"ARMY ANT" BEHAVIOUR IN THE PONERINAE: A RE-ASSESSMENT

D.J.C. Fletcher, Department of Entomology, University of Natal
Pietermaritzburg. South Africa.

Wilson (1971) has said that it is seldom recognized that the behaviour patterns characteristic of the doryline "army ants" also occur in some groups of the primitive subfamily Ponerinae. This idea appears to have originated with Wheeler (1910) who observed that certain ponerine ants carry out raids that are suggestive of the predatory forays of the dorylines, (see also Schneirla, 1971). This idea may be criticised on two grounds.

Firstly, it is based on fragmentary field observations almost totally unsupported by experimental evidence. Secondly, it has led to our looking at much of ponerine behaviour from the standpoint of doryline behaviour. This is a risky procedure, because objectivity might be impaired, and because it results in behavioural similarities between the two groups being emphasized at the expense of the differences. The following definitions make clear what behavioural characteristics have been sought among the Ponerinae.

Schneirla (op. cit.) defined army ant raiding behaviour as, "large scale predation in the manner of all dorylines, characterized by a regular relationship to emigrations and cyclic colony function". Wilson (1958, 1971) emphasized that the diagnostic features of this type of behaviour are nomadism and group-predation. The former he defines as "relatively frequent colony emigration" and of the latter he says:

> "Group-predation includes both group raiding and group retrieving in the process of hunting live prey. These two processes must be carefully distinguished from each other since they involve quite different innate behaviour patterns and are not invariably linked. Many ant species, particularly those in the higher subfamilies, engage in group retrieving of prey, but relatively few nondorylines also group raid".

On the basis of these definitions, Wilson (1958) surveyed what was known about "army ant" behaviour in the Ponerinae, to enable him to draw conclusions concerning the possible evolution of the more advanced types of raiding displayed by such doryline genera as Eciton, Anomma, Dorylus and Labidus. The results are interesting, but how real are the supposed similarities between the ponerine and doryline methods of raiding?

One of the most important differences concerns odour trail communication. A brief account of the typical doryline behaviour is given by Wilson (1971) in which he describes the advance of a raiding column of Eciton burchelli. "No leaders take command of the raiding column. Instead, workers finding themselves in the van press forward for a few centimeters and then wheel back into the throng behind them, to be supplanted immediately by others who extend the march a little farther. As the workers run onto new ground, they lay down small quantities of a chemical trail substance from the tips of their abdomens, guiding others forward".

There is a striking contrast between this behaviour and that of the termitophagous ponerine raider, Megaponera foetans. Collart (quoted by Wheeler, 1936) removed the leading ant from a raiding column of this species and found that when they reached the point of removal the following ants came to a halt. They resumed their march only when the "ant-guide" was returned to them. Deprived altogether of this single ant a column will turn about and return to its nest. Recently, I have been able to confirm and extend these observations in the laboratory using a queenright colony living in a nest box having access to a large arena. Frequent raids are conducted in the arena on parts of termite colonies that I provided and each raid is organised as follows.

A scout ant, which is almost invariably a major worker, locates the termites and returns to the nest box laying an odour trail. Shortly after entering the nest it reappears at the head of a large column of workers from which it is easily distinguished by its peculiar trail-laying gait and by the contrast in size between it and the minor workers that almost always seem to head the column. Occasionally, the scout appears to have difficulty in following its own previously laid odour trail and it then loops back. Whenever it does this, the following ants mill about unable to go farther. At this stage they are absolutely dependent on the scout for guidance. When Collart's experiment of removing this ant was repeated, the others behaved as they do when a trail comes to a natural end in the vicinity of a termite nest - they massed for an attack. But finding nothing to attack, they searched the area for several minutes and then returned to their nest along the outward route.

While following a trail-laying scout, some of the workers may be seen to reinforce the odour trail and once the attack on the termites has begun, a number of the ants run back along the trail to the nest where they recruit others. These later recruits do not have to be led, but follow the now well-established trail independently. Later, when the termites are being transported to the nest, the trail is heavily reinforced and two-way traffic becomes conspicuous as many of the ants return to gather more termites. No doubt this behaviour also occurs in the field if the termite colony is not situated too far from the nest (unpublished data).

Although more experimental data are urgently needed, there is ample observational evidence to suggest that the behaviour of Megaponera is typical of many ponerines. For example, Schneirla (op. cit.) described a raid by Termitopone laevigata in Panama during which the column of ants moved in single file and was "headed by one or two ants that moved steadily forward indicating that the trail may have been made before". At the end of the raid the termite-laden ants "filed back over the same trail". Wheeler (1936) said that the termite raids of Ophthalmopone ilgi in Abyssinia are very similar to those of M. foetans and he also mentioned numerous observations by Emerson of groups of Termitopone commutata workers marching in single file, either on their way to raid termite colonies or returning with their prey. On one occasion they were observed moving back and forth from their nest while raiding a trail of Syntermes territus. Similarly, Arnold (1915-26) noted that although the workers of Paltothyreus tarsatus generally go about singly, they occasionally foraged in short columns in single file. I have also seen them going to-and-fro from their nest on a fairly broad trail while attacking a nearby termite colony.

