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Abstract

Eighty percent of the prey captured by the ponerine ant *Amblyopone silvestrii* in nature were geophilomorph centipedes. In the laboratory observation, this ant showed skillful hunting behavior which is highly specialized on large, linear-shaped soil arthropods. Specialization on centipedes, migratory behavior and hemolymph feeding are common in the members of the Amblyoponini and the Leptanillinae.

Introduction

In spite of a general impression that ants are polyphagous insects, many specialist predators have evolved, particularly in the two subfamilies Ponerinae and Myrmicinae (Hölldobler and Wilson 1990; Masuko 1992). Specialization on relatively large prey is, however, rather uncommon and known only from a few groups in extant ants. The ponerine tribe Amblyoponini is a representative of this minority and some of its members (genera *Amblyopone* and *Onychomyrmex*) are known to predate especially upon chiro-pods (Hölldobler and Wilson 1990), but information concerning this feeding has been fragmentary or only narrative. In this paper, quantitative data are presented for the prey menu in nature of *Amblyopone silvestrii* and the specialized hunting behavior is described.

Materials and methods

Amblyopone silvestrii is 4-5mm long, reddish-brown in color, and is distributed from Hokkaido to Ryukyu Islands in Japan. Colonies for the present study were collected in the evergreen broadleaf forest at Cape Manazuru, Kanagawa Prefecture. The forest is dominated with the trees *Cinamomum camphora* and *Castanopsis cuspidata* var. *sieboldi* (Miyawaki et al. 1972). When nests of *A. silvestrii* were found in the soil during excavation, the galleries were carefully searched for the ants, their symbionts (mostly the millipedes *Ampelodesmus granulatus*), and prey retrieved by the ants. The prey items were preserved in Kahle's solution on the spot for later identification and measurement in the laboratory. The length of prey organisms was measured with the method basically the same as applied to collembolans by Tamura (1974): Specimens were laid on their side in an alcohol filled depression of a color reaction plate. This glass plate was placed on the stage of a stereomicroscope and observed at the magnification of 50X. Using a drawing tube attached to the microscope, the body length of the prey was precisely drawn as a line on a paper by tracing the central body line from the anterior tip to the posterior one. This line drawing was then enlarged

about 3 times with a photocopy machine, and its length was measured with a curvimeter of the least scale of 1cm. With this method, the prey body lengths could be precisely determined to 0.1mm.

Collected colonies were housed in polystyrene observation nests measuring $10 \times 11 \times 2$ cm or $10 \times 19 \times 2$ cm, and the bottom of each nest was covered with the plaster-of-Paris mixed with activated carbon powder (Fig. 1). A nest chamber was excavated in the center of plaster floor, and the tops of terraria and nest chambers were covered with clear glass, which permitted observations of the ants, both inside the nest and in the foraging arena. Ants were easily reared on the prey such as centipedes collected in the field or small-sized mealworms cultured in the laboratory. Nests were kept at $20^\circ - 25^\circ\text{C}$. Most behavioral observation was made with a stereomicroscope attached to a swing arm. The ant's behavior was tallied with a tape recorder.

The scanning electron micrograph was taken with a J.E.O.L. JSM-25 microscope. In place of critical-point-drying, specimens were treated with hexamethyldisilazane (Nation 1983).

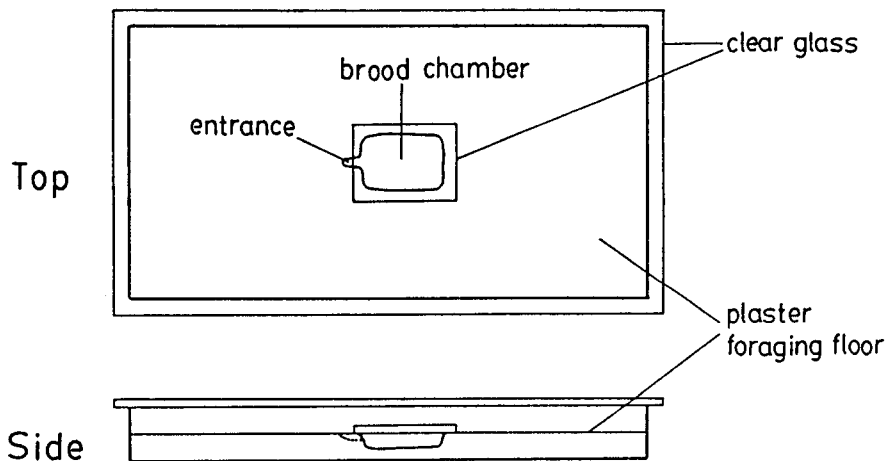


Fig. 1. Artificial nest for laboratory colonies of *Amblyopone silvestrii*. Size= $10 \times 19 \times 2$ cm.

