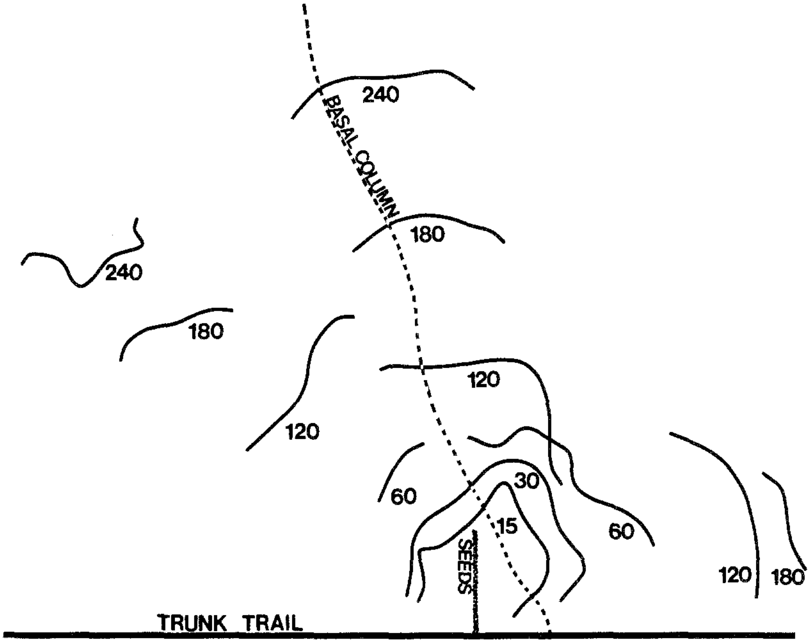

Fig. 2. Progression of swarm fronts for raids initiated by laying a 1-m-long trail of seeds from a canary food mix out from the trunk trail of colony 51-82. Numbers are times in minutes from the moment a column of ants first advanced to the end of the seed trail. Curved solid lines indicate swarm fronts; the dashed line shows the course of the only column present at 360 min.

Rainfall can influence foraging intensity. Raiding activity is strongest on moist days, and raiding (particularly swarm raiding) is significantly curtailed during dry spells. Workers likewise respond more aggressively toward disturbances on moist days. For example, when I placed my finger near the center of colony 65-82's trunk trail, 39.5 ± 17.3% ($N = 7$) of the ants passing by on the trail attacked me on moist days, but only 3.9 ± 5.4% ($N = 9$) climbed the finger on dry days (under both conditions there were on average about 270 ants/min on the trail).

Hypogaeic raiding can be inferred from the occasional emergence of raids from holes in the ground away from a colony's nest site and trunk trails, but the frequency and dynamics of such raids are unclear. Nest dissections and analysis of midden contents have yielded only foods that the ants commonly collect on the ground surface, and it is assumed the majority of foraging activity is epigaeic (except possibly in south India).

Epigaeic raids usually stay at ground level, although some ants ascend vegetation for short distances (rarely beyond 10 cm). Most raids proceed around

