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Marauder Ants (*Carebara* in Part)



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Synonyms

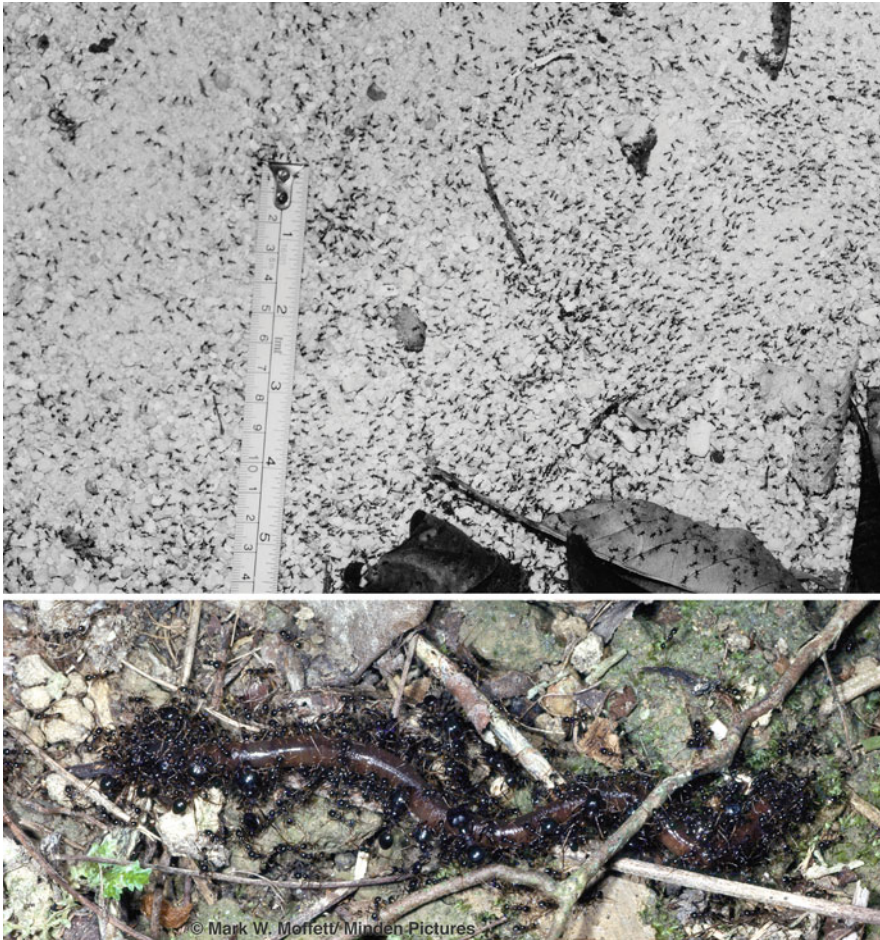
Pheidologeton

The term marauder ant refers to the two species *Carebara diversa* and *C. silenus*, myrmicine ants until recently placed in their own genus, *Pheidologeton*. This is a monophyletic group of behaviorally and ecologically distinct ants [1]. The better-known species, *C. diversa*, is most common in disturbed habitats extending from India across Southeast Asia to southern China and Taiwan, while *C. silenus* resides in forests of the Malay Peninsula, Sumatra, Java, and Borneo. These species warrant attention because of their extreme physical castes and a remarkably flexible foraging strategy that includes finding food en masse, at a scale similar to many doryline army ants, with the collective foraging raids of marauder ants reaching into the tens of thousands of participants [2] (Fig. 1).

Foraging

Much of the interest in marauder ants arises from their similarities to army ants. In comparing these two groups, it is important to contrast solitary foraging with collective foraging, the quintessential army ant trait. Solitary foraging is the norm for most ants, including the workers of many species that are said to raid. In such species, the workers actually search for a resource (often food but slaves in the case of slave-making ants) on their own and recruit over a distance to it. The raids that result from this act of recruitment function not so much to locate food as to harvest food already found. In contrast, marauder ants and army ants do not have such solitary workers (“scouts”) that travel a substantial distance alone.

