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Swarm Raiding in a Myrmicine Ant

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Doryline ants (commonly known as army ants) are among the best studied social animals [1]. This can be attributed in large part to their dramatic raiding behavior. While the majority of doryline species forage in narrow columns, a few raid in broad swarms [1]. Swarm raiding, though rare, has been studied intensively [1, 2], and has long been recognized as one of the most impressive examples of coordinated group activity shown by animals [1]. To date swarm raiding has been found only in doryline ants. I report the discovery of massive swarm raiding in the myrmicine species *Pheidologeton diversus* (Jerdon); the raids of this highly polymorphic Asian ant (Fig. 1) are remarkably convergent with those of army ants.

P. diversus colonies have one or two stable trunk trails (i.e., relatively long-lasting orientation trails [3]), which extend 5–100 m from the nest. Trunk trails often remain in use for weeks, during which time ants move along them continuously, day and night. A variety of other ants, including certain dorylines [4], also produce trunk-trail foraging routes.

The great majority of ants search for food solitarily [5]. This is also true for most species with trunk trails, since workers depart from the trails singly to search for food. However, in *P. diversus*, as in doryline ants, trunk trails serve as the departure points of raids: solitary foraging, insomuch as it can be said to occur, is restricted to the advancing fronts of these raids (other than at the raid front, solitary ants rarely travel even 5 cm from a trail). Raids originate at any time of day and from any point along the trail; they advance for variable distances and then usually retreat. Raids are apparently influenced little by the courses of recently retreated raids, and will advance readily over previously unvisited ground [6].

A raid begins when ants abruptly move out from some point along a trunk trail or from the nest entrance and then advance at 10–20 cm/min in a narrow column. After the column extends between 0.5–3.0 m, the ants at its terminus spread out to form a narrow group, and progress begins to slow. A minority of these column raids further expand into larger, fan-shaped raids (Fig. 2) which sometimes advance at least 20 m. Within a narrow region along the advancing margin of these raids, ants move about in large numbers, forming a swarm. Behind this region, most ants move in a fan-shaped network of columns. The raid funnels back to a single, basal column, which lengthens as the raid progresses.

The raids of *P. diversus* can reach 6 m in width and contain tens of thousands of individuals. Such raids resemble those of swarm-raiding doryline ants, yet they advance slowly, usually 1.5–2.0 m/h, while doryline swarm raids often sweep ahead at 10–20 m/h [1]. A disparity in worker movement patterns probably accounts in large part for this difference. In contrast to doryline ants [1], workers at the raid front do not advance rapidly and directly on to uncharted territory and

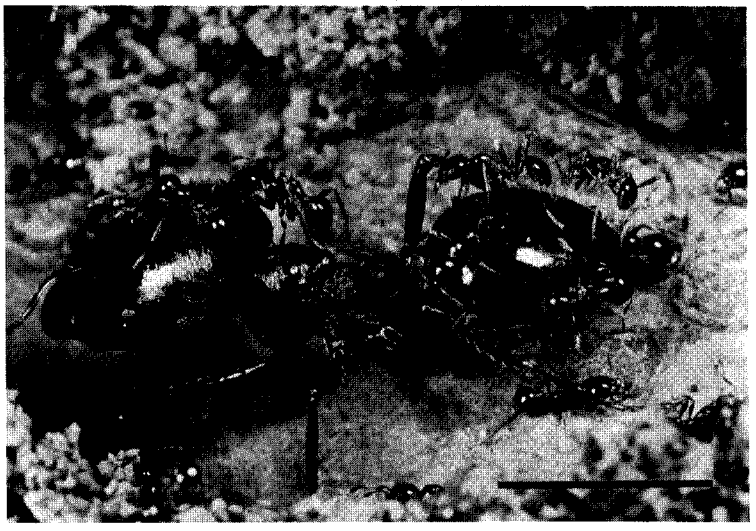

Fig. 1. *Pheidologeton diversus* foragers, including several minor workers riding on a large major (scale bar = 0.5 cm)