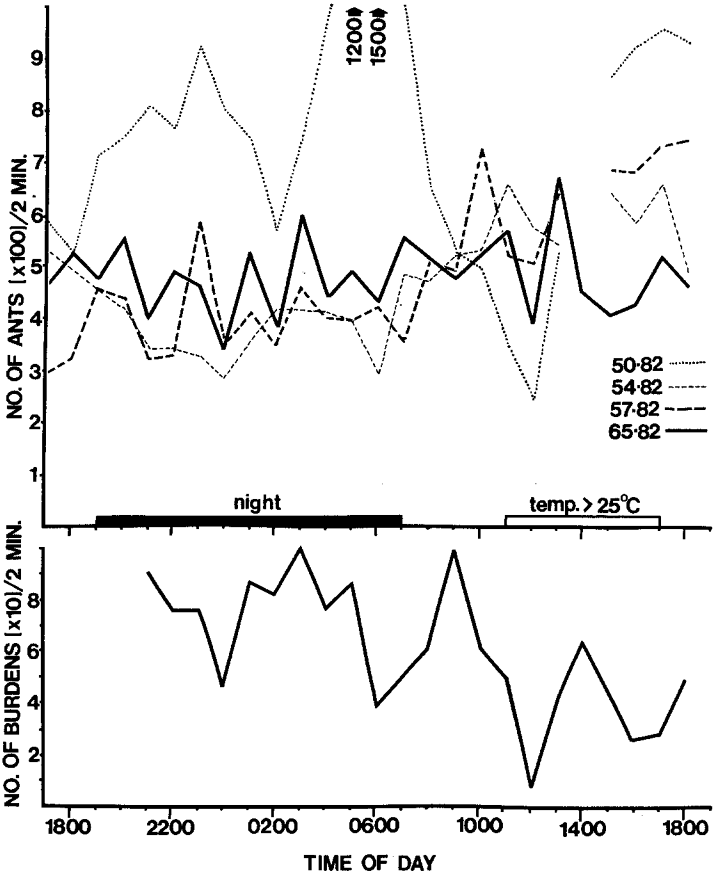

Fig. 3. Activity patterns of four *P. diversus* colonies during a 26-h period with no rain. Ants crossing a point on the trunk trail(s) of each colony were counted for 2 min separately for outgoing and incoming traffic. Second counts of traffic for colony 65-82 taken 5 min after the first differed from the first counts by a mean of 11.7% (and never more than 21%), indicating that 2-min counts were long enough to be representative of the ongoing activity level. Top: Total worker traffic for each colony. Note that data for outgoing and incoming worker traffic (combined for this graph) also showed no diurnal/nocturnal rhythm. Colonies 50-82 and 57-82 had two trunk trails; in both cases the activity on one trail showed no clear relationship with that on the other. Bottom: Number of food items arriving at the nest of colony 65-82 in 2 min. The proportion of the returning ants that carried food similarly lacked any obvious temporal pattern.

the base of trees without climbing the trunks more than 30 cm, but once a raid extended 9 m up a tree.

The pattern of raiding was documented by mapping colony activities and from prolonged observations on selected plots of ground. Sometimes (especially in dry weather), no group-hunting activity was located, and the ants on the trunk trail carried little or no food. More often multiple raids progressed concurrently from widely separated parts of the trunk trail system. For example, the activities of colony no. 61-82 were mapped every day for 6 days at 0630–0900 h (Fig. 4). Column raids were more common than swarm raids. Raids shifted rapidly, so that afternoon checks on the colony usually indicated a trail system differing substantially from that recorded the same morning or the next day. As for most colonies, much of the raiding activity was directed out from the end of the trunk trail. Many raids advance only a few meters from trunk trails; thus areas nearest the trunk trails tend to be crisscrossed by raids most often (Table II).

Raids often cross the paths of recently abandoned trails and raiding columns (e.g., Fig. 4). Raiding workers show no obvious change in behavior upon reaching abandoned routes, neither avoiding the routes nor turning to follow them. This has been documented for raids that had retreated as little as 6 h earlier, suggesting that the courses taken by raids can be largely, if not entirely, independent of those of previous raids. Yet at least some group advances are influenced by past foraging activities: columns of ants have been observed to advance along the routes of trunk trails abandoned up to 4 days previously.

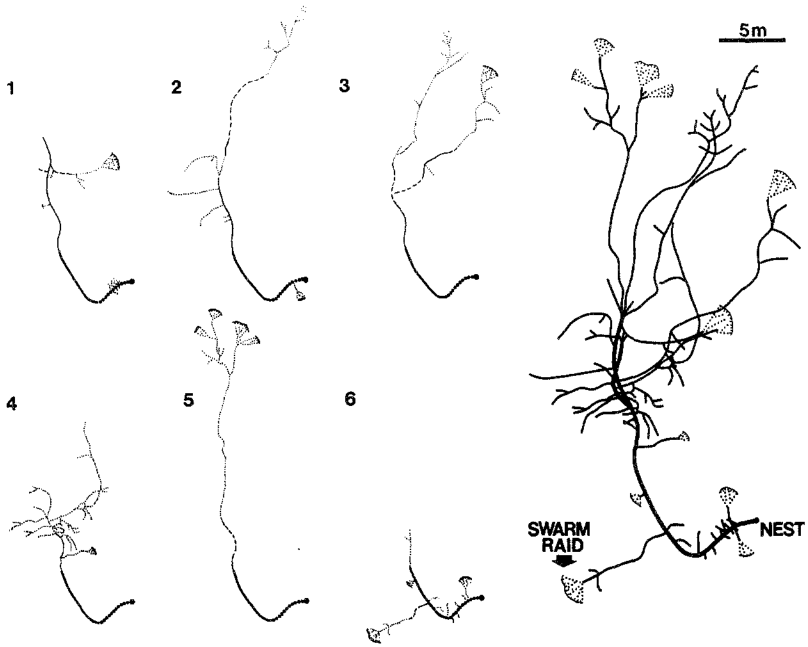

Fig. 4. Six sequential daily maps of the activities of *P. diversus* colony 61-82, which had one trunk trail. At the left are the individual maps; at the right all these maps are overlaid. Map symbols for the overlaid map are as in the legend to Fig. 1; symbols for the remaining maps follow. Wide dotted line, sunken trunk trail; thick solid line, trunk trail with soil cover; thin solid line, trunk trail with soil walls; dashed line, poorly constructed trail; fine dotted line; ant column. Rain averaged 6.5 mm/day, falling nightly except before day 4.

