OECOPHYLLA LONGINODA, AN ANT PREDATOR OF ANOMMA DRIVER ANTS (HYMENOPTERA: FORMICIDAE)*

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Ants of the subgenus Anomma, one of 6 subgenera composing the genus Dorylus, are commonly referred to as "driver ants." The driver ant receives its name apparently because it "drives everything before it capable of muscular movement, so formidable is it from its numbers and bite . . ." (Savage, 1847). Of the Dorylus subgenera, Anomma is most conspicuous. Its species are aggressive, primarily epigaeic foragers (i.e. surface adapted as opposed to subterranean) with colonies consisting of up to 22 million individuals (Raignier and van Boven, 1955). Although the ferocity of the Anomma driver ants has been fictionalized and tales of their behavior are incorporated into African folklore, their pugnacity has been repeatedly documented (Loveridge, 1922; Raignier and van Boven, 1955; Savage, 1847, 1849; Wheeler 1910, 1922). The driver ants have also been described as clearly dominant animals (Weber, 1943). Without a doubt, they appear as efficient predators, having evolved a system of group predation of significant adaptive advantage in tropical environments.

However, these carnivores are themselves not without predators. Bequaert (1922) reports Anomma species from the stomachs of 4 species of African toads (genus Bufo) and 3 species of African frogs (in the genera Rana, Kassina, Hemisus). He also reports that driver ants are commonly eaten by African skinks of the genus Mabuya and by pangolins (scaly anteaters) of the genus Manis. Chapin (1932) indicates that driver ants are eaten by several species of African birds, including the Guinea fowl, Phasidus niger Cassin. My own observations in Ghana place the domestic chicken among Anomma predators, for driver ants frequently forage in village refuse heaps where chickens are also regular visitors. These chickens walk along the columns and clusters of worker ants, picking up and swallowing individual workers while carefully avoiding any other contact with the ants. Insects and other arthropods have not been observed as important Anomma predators. While flies of the genera

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Bengalia (Calliphoridae) and Stylogaster (Conopidae) are recorded as Anomma predators (Cohic, 1948), the term predator is applicable only in the case of Bengalia. Bengalia flies fly about and land near Anomma columns and eventually dart toward individual workers, stealing their prey or brood (Bequaert, 1922). Stylogaster, on the other hand, is parasitic on insects, particularly cockroaches, that flee before Anomma foraging swarms, and on tachinid and muscid flies that are attracted to such swarms (Smith, 1967). Stylogaster is also abundant over the swarms of New World dorylines, and parasitizes cockroaches and tachinid flies (Rettenmeyer, 1961). The eggs of these conopids are inserted into the host cuticle, and the larvae are internal parasites.

During May and June of 1971, while collecting driver ants in Ghana, I observed on 5 separate occasions the ant Oecophylla long-inoda (Latreille) (subfamily Formicinae) successfully attacking Anomma workers. It became apparent that O. longinoda is a common predator of driver ants and that it may be one of the very few insect predators of the subgenus.

Two other species of ants were seen to attack Anomma, but each case involved unusual circumstances. In the first case, workers of the ponerine ant Paltothyreus tarsatus (Fabricius) carried off the larvae and pupae of D. (Anomma) nigricans Illiger that had been discarded while the nest of the Anomma colony was being excavated. In the second case, a small species of Crematogaster dragged away Anomma workers that had been injured by an automobile that passed over an Anomma column. (Note: driver ants move in columns, usually along well marked trails, during foraging and during emigration or nest relocation). Cohic (1948) also records an encounter between Crematogaster and Anomma.

O. longinoda, commonly referred to as the red tree ant, is concentrated in several areas in the Ethiopian Region and is considered to be an efficient predator with a painful bite (Vanderplank, 1960). This ant is dimorphic, with its maxima caste performing the foraging tasks (Weber, 1949). Although O. longinoda previously has been recorded as a predator of Anomma by Cohic (1948), Ledoux (1950), Vanderplank (1960), Way (1954), and Weber (1949), the extent of this predation was, in most cases, not indicated. Note: the major weapons in predatory attack for both Oecophylla and Anomma are the mandibles. O. longinoda, a formicine ant, is stingless, while Anomma workers possess what appears to be a functionless sting.

Of the 5 observations of Oecophylla predatory behavior, 2 oc-

curred in the coastal scrub and grassland region at Legon and 3 in the moist semi-deciduous forest region (2 at Kade and I at Tafo), and each involved predation on the species Anomma nigricans. Although all African populations of Oecophylla are considered to be one species, the observations at Kade involved the commonly occurring dark form.