There is marked difference in the location of prey between Megaponera foetans and members of the Dorylinae. The food of the Dorylinae is more or less continuously distributed, numerous victims being flushed throughout a raid, so the direction taken by a raiding column matters little. On the other hand, the prey of Megaponera is discontinuously distributed and the destination of a column is predetermined. It is reasonable to hypothesize that any species of ponerine ant that has a specialized, discontinuously distributed prey will show group-predatory behaviour of the Megaponera type rather than an army ant behaviour of the doryline type. In several cases I have been able to test this hypothesis both by observation and experiment.

I have shown elsewhere (Fletcher, 1971) that Leptogenys attenuata and L. nitida both specialize in feeding on terrestrial crustaceans, particularly on the isopod, Philoscia mina, which is easier for the ants to capture than the more mobile amphipod, Talitriator eastwoodae. I mentioned also that both kinds of prey are localized by their microclimatic and food requirements and that the isopods tend to cluster. Experiments showed that as a result of this localization of prey the foraging efficiency of both species is enhanced by recruitment. The manner of this recruitment is very similar to that of Megaponera, foragers being led in small groups on miniature "raids" by a trail-laying scout to the site of its previous foraging success.

This work has recently been extended by Blomefield and Fletcher (unpublished data) to include a third member of this genus, L. stuhlmanni. Here too, behaviour of the Megaponera type has been recorded, groups of up to about 20 workers being led to the hunting grounds by a successful scout. This species is of additional interest, in that we have found it to prey not only on isopods and amphipods but also on termites. It thus represents a link between the obligatory termite raiders of the L. processionalis type (see Wheeler, 1910, 1936) and the species that are specialized crustacean feeders. Although L. stuhlmanni does not seem to raid the actual termitaria, but instead to capture foraging termites, its behaviour strongly suggests that the raids of the purely termitophagous species are also of the Megaponera type.

The behaviour of L. nitida has permitted a further extension of the hypothesis. Although its method of recruitment to a foraging site is initially very similar to that of L. attenuata, a marked difference soon appears as a result of the small size of the workers. Each one is only able to transport the smallest of isopods so group retrieval is obligatory for larger prey. Through a rapidly increasing tempo of recruitment a continuous odour trail is established to the foraging site and workers pass along it both singly and in groups, the latter dragging their prey co-operatively. (Fletcher, op.cit.). It thus seemed possible that even those ponerines that are less specialized in their feeding habits and that practise group retrieval of their prey might also forage in essentially the Megaponera manner.

This expanded hypothesis has so far been tested only in the case of the large ponerine, Plectroctena mandibularis, which preys upon millepedes and on the alates of various ant and termite species during and after their mating flights. The workers hunt solitarily and bring in most prey on their own, but group retrieval is necessary for the transport of the larger millepedes. Having immobilized a millepede by stinging it, a "scout" lays an odour trail to the nest and soon returns leading a group of up to 12 recruits. Together they partly carry and partly drag the prey back to the nest (unpublished data).

In the light of the foregoing evidence, it seems that Wilson's sharp distinction between group raiding and group retrieving cannot be strictly upheld. By no means all the behaviour patterns involved are different and even those that are, may be possessed by the same ant, as in L. nitida and P. mandibularis. Moreover, it appears that the foraging behaviour of the ponerines considered here is more closely allied to that of the trail-laying Myrmicinae and Formicinae than it is to the raiding behaviour of the Dorylinae. Indeed, it is but another short step from odour trail recruitment combined with group retrieval, to odour trail recruitment combined with the cutting up of prey and transporting it piecemeal, both of which are commonly practised by the higher ants.

Referring back to the earlier quoted definitions of army ant raiding behaviour, there remains the question of whether there is an association of the doryline type between nomadism and group-predation in the Ponerinae.

There is but a single record of emigration in Megaponera foetans, that of Arnold (1914), yet Wheeler (1936) saw it as evidence of "frequent changes of domicile, probably necessitated, as in the Doryline ants, by the need of ever fresh supplies of prey". This unjustified conclusion was generalized by Wilson (1958) when he said that much the same considerations also applied to the other group of foraging, obligatory termitophagous ponerines. Whether or not M. foetans is truly nomadic remains unknown, but there is evidence to suggest it is not. Wheeler's assumption that it frequently requires to change its trophic field is not well founded. Termite colonies are exceedingly populous and even regular raids by Megaponera are unlikely to make much impression on them. Wheeler himself records, in connection with Collart's "ant-guide" experiments, that Ghesquière and Schouteden repeatedly observed columns on their outward march pass termitaries without any attempts to plunder them.

The Megaponera colony I removed to the laboratory also had many termite colonies within easy raiding distance. In the laboratory, the ants excavated their own nest and in the field their tunnels were together several metres long, indicating protracted domicile (unpublished data).

Leptogenys stuhlmanni is highly nomadic, sometimes emigrating more than once a week. But in spite of the fact that its emigrations appear to be related in some way to the availability of prey, there is no evidence of cyclic colony function associated with the brood (see Schneirla's definition). Colonies move at irregular intervals both when brood is present and when it is absent as in winter (Blomefield and Fletcher, unpublished data). More data on nomadism in other species are needed.

To conclude, while it is possible that a few ponerine, and ponerine related genera, show a primitive army ant raiding behaviour of the doryline type, it is clear that some, and probably many, of the genera from which evidence has been drawn for such behaviour, have a fundamentally different raiding pattern. The behaviour of ponerine ants is a large and a virtually untouched field for research, and future investigations should be undertaken free from the bias of the past.

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