Table II. Discovery of Single Palm Nuts Placed Varying Distances from *P. diversus* Trunk Trails

Distance of bait from trunk trail	Number of experiments	Number of baits discovered by the colony after		
		1 day	3 days	6 days
20 cm	15	7	12	15
1 m	15	5	8	13
4 m	15	0	4	8

Also, temporary trails abandoned for up to 1–2 days are commonly reestablished. However, it is unclear whether advance along old routes is equivalent to raiding. Also, I have never documented an unequivocal example of a raid orienting along the path of a previous transient raid.

In India, ants were observed carrying booty (particularly seeds) down holes (or, in two cases, under leaves) along the basal column formed by workers during raids or along other temporary routes. These appeared to represent booty caches similar to those documented for army ants (Schneirla, 1971). Once the ants carried whole uncooked rice grains from a bait into one hole along a route and soon began to carry out mostly fragmented pieces from an adjacent hole. Booty caches were never seen in the Malay Peninsula or elsewhere in Southeast Asia.

Raid Advance in Relation to Food Distribution

Raids of *Pheidologeton diversus* are not directed toward specific food sources; instead food is usually taken more or less continuously as the raid progresses. Even rich food items are discovered only serendipitously along the advancing fronts of raids. Raids often miss such items: on one occasion a column raid passed within 3 cm of a large fruit, then continued to advance and later retreated without locating the fruit.

Raids are capable of responding to local variation in food density. In one experiment a swarm raid passing through a food-poor area was diverted from its original course with a trail of scattered sesame seeds. The ants tracked the band of seeds for its full 15-m length (Fig. 5). Most raids proceeded in roughly a straight line, suggesting that only prominent differences in density can substantially shift raid direction. For example, a dense column of seeds 1 cm in width was usually tracked precisely by a column raid. In contrast, a few spaced seeds had little impact on the route taken by most raids (Fig. 6).

Is food discovery required for continued raid advance? No: column raids

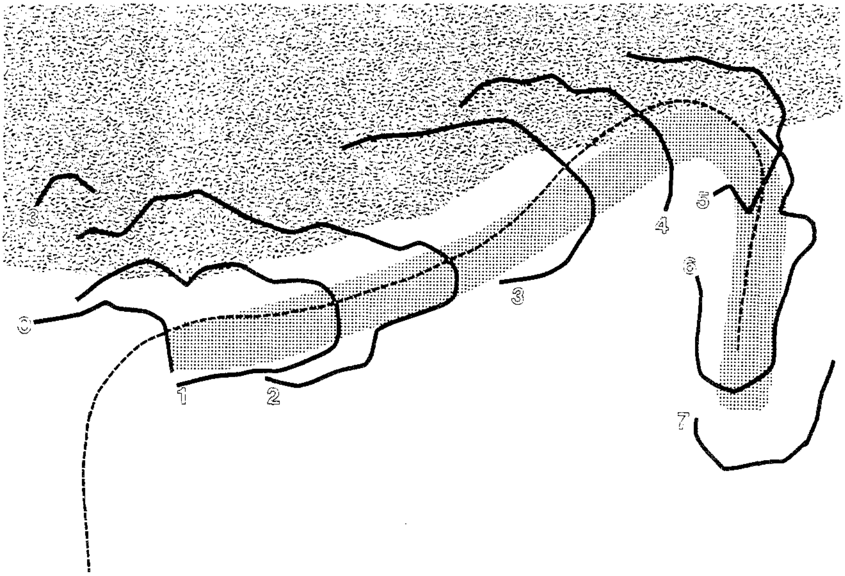

Fig. 5. Response of a *Pheidologeton diversus* raids to a moderate food density. At 1145 h (hour "0"), I scattered sesame seeds as evenly as possible within a 1-m-wide band indicated by the dot stippling, beginning off to the side of an advancing swarm raid, with 1.0 g of seeds/m^2 (i.e., about 1 seed/ 20 cm^2). The raid itself was not disturbed. I mapped the location of the raid front at hourly intervals (solid curved lines) and the course of the basal column of the raid at the end of the observations (dashed line). In addition to the seeds, the ants collected food within the area of leaf litter and vegetation demarcated in the upper part of the diagram; the remaining area was bare ground. By hour 7, the raid had tracked the band of seeds to its end and advanced beyond. The raid had retreated by the next morning.

were found to advance 50 cm or more without taking any food, and swarm raids often passed through areas where little, if any, food was taken. Raids usually went under or around boards placed before them, but I was able to force one swarm raid to advance over a 40-cm-wide board by blocking other possible routes, despite the absence of food.