Discussion

O. longinoda attacks both emigrating and foraging columns of Anomma, but attacks the columns at a limited number of selected points. In some cases the Anomma trails over which the columns move are marked by soil particle walls, while in other cases, the columns march along completely exposed trails or trails covered in part by grasses and organic debris. Some trails are subterranean or covered with soil particle ceilings built by the Anomma workers. In the observations reported here, the Anomma trails either had soil particle walls or were partially covered by organic debris (primarily leaves).

Single Anomina workers are removed from the column by individual foraging O. longinoda workers. The O. longinoda workers are either positioned outside of the soil particle walls or on leaves and twigs adjacent to or overhanging the Anomma column. An O. longinoda worker quickly thrusts its head into the column, grasps an Anomma worker in its mandibles and pulls it from the moving column. In one case (Tafo) the O. longinoda workers removed Anomma workers from a diffuse column expansion. The Anomma workers are rarely alarmed by the removal of a single sister worker, although in one instance, the O. longinoda attack was so widespread that the Anomma column was subsequently disrupted. O. longinoda workers are obviously afforded some protection by the trail wall or by the space between the column and their position on the surrounding vegetation (Fig. 1). Anomma workers are generally excitable and easily disturbed, and thus it is surprising that they are usually so little disturbed during an Oecophylla attack.

Way (1954) notes that O. longinoda grabbed A. nigricans workers from the column, but adds that the Anomma workers had "strayed from the main stream." While it is true that the Anomma workers selected by O. longinoda foragers are peripherally located in the column, they are not usually "strays." Way (1954) also reports that Anomma soldiers were never taken, but I observed on several occasions soldiers being attacked and immobilized. Although most Anomma workers attacked were not of the soldier caste, this may

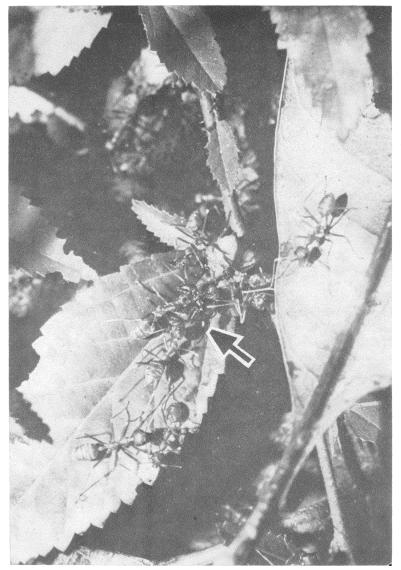


Fig. 1. Captive Anomma worker (indicated by arrow) and attacking O. longinoda foragers at the beginning of the immobilization phase of predatory attack.

be merely a reflection of the polymorphic proportions of the colony population.

While the removal of Anomma workers from the column is performed by individual O. longinoda workers, the immobilization of prey is the result of group action. O. longinoda workers surround the initial foraging worker and its Anomma captive and bite and grasp the Anomma worker extremities, and at the same time begin pulling (Fig. 1). Additional O. longinoda workers are recruited to this task, perhaps by the secretion of alarm substances. The mandibles, legs, antennae and parts of the alitrunk, petiole, and gaster are grasped (Fig. 1). Anywhere from 5 to 20 O. longinoda workers arrange themselves around the Anomma worker. In all cases, regardless of Anomma worker size, captured workers were incapable of mounting an adequate defense and were unable to bite their captors (i.e. they are unable to reach the O. longinoda worker because of their position in its mandibles).

The Anomma worker is immobilized through prolonged stretching, and this method of prey immobilization is common in Oecophylla (Gressitt, 1956; Ledoux, 1950; Vanderplank, 1960; Way, 1954; Weber, 1949). The stretching of prev, spread-eagle fashion, may be common to predaceous ants whose mandibles, perhaps in combination with their stings, are not efficacious, at least at the individual level, in quickly killing or immobilizing prey. For instance, New World doryline swarm raiders, such as Eciton burchelli (Westwood) and Labidus coecus (Latreille) stretch their large prey until it is torn to pieces (Schneirla, 1971). In this case, not only does the stretching serve to kill the prey but to subdivide it as well, thus facilitating the transport of the prev back to the bivouac. The O. longinoda mandibles do not appear to pierce the integument of the Anomma workers, although Way (1954) notes that the soft cuticle of limb and abdominal joints of prey is sometimes breached. He further reports that the O. longinoda workers sometimes curl their gasters dorsally and spray "poison" on these wounds.