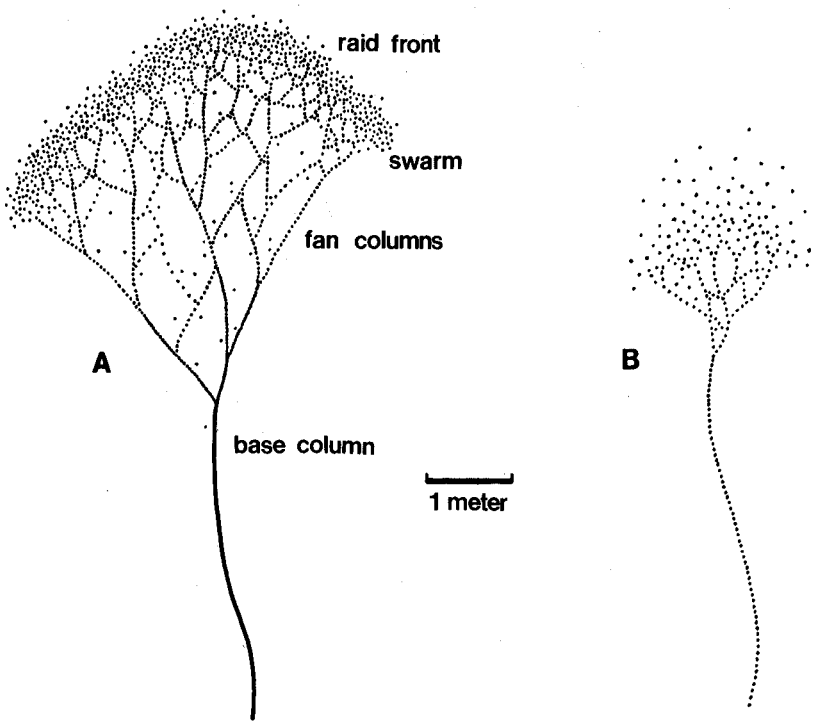

Fig. 2. Two extremes in the raiding pattern of *P. diversus*. In pattern A, worker density is high and concentrated at a well defined raid front. Raids of this description vary from 2 to 6 m across. Pattern B is characteristic of most smaller raids. Workers are relatively spread out, so that, in extreme cases, scattered individuals advance as much as 50 cm ahead of other ants

then retreat; rather they meander considerably, and without the rapid turnover characteristic of ants at a doryline raid front.

Whereas the recruitment techniques of other predatory ants allow the capture of agile prey up to at most a few times the body weight of individual foragers, *P. diversus* and dorylines capture relatively formidable prey, including prey having dry weights hundreds or thousands of times greater than that of the ants participating in prey capture. In *P. diversus,* common prey include cockroaches, centipedes, orthopterans, and earthworms up to 10 cm in length. Workers rush at prey encountered during the advance of a raid, piling on until the quarry is securely pinned down and can be torn apart.

As the raid advances, the ground traversed is covered repeatedly by many individuals within the swarm. This leads to the ferreting out of an impressive variety of foods other than difficult prey. For example, the ants also catch smaller prey, even such tiny, elusive insects as collembolans and fruit flies. And, unlike doryline ants, which have diets composed almost entirely of animal material [1], in *P. diversus,* seeds, nuts, and fruits form an important part of the diet: usually almost half the material carried to the nest is of vegetable origin [6].

A variety of ants other than *P. diversus* and doryline ants have been referred to as "raiding" or "group raiding" ants. These include slave-making ants, cerapachyine ants, and certain ponerine ants, all of which attack other ant colonies or formidable prey. In *P. diversus* and doryline ants, workers search in groups for live prey and other food, while, with few known exceptions [7], the foragers of these other raiding ants search for prey and other food solitarily and then recruit workers over a distance to it. The difference is fundamental: the raids of both *P. diversus* and doryline ants are not directed toward specific food sources. Indeed, this feature is the crux of the army ant foraging strategy.

Doryline ants foraging in swarm raids are characterized by their large colonies, relatively broad diets, and the efficiency with which they kill massive prey [8]. Tropical Asia lacks epigaeic doryline species of this description, although such ants are conspicuous in Africa (i.e., some *Dorylus* spp.) and Central and South America (i.e., *Eciton burchelli* and *Labidus praedator*). In Asia, *P. diversus* and probably some other related *Pheidologeton* species have apparently preempted this army ant niche.

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1. For a review see: Gotwald, W.H., in: Social Insects, Vol. IV, p. 157 (H.R. Hermann, ed.). New York: Academic Press 1982. Note that the Dorylinae are probably triphyletic (see Gotwald, ibid.)
2. Franks, N.R., Fletcher, C.R.: Behav. Ecol. Sociobiol. *12*, 261 (1983)
3. Hölldobler, B., Lumsden, C.J.: Science *210*, 732 (1982); Hölldobler, B.: Behav. Ecol. Sociobiol. *1*, 3 (1976)
4. For example, *Neivamyrmex nigrescens* (Schneirla, T.C.: Anim. Behav. *11*, 583 (1963))
5. My use of the term 'solitary foraging' (to contrast with 'group foraging') encompasses foraging types I–IV of G. Oster and E.O. Wilson (pp. 248–251 of: Caste and Ecology in the Social Insects. Princeton Univ. Press 1978). Although workers search for food separately, in many species recruitment must occur before the retrieval of an intractable food item can begin
6. Moffett, M.W.: in preparation
7. *Leptogenys ocellifera* shows limited group foraging behavior (Maschwitz, U., Mühlenburg, M.: Oecologia *20*, 65 (1975)) and *Onychomyrmex* spp. invariably forage in groups (Hölldobler, B.: unpublished)
8. Wilson, E.O.: The Insect Societies. Cambridge: Harvard Univ. Press 1971