A lack of food in the raided area can change raid characteristics and eventually lead to raid retreat. Raids passing into areas with little food often slow their advance, and the ant density within the raid decreases as the flow of ants out of the raid increases [similar behavior has been reported for army ants (Schneirla, 1971)]. The sparsity of food on most tree trunks could explain why raids rarely ascend trees. In cases where a raid climbed higher than 1 m, either the trunk was covered with epiphytes harboring food or the ants fed directly on tree bark.

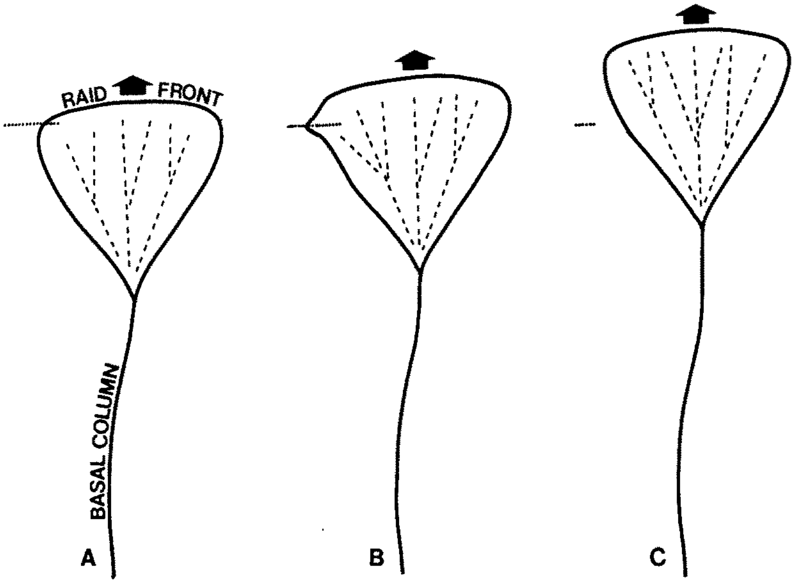

Fig. 6. Response of a *P. diversus* swarm raid to low food density. Sesame seeds were placed 1 cm apart in a 40-cm line. After initially contacting the seed trail (A) the ants extended their foraging activities along the seed trail slightly (B) but never tracked the trail to its end (C). The seeds had no discernible influence on raid direction.

Bulk Foods

Raiding patterns are altered after the ants encounter large food items. Such items can stop raid advance (Fig. 7). Fruit or other "bonanzas" located by raids usually initiated intense raiding activity in their vicinity after an initial rapid buildup of ants at the site (Fig. 8), a phenomena termed "recruitment overrun" by Topoff *et al.* (1980) with respect to *Neivamyrmex nigrescens*. This often led to the discovery of additional fruits, setting off further raids, which explains the dense trail networks often found under fruiting trees. Networks of similar appearance sometimes occurred beneath lights at night where the ants harvested from a rain of falling insects, much as described for *Labidus* and *Neivamyrmex* ants by Rettenmeyer (1963, p. 304).

Harvesting intensity can reach an awesome scale: in India one column about 40 workers in width led up a cacao trunk to a rotten pod 19 cm long. At least 6000 ants passed in and out of the pod each minute, emptying it within 24 h.

The harvesting of bulk foods can continue for long periods. The ants can harvest 300 g of seeds from a canary food mix within 8 h; for as long as 16 h they will thoroughly churn up the soil within a 10- to 20-cm radius of a spot where 2 Tbsp of cooking oil was spilled. The longest periods of harvesting

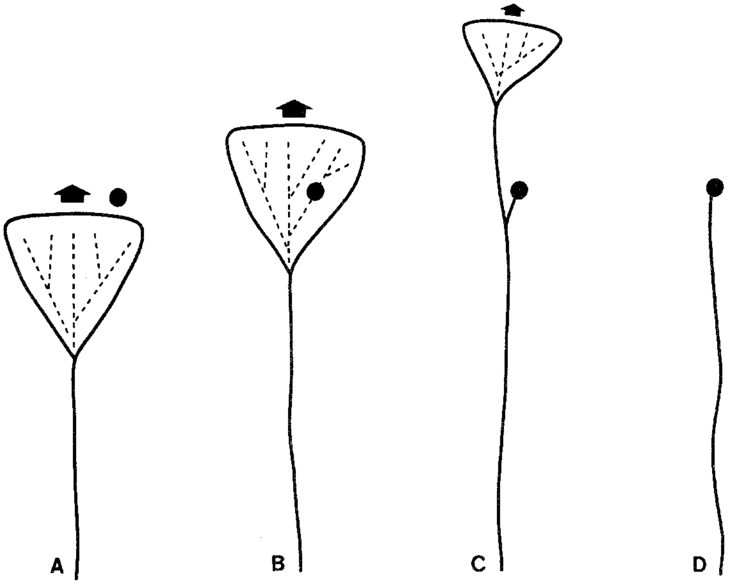

Fig. 7. Response of a *P. diversus* swarm raid to a rich food source. A 300-g bait of fresh beef was placed in front of the raid (A). The ants encountered the bait (B) and advanced about 1.5 m beyond (C), then drained back to the bait (D). The ants then harvested the bait continuously over the next 4 days.