The crux of collective foraging is that raids are not directed toward a specific resource, since the ants in the lead of a raid do not follow signals left by nestmates that passed through the area earlier. Instead, the search for resources involves multiple individuals acting collectively. Rather than looking for food side by side, as human hunters might, the foragers advance in continuous columns, which sometimes end in swarms. Marauder ant workers near the forward edge of a column or swarm raid run around up to a few centimeters onto uncharted ground before others replace them to extend this search. Because foragers seldom stray far from other ants, each worker has only a small, temporary influence on a raid’s progress, nor does the continued progress of a raid depend



Marauder Ants (*Carebara* in Part), Fig. 1 Top: Ants within a swarm raid of *Carebara silenus* in an area about 20 cm wide. Bottom: A typical large earthworm being transported by *Carebara diversa*

on those workers locating food (albeit desirable food amplifies raid intensity and can shift a raid's direction [3]).

Marauder ants raid around the clock. Most raids take the form of narrow columns, as do those of many army ants and the few other species with collective foraging. However, some raids can expand to four or more meters wide. In these swarm raids, many ants at once conduct their searches along a broad raid front that takes a fan shape, narrowing behind to a column that ultimately extends to the nest, a configuration remarkably similar to swarm raid of army ants. Marauder swarm raids can progress more than 20 m before withdrawing. Swarms move forward 2–3 m per hour in *C. diversa* and 4.5 m/h in *C.*

silenus, less quickly than the best-known army ants (certain African *Dorylus* driver ants and New World *Eciton burchellii*), but speed similar to the swarm raids of other *Dorylus* species [4]. The column raids of marauder ants can advance two or three times as fast.

Marauder ants, like army ants, depend heavily on group predation. That is, within a raid they search for and often catch, kill, and retrieve live prey in groups. *C. diversa* seize everything from springtails and fruit flies to grasshoppers, scorpions, and small frogs or geckos (though, unlike some army ants, they do not attack social insect colonies). Besides that, about half of *C. diversa*'s diet is a smorgasbord of plant material, including seeds, nuts, fruits, and, when other food is scarce,

tree bark. Collective foraging permits the ants not only to search out and surprise prey but also to fend off competing ants from other kinds of food and to harvest it without delay.

Worker Castes

In all such activities, the ants rely on a division of labor [5] (Fig. 2). *C. diversa* has the most extreme polymorphism of any ant species, as measured by its range of worker sizes. The largest workers, or majors, have heads ten times as wide and dry weights 500 times those of the superabundant minors, which account for at least 99% of the colony. Except for a gap in the distribution of head widths between all the similar-sized minors and the next largest (media) ants, workers of every possible size exist between the extremes (Fig. 3).

During a raid, the minor workers are first to reach the front. Marauder ants lack stingers, and the minors act in hordes not only to find but also to subdue prey. Being numerous, tiny, and disposable, the minors are often killed in struggling with prey. By the time the quarry is restrained, the more valuable larger ants arrive and give crushing blows with the mandibles, chopping off any part of the prey that moves, at little risk to themselves. Removing any flailing appendages need not kill the prey, and immobilized invertebrates are often found whole inside the nest, where they seem to be stored until eaten.

All the workers jointly carve soft or unmanageably sized or shaped items to pieces, which teams of minors and an occasional media efficiently haul away singly or by group transport. As many as 100 *C. diversa* can fetch a 10 cm earthworm 5000 times the weight and 10,000 times the volume of each of its carriers; the assembled ants' travel speed only reduced to a quarter of that of unburdened workers [6] (Fig. 1).