After the Anomma worker is immobilized, it is usually carried by one or two Oecophylla workers to their arboreal nest. If the Anomma worker is not completely immobilized, more than 2 workers may cooperate in carrying it to the nest. In one observation, the Anomma worker was pulled at and stretched for 20 minutes, resulting in almost complete immobilization. Four O. longinoda workers then proceeded to carry the worker up a tree trunk, I grasping the Anomma mandible, I an antenna and I each the metathoracic legs. The Anomma worker occasionally moved its legs, catching its tarsal

claws on lichens and mosses growing on the bark. Eventually 2 workers managed to carry it up into the tree. Way (1954) timed the stretching of a honeybee by O. longinoda workers and found it also lasted 20 minutes.

The predatory attack of O. longinoda on Anomma driver ants is thus divisible into 3 phases: (1) the attack phase, in which an individual Anomma worker is seized and removed from the column; (2) the immobilization phase, in which additional O. longinoda workers are recruited to stretch the Anomma worker until it is no longer able to move; and (3) the transfer phase, in which the immobilized Anomma worker is carried to the Oecophylla nest.

Although in all observations the *Oecophylla* workers carried off many *Anomma* workers, the number may not be significant with respect to the total number of *Anomma* workers comprising a colony. Way (1954) notes, in his observations of *Oecophylla* attacks on *A. nigricans*, that in one case, in a period of an hour, 348 *Anomma* were carried into one tree and 252 into another.

The importance of driver ants in the diet of O. longinoda cannot be calculated at this point. It is known that insect prey and sugars are essential for the survival and reproduction of an O. longinoda colony (Vanderplank, 1960). The role of Anomma as a food source may depend, to a large extent, on chance movements of Anomma columns into Oecophylla colony territories. Obviously the probability of such an occurrence depends, in part, on the colony densities of prey and predator in a given area. The efficiency of foraging behavior in Anomma may in itself increase the probability of chance encounters with Oecophylla. Numerous foraging columns, for instance, may simultaneously work out from an Anomma nest, may frequently change direction, and may start anew each day, thus enabling the colony, in its search for nutrient sources, to probe the environment in many directions.

Are the roles of predator and prey in the Oecophylla-Anomma interaction ever reversed? Evidence for such a reversal might be found in the prey materials carried by Anomma workers back to the nest. I made II extensive surveys of prey taken from Anomma foraging columns in areas where O. longinoda is also found, and in only one sample was there such evidence. It contained the gaster of an adult O. longinoda worker. It appears that O. longinoda is not often attacked by Anomma, though it is not likely that Oecophylla could effectively resist an Anomma foraging swarm. However, it is probable that the arboreal nests of O. longinoda are simply out of reach of Anomma foragers. My own observations indicate that while

Anomma does forage in trees at heights greater than 10 feet, they are less likely to do so than they are to forage in lower vegetation. Cohic (1948) reports that while he observed D. (Anomma) nigricans foraging in trees to heights of about 10 meters, the nests of Crematogaster and Oecophylla were spared or avoided.

SUMMARY

- 1. O. longinoda is an important predator of Anomma driver ants and may be the single most important insect predator of Anomma in areas where the two are sympatric.
- 2. In attacking Anomma, an O. longinoda worker reaches into a moving Anomma column (foraging or emigrating) and seizes an individual Anomma worker in its mandibles, pulling it quickly from the column. This is termed the attack phase of the predatory interaction.
- 3. After the *Anomma* worker is removed from the column, the initial *O. longinoda* forager is joined by sister workers, which together immobilize the prey through prolonged stretching. This is termed the immobilization phase.
- 4. When the *Anomma* worker is sufficiently immobilized, it is carried back to the *Oecophylla* nest by 1 or more workers. This is termed the transfer phase.
- 5. Individual *Anomma* workers are unable to successfully defend themselves, and little or no alarm is generated in the column when the worker is removed.
- 6. All Anomma workers, regardless of size, including soldiers, are subject to O. longinoda attack.
- 7. Immobilization of prey through prolonged stretching may be employed by predaceous ants whose mandibles and/or stings are ineffective in subduing prey at the individual level.
- 8. O. longinoda is an effective predator of Anomma because, (a) it usually attacks the Anomma column at a limited number of points and generally avoids disrupting Anomma movement; (b) it seizes and removes Anomma workers from the column quickly, thus avoiding a widespread alarm response; (c) it attacks from defensively advantageous positions outside of the column, reducing its vulnerability to Anomma alarm response.
- 9. In areas densely populated by O. longinoda (where the probability of chance encounter is high), an Anomma colony may lose several hundreds, theoretically thousands, of workers per day to Oecophylla predation.

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