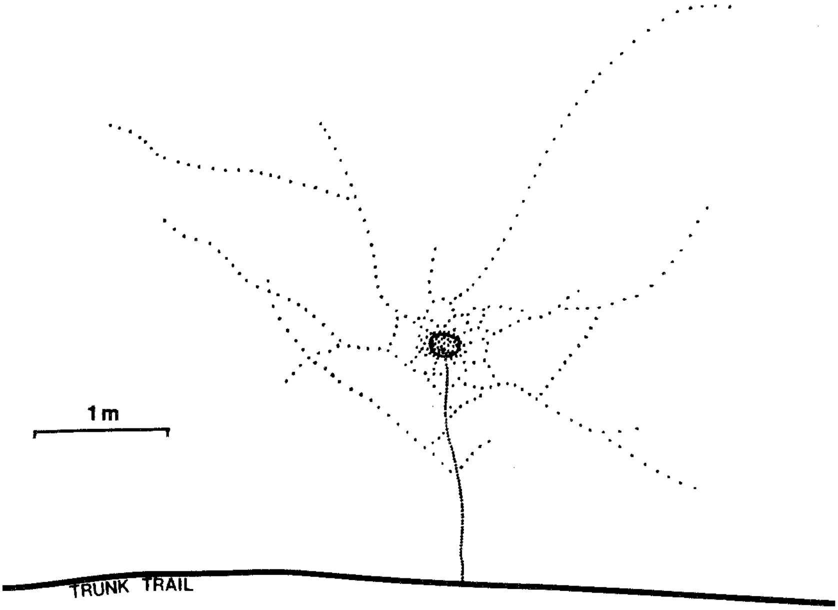

Fig. 8. Response of a *P. diversus* column raid to a large fruit. An increase in the flux of workers into the raid was followed by the formation of this column network within 30 min.

recorded were 6 days for a large fruit of the tree *Caryocar nuciferum* (Theaceae) and up to 8 days for fallen clumps of palm nuts.

Origin of Trunk Trails

Following a period of advance, most raids slowed to a stop and then retreated. Trunk trails originated when the basal trail of a raid continued to be used long after the cessation of the original raiding activity which formed the trail. Raids in which carcasses or fruit were uncovered often had their basal trails develop into trunk trails in the course of the long-term exploitation of these resources. Some of these trails far outlasted this initial source of food. However, most trunk trails were not formed initially to bulk foods; in these cases it was usually unclear why a trunk trail developed from a particular raid.

Swarm raids following heavy rain are apparently the most likely candidates for trunk trail formation. Activity on the basal trail of such raids is generally high, so that many ants are available to take part in trail construction; building activities are facilitated by the damp soil.

Intraspecific Competition and Foraging Dynamics

The 7000-m^2 study area at the Singapore Botanical Gardens was densely occupied (Fig. 9), encompassing trails from between 6 and 11 colonies (7.9 ± 1.6 colonies for nine complete mappings during a 100-day period). Distances to nearest conspecific nests had a mean value of 15.3 ± 4.4 m. The distribution of nests appeared to be primarily the result of the availability of nest sites, since most colonies nested at the bases of large trees.

Territories of *P. diversus* were spatiotemporal (*sensu* Hölldobler and Lumsden, 1980): only areas occupied by the current raids and trails were defended. Thus some areas were foraged intermittently by two or more colonies (although overlap was often minimal; note Fig. 1). When the raids of two colonies collided, small knots of fighting workers developed and the raids drained back in opposite directions. Raids colliding with foreign trails also provoked fighting, but that this did not invariably lead to raid retreat was indicated by the occurrence of trails that crossed. The colony with the more recently formed trail crossed the other using low-lying sticks or vegetation or, sometimes (but not for long), the soil cover of the older trail. In two of the five instances observed both trails continued beyond the intersection as well-constructed trunk trails lasting 9–13 days, even though knots of fighting workers were common near trail intersections and piles of up to 300 dead ants were sometimes found. The first colony to abandon its route was that with the newer trail in at least four of the five cases.