There are other aspects to the marauder ant division of labor. Upward of 20 minors ride on some large majors; being carried is expected to be an overall energy savings [5]. Additionally, *C. diversa* medias extract seeds from grass stalks, which the minors then carry off, effectively forming a conveyor belt. Mostly the larger

workers mill seeds with their mandibles, usually inside the nest. A specialized caste of replete media and major workers, gasters engorged with food, reside permanently within peripheral nest chambers, and regurgitate meals to nestmates.

Modification of the Environment

The ephemeral raids are just part of *C. diversa* strategy in managing its environment [3, 7]. These ants construct stable trunk trails from their nests, usually one or two at a time, which can reach 100 m in length, in places underground. In southern India, *C. diversa* cache food along these trails. Trunk trails are best known in ant species that forage out from them solitarily, but they also exist in some army ants, in which the routes can similarly last 2 or more months [4, 8]. *C. diversa* trunk trails are replaced at intervals by alternative trunk trails that build up after raids head out in a new direction. Medias and majors act as heavy-duty road equipment, clearing trunk trails by clearing away fallen debris with their heads or dragging off, or gnawing at, obstructions. Mostly the minors chisel the ground surface, making the trail suitably smooth for easier transit.

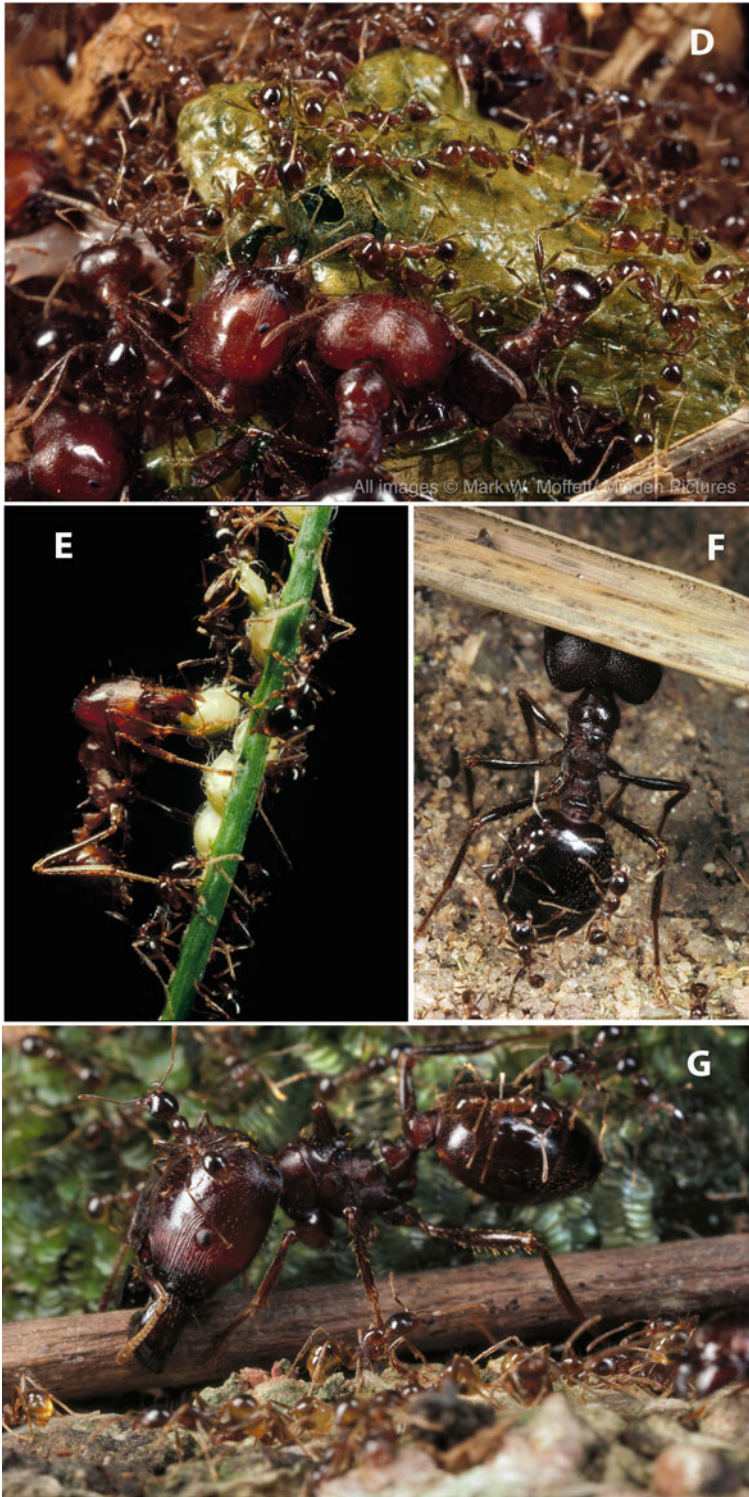
Raids extend from trunk trails or directly out of the nest. Trunk trails expand the territory over which the ants can travel and swiftly assemble and provide safety too. Their flanking soil walls and roof reduce disturbances from other ants. The structures are built by the smaller workers, although majors tamp the covers into position from time to time with their heads. Similar earthen arcades are made during the course of a raid by army ants, but in marauder ants, the covered trail effectively becomes an extension of the nest and may eventually sink below ground. A pattern tends to emerge when a trail is heavily used, with incoming ants following the midline, relegating the outbound worker traffic to each side, an arrangement that reduces congestion.