Rich food finds were vigorously defended. Wide bands of fighting workers developed when two colonies attempted to harvest the same bait [in experiments

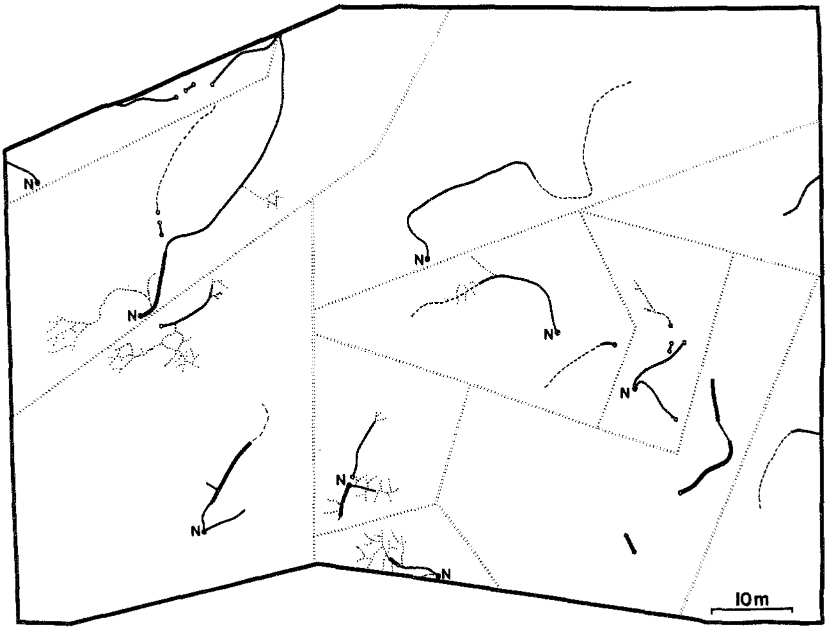

Fig. 9. A map of *P. diversus* trails within the 7000-m^2 Botanic Garden study area, showing the locations of nests (N) and trails. Dotted lines separate the areas currently foraged by different colonies; other symbols as in the legend to Fig. 4.

usually piles of seeds from a canary food mix (Moffett, 1987)]. These bands often shifted until one colony completely drove the other away from the food site.

Interspecific Competition and Foraging Dynamics

Interactions with other ant species were documented with 40 baits each of honey water, cooking oil, lean pork, seeds from a canary food mix, and cooked rice positioned at various sites within the Botanic Gardens study area over a 3-week period. Of the 200 baits, 71 were preempted by *P. diversus* within a 24-h period, including several examples of every type of bait presented. Forty-three of these 71 baits had initially been harvested by other ant species but were usurped at some point by *diversus*.

Once taken over by *P. diversus* no bait was relinquished to other species (except possibly one rice bait, which was more likely abandoned by the *diversus* and later consumed by another, unknown species). *P. diversus* aggressively defended food from all intruders. Indeed, during my observations no ants harvested from baits controlled by *diversus* except one *Diacamma rugosum* individual observed lowering itself from grass blades to drink from a honey-water bait below and a case of *Tetramorium* ants emerging from beneath a boiled rice bait. In both cases the success of the second species was short-lived.

These observations indicate that *P. diversus* is highly successful in its competitive interactions with many ant species. Raiding workers are usually able to drive competitors from food through sheer force of numbers and successfully defend the food until it is completely harvested. Yet I have seen *Tapinoma* sp., *Meranoplus bicolor*, and *Solenopsis geminata* repel advancing raids apparently by using noxious chemicals, while *Oecophylla smaragdina* and (less often) *Proatta butteli* can deter this species through direct physical assaults. Swarm raids were clearly more successful at driving away competitors than column raids, presumably because of the greater number of ants involved.

The aggressiveness of the ants in *P. diversus* raids was shown by this species' success in forcing a ring of 150–250 *Oecophylla smaragdina* workers up the trunk of a *Lansium domesticum* tree (Meliaceae) and out onto lateral branches. This was observed four times, and in each case the *P. diversus* ants then ate the bark of the tree for several hours. Yet the *O. smaragdina* colony involved was relatively small (encompassing only two other 8- to 10-m-tall adjacent trees). As in *Anomma* driver ants (Gotwald, 1974a) it is doubtful that the *diversus* ants could have competed against a full-sized colony. In addition, I often observed *Oecophylla* ants plucking *diversus* workers from columns, exactly as described for *Anomma* ants by Gotwald (1972).

DISCUSSION

Group Hunting: General Considerations

Army ants (doryline and ecitonine ants) group-hunt, that is, workers search for food together in a cohesive, relatively rapid, and continuous group advance (or ''raid'') (Oster and Wilson, 1978); solitary hunting is essentially absent, being reduced to short episodes along the advancing margin of a raid. ''Group predation'' is a more general term than ''group hunting'': it applies to any species in which workers attack live prey en masse, using a common path or trail both to reach the prey (''group raiding'') and retrieve any booty (''group retrieving'') (Wilson 1958, 1971). In contrast to army ants, workers of most group-predatory species hunt prey solitarily and then recruit nestmates over a distance to it. Such behavior has been documented for many ponerine genera (Fletcher, 1973; Maschwitz and Mühlenberg, 1975; Longhurst and Howse, 1979, Hölldobler and Traniello, 1980; Hölldobler 1982, 1984; Peeters, 1984) and in other ants (e.g., Hölldobler, 1973; Longhurst *et al.*, 1979). Unfortunately, the foraging behaviors adopted by these ants have generally been confounded with group hunting (e.g., Wilson, 1958; Schneirla, 1971; Gotwald, 1982).