Another part of the *C. diversa* foraging strategy comes into play where food is locally bountiful, whether the ants discover a single massive food item like a vertebrate carcass or a patch of fallen fruit scattered beneath a tree. The ants build



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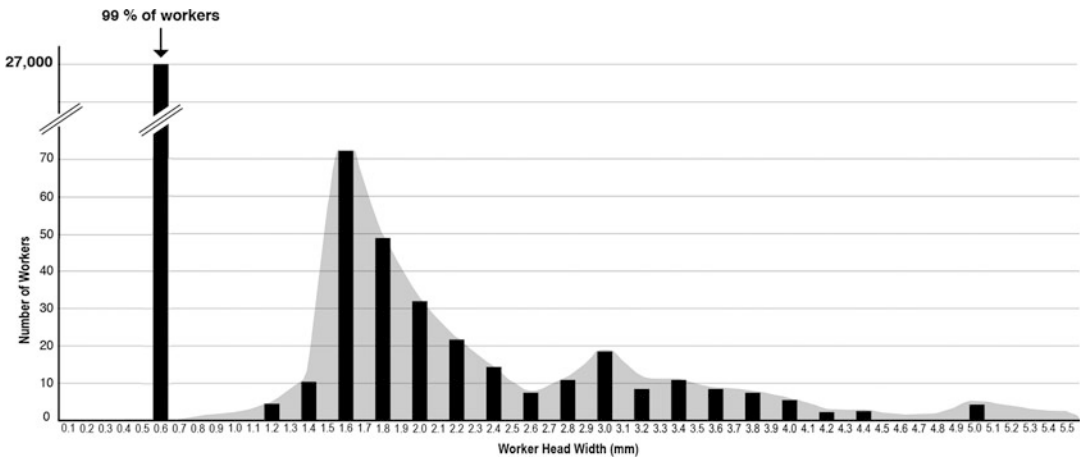
Marauder Ants (*Carebara* in Part), Fig. 2 (continued)



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Marauder Ants (*Carebara* in Part), Fig. 2 Division of labor among media and major workers (*Carebara diversa*): (a) carry minor workers; (b) haul the colony's brood during

a nest disturbance or migration; (c) kill and discard ants of other species disturbing trails (only minor workers participate in wars between marauder ant colonies); (d) give a



Marauder Ants (*Carebara* in Part), Fig. 3 Polymorphism in *Carebara diversa*. The bar graph shows the size distribution for a portion of a colony from Singapore; the number of minor workers had to be approximated. The distribution in gray shows my estimate for the distribution

of ants in the colony as a whole: The very largest ants are extremely rare but important behaviorally and might well form a fourth peak in the size distribution (“supermajors”). (Photographs copyright Minden Pictures, all rights reserved)

elaborate scaffoldings of soil, at times upward of a quarter meter wide, to feed on these objects. Upon encountering such a bonanza, the ants quickly raid outward in columns to establish a trail network that permits them to harvest from and control the surrounding region for many days.