The confusion between group-hunting and other strategies is in part the result of a widespread failure to recognize two largely independent stages in the process of obtaining food: the search for food (''foraging'' in a narrow sense) and the harvesting of food (encompassing recruitment to food, and the killing, tearing apart, transport, and consumption of food). Many classifications of ant foraging strategies will have a greater heuristic value when these two activities are clearly distinguished.

Group hunting (and the concomitant loss of solitary hunting) is perhaps the key innovation in the evolution of doryline and ecitonine ants. This strategy is apparently very rare outside of the army ants, having been clearly demonstrated only for *Onychomyrmex* (Hölldobler *et al.*, 1982; Hölldobler and Taylor, personal communication) and to a limited extent in *Leptogenys ocellifera* (Maschwitz and Mühlenberg, 1975). Further documentation will be required to determine if group hunting occurs in *Simopelta* (Gotwald and Brown, 1966). *Leptanilla* ants have been treated as army ants (Wilson, 1971), but laboratory observations by K. Masuko (personal communication) suggest that group hunting is poorly developed or absent.

Group Hunting in *Pheidologeton diversus*

Similarities of certain ponerine genera to the behaviors associated with army ants (Wilson, 1958) could conceivably be in part a reflection of close phylogenetic ties between these groups (Gotwald, 1982). In contrast, similarities of this kind between *P. diversus* and army ants clearly represent convergences.

Pheidologeton diversus shows true group hunting, in that the search for food is essentially restricted to the advancing margins of raids, and the course of a raid is not dictated by scout ants recruiting from a distance. As a consequence, any given worker has, at most, a small and temporary influence on raid progression; conversely, the movements of each worker are tightly constrained by that of the raid. Solitary workers do not travel far from trails and take very little food. Such workers can recruit to food, but judging from the experiments of Chadab and Rettenmeyer (1975) similar behavior is possible in *Eciton*. The proclivity of *P. diversus* workers to move ahead of other ants at raid fronts [in extreme cases up to 50 cm (Moffett, 1984, Fig. 2)] and wander short distances from trails may be somewhat greater than in army ants, perhaps because this species has compound eyes [army ant workers are blind or have their eyes reduced to single facets (Schneirla, 1971; Gotwald, 1978a)].

P. diversus raids are structured remarkably like those of army ants (Moffett, 1984). This study documents further similarities in group-hunting dynamics. As in army ants (Torgerson and Akre, 1970), advancing groups can orient along abandoned trails, but the available evidence indicates they do not necessarily do so. Also, raid advance is not intimately tied with food discovery, so that raiding can continue over areas without food. This is probably also true for army ants; for example, the raids of *Eciton burchelli* and some *Anomma* species often climb trees offering little food on the main trunk (Rettenmeyer, 1963; Chadab-Crepet and Rettenmeyer, 1982; Raignier and Boven, 1955).

The raids of the army ant *Eciton burchelli* appear to avoid the paths taken by previous conspecific raids (Franks and Bossert, 1983). This species feeds in large part on social hymenoptera, which can take months to return to preraid densities; nonsocial prey recover within a week (Franks, 1982). Avoidance of old raid tracks should be advantageous, since social insect densities are low in previously raided areas. *P. diversus* showed no signs of raid track avoidance (Fig. 5). This could be a result of the quickness with which many of the foods of this species rebound to former densities: raids passing over areas raided the previous day often still took considerable food. The raids of *Labidus praedator* (Willis, 1967), *Aenictus gracilis*, *A. laeviceps* (Schneirla, 1971), and *Anomma* ants (Gotwald, personal communication) apparently also do not avoid old raid tracks. Like *P. diversus* (Moffett, 1987), these ants depend relatively less than *E. burchelli* on slowly renewable social insect prey (Willis, 1967; Gotwald, 1974b). The courses of raids in such species may be more directly influenced by food densities than in *E. burchelli* (Franks and Fletcher, 1983): *diversus* raids are capable of tracking areas of high food density, as can apparently occur in *L. praedator* (Willis, 1967) and *Anomma* ants (Raignier and Boven, 1955).

Advantages of Group Hunting

Why search for food in groups? The rate of food discovery during group hunting is sharply reduced over that which would result if the ants split up and hunted separately, since the ants in a raid spend most of their time repeatedly covering the same ground. The advantages of group hunting must outweigh this shortcoming by yielding a sufficiently increased probability that discovered food is successfully returned to the nest. Such advantages relate to harvesting efficiency, competition, and the potential for capturing formidable prey. Only the latter has been discussed in any detail for army ants (i.e., Wilson, 1971). Advantages in all three areas are important in *P. diversus*.

At any given moment the swarm behind the raid front can be viewed as a pool of potentially recruitable workers which has been transplanted from the nest to an area considerably closer to where food discovery occurs (the raid front). This characteristic is used most effectively in exploiting food finds requiring many ants, for instance, large or intractable food items. In most ants that search for food solitarily and recruit assistance at a distance, the buildup of workers at the food can be much more time-consuming than in group-hunting species (Chadab and Rettenmeyer, 1975). Also, solitary hunters must leave food finds unattended for long periods while recruiting others. This is a serious drawback of most foraging strategies involving recruitment, as other ants can usurp the food while it is unattended (Oster and Wilson, 1978) or (in the case of prey) the food itself may move elsewhere. Group hunting leaves little or no time for this to occur. The strategy also confers *P. diversus* with another competitive advantage: experiments with baits have demonstrated that other species, occasionally even the tenacious ant *Oecophylla smaragdina*, can be driven from food by the sudden deluge of *diversus* workers in an advancing swarm raid.

Trunk Trails

P. diversus invests so much in the defense and maintenance of its trunk trails (Moffett, 1987) that it often seems more legitimate to view such trails as an extension of the nest than as part of the foraging system. Trunk trails (i.e., routes used daily as a base from which raids extend) are occasionally formed during the statatory period by army ants such as *Eciton hamatum* and *E burchelli* (Rettenmeyer, 1963, p. 327; Schneirla, 1971, p. 96), *Neivamyrmex nigrescens* (Schneirla, 1963), and *Anomma nigricans* (Cohic, 1948). Trunk trails also occur among other myrmicine ants (e.g., Hölldobler, 1976; Hölldobler and Möglich, 1980; Shepherd, 1982; Moffett, 1986), which hunt out from the trails solitarily.

The trunk trails of *P. diversus* have several functions. The trails expand the trophophoric field by making distant regions accessible. Furthermore, a well-maintained trail provides for more rapid traffic flow to and from distant areas (Moffett, 1987). In *diversus* traffic along the route is protected from disturbances from foreign ants, *Bengalia* flies (Jacobson, 1910; Bequaert, 1922), and other sources by the trail's physical structure (Moffett, 1987). However, these trails appear to play a less prominent role in separating foraging areas than in species such as *Pogonomyrmex badius* (Hölldobler, 1976), as the trails of conspecific colonies do occasionally cross. Trunk trails are also available as emigration routes (Moffett, 1988), as in certain other myrmicine species (e.g., Harrison and Gentry, 1981) and army ants (Schneirla, 1971; Gotwald, 1978b).

In some myrmicine species (Hölldobler and Lumsden, 1980) and possibly in army ants (judging from Schneirla, 1963), trunk trails serve primarily to orient foragers into "disjunct" food patches (patches in which the food is dispersed such that, on average, appreciable search time is required to locate individual items in the patch). Qualitative observations suggest that *P. diversus* trunk trails can likewise respond to such food patchiness. For example, when part of the environs of a nest was clearly richest in food (e.g., for a colony located near a fruiting tree), the colony's trunk trail usually extended into this area.

P. diversus trails are also used in the long-term exploitation of "conjunct" patches such as bulky food items (or a heap of seeds). Army ants are not known to use trails in this way: the army ant diet is limited to foods that can be harvested within the duration of a raid. Prey too large for transport are abandoned when a raid ends (Rettenmeyer, 1963, p. 422; Pullen, 1963).

Origin of Group Hunting

The evolution of raiding and nomadism (see Wilson, 1958) in army ants and certain ponerines has been addressed by Wilson (1958, 1971) and Schneirla (1971), but the emergence of the group-hunting pattern itself has never been considered. One possibility is that group hunting in *P. diversus* and army ants represents a modified trunk trail formation process. Indeed, the basal trails of raids can be viewed as trunk trails, albeit relatively short-lived ones. The advantages discussed for group hunting at least potentially hold to a lesser extent for solitary hunting species with trunk trails. Indeed, trunk trail dynamics in certain ants of this description include elements suggestive of group hunting [e.g., *Pheidole militicida* (Hölldobler and Möglich, 1980), *Veromessor pergandei* (Wheeler and Rissing, 1975)], and hopefully additional studies on the development of individual trails will further clarify the extent of these similarities. Conceivably the ancestors of group-hunting ants searched for food solitarily from trunk trails, and the acceleration of trunk trail ontogeny into a raiding process (and concomitant reduction of forager autonomy) occurred to increase the efficiency with which formidable prey are captured or because of other advantages of group hunting. If so, intermediate stages in the evolution of group hunting should be sought among the ants that use trunk trails, especially those related to army ants or to *P. diversus*.

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