Comparison Between Species

The two species differ in several notable ways [9]. Trunk trails are unknown in *C. silenus*, so that raids arise directly from the nest or branch from other raids. The species harvests far less plant matter than *C. diversa*. Despite its faster raids, *C. silenus* also rarely succeeds in capturing massive or agile prey, mostly taking invertebrates not more than a few times the size of its minors.

Colonies attain populations of 250,000 in *C. diversa* and 100,000 in *C. silenus* [10]. Both species tend to nest at tree bases, at least *C. diversa* making use of preexisting cavities in part. The workers form thick masses within these spaces, with the minors often stretching out between the various larger ants and brood, linking them together though without forming the neatly arranged chains seen in army ants. Colonies of *C. diversa* often emigrate every few weeks or months, in line with some *Dorylus* and New World *Labidus* army ants [4], but less often and not as regularly as such plainly nomadic army ants as *Eciton burchellii*. Marauder ant emigrations make use of what had been the colony trunk trail and require a few nights to be completed. Aggressive ants patrol outward from the migration route where it crosses bare ground (behavior otherwise only seen when a trail or nest is disturbed). A *C.*

Marauder Ants (*Carebara* in Part), Fig. 2 (continued) death blow to the prey at the raid front, in this case a frog; (e) extract seeds from grasses; (f) push obstructions off the trail with the head; (g) gnaw obstructions along a route that can’t be pushed away. Among the behaviors not illustrated are serving in the nest as a replete and “tamping” a trail’s sagging soil cover. The frequency of participation by the

variously sized workers depends on the job [2], but the medias are most uniquely important in task E and also occasionally assist the minors in transporting food, depositing soil on puddles and building earth covers over trails, while usually the majors, and especially the largest “supermajors,” perform task F

silenus queen observed in transit ran under her own power accompanied by a retinue of several hundred minors that swelled the column as she passed.

Where marauders differ most significantly from the army ants is in the mode of colony foundation [10]. New colonies don't form by fission. Rather, the virgin queens go on mating flights, as they do in most ants (Fig. 4). Some colonies may be founded by multiple queens (pleometrosis). How a nascent colony forages is unknown.

A variant of collective foraging exists in a partially subterranean *Carebara* species related to marauder ants. In Peninsular Malaysia, *C. affinis* workers extend weak columns a few meters across the ground surface over periods of hours, a slow-motion activity that leads to the ants collecting tiny seeds or sporadic tiny insects [11, 12]. Species like *C. affinis* might hold clues to the evolution of the remarkable collective foraging of both marauder ants and army ants, given that, for example, the ancestors of *Dorylus* and *Ectiton* were subterranean [13, 14]. A likely scenario is that raids arose when an ancestral species, foraging in interstices underground, could only locate food by working in numbers to clear passages, yielding trails that their search parties would add



Marauder Ants (*Carebara* in Part), Fig. 4 A dealate *Carebara diversa* queen collected after a mating flight. The queens dig into the soil and attach their first eggs to a smooth patch beneath their gasters. (Photograph copyright Minden Pictures, all rights reserved)

to over the long term. When this species shifted to moving collectively on the ground surface, its ants would be able to jointly forage far faster, transforming what had been a system to incrementally build trunk trails into full raiding behavior. Collective foraging would have evolved as an accelerated trail production process in which group advance becomes disengaged from food discovery, most likely as a result of difficulties of foraging in the soil that have since been overcome by more efficient subterranean species [3, 12].

Cross-References

- ▶ [Army Ants](#)
- ▶ [Group Transport](#)

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