Results

1. Prey content in field

Since the life of *A. silvestrii* is totally hypogaecic, information on their diet in nature is only available from captured prey found in their nests. A total of 30 prey items were obtained from 28 nests between June 1981 and September 1985. Of them, 27 (90%) were centipedes, most of which were geophilomorphs (Table 1). *Prolamnonyx holstii* was the most dominant prey species ($n=18$). This centipede is known to be the most abundant among geophilomorphs distributed in the Manazuru forest (K. Ishii, pers.comm.). *A. silvestrii* is thus admittedly a specialist predator of geophilomorph centipedes, but they also casually hunt other long-bodied predaceous soil arthropods (Table 1). In capturing geophilomorphs, the ants show a stereotypic but skillful hunting sequence toward such large, linear-shaped organisms (see below).

The length of preserved prey with intact or nearly intact bodies was measured by means of a photocopy and a curvimeter. The mean body length of geophilomorphs was 13mm (SD=6mm, range 6–30mm, n=11), and a lithobiid centipede was 7mm long and 2 cantharid beetle larvae were 4mm long each. Thus, the body length of the measurable 14 prey items varied from 4 to 30mm, averaging 11mm (SD=6mm). It is clear that *A. silvestrii* predominantly hunts the organisms of relatively large body size ranging from the same to several times as long as the ant itself (4–5mm).

Table 1. List of 30 prey items recovered from 28 nests of *Amblyopone silvestrii* in the field.

Species	N	(%)
Chilopoda		
Lithobiomorpha		(10)
Lithobiidae		
<i>Monotarsobius holstii</i>	1	
<i>Monotarsobius eleganus</i>	1	
<i>Monotarsobius</i> sp. (undetermined)	1	
Geophilomorpha		(80)
Mecistocephalidae		
<i>Prolamnonyx holstii</i>	18	
<i>Dicellyphilus latifrons</i>	1	
<i>Tygarrup monoporus</i>	1	
Geophilidae		
<i>Ceiletha macropalpus</i>	3	
<i>Mesogeophilus</i> sp. (undetermined)	1	
Insecta		
Diplura		(3)
Japygidae		
<i>Japyx</i> sp. (undetermined)	1	
Coleoptera		(7)
Cantharidae sp. larva (undetermined)	2	
Total	30	(100)

2. Prey preference in laboratory

Food preference of *A. silvestrii* was examined by giving small-sized soil invertebrates to laboratory colonies. The ants readily attacked intact individuals of several species of geophilomorph, lithobiid and cryptopid centipedes, and all of these were finally consumed by the larvae. The other accepted organisms (namely those captured intact and consumed) were: Termite adults and nymphs (*Reticulitermes speratus*), ant larvae and pupae (*Brachyponera chinensis* and *Camponotus kiusiuensis*), tabanid fly larvae, early instars of mealworm (*Tenebrio molitor*), canthalid, elaterid and ptilodactylid

beetle larvae, diplurans (*Campodea* and *Japyx*), symphilans (ScutigereLLidae), and an undetermined species of whiteworm. In contrast, staphylinid beetle adults and trombiid mites were ignored by the ants despite frequent contacts in the foraging arena of artificial nest. And sugary solution was always neglected by the ants.

Among geophilomorphs tested, *Scolioptanes* was always immune to the attack by *A. silvestrii*. When workers gripped this centipede with the mandibles, it bled hemolymph from the wound made by the ants. This hemolymph was so sticky that the ants were frequently much entangled into immobility. Furthermore, this substance appears to be highly distasteful to ants, which, attached with even a small quantity, immediately retreated, apparently in distress, and began self-grooming. The ants that had been heavily glued with this substance were occasionally found to be dead in the foraging arena the next day. The hemolymph of lithobiomorph centipedes is also gluey, but in most cases the ants overcame this substance and subdued the centipedes.

3. Prey capture

In the laboratory nest, *A. silvestrii* workers explore the foraging arena singly, without any sign of cooperation with other workers. When a worker comes across a nestmate during foraging, they may, at most, only briefly palpate each other with the antennae. Encounter with prey is usually haphazard. When the prey stands still, foraging workers become aware of its presence mostly by faint antennal touching. It was, however, often observed that without any direct contact the ants did perceive a centipede which was moving within a range of 1cm. Probably this was done by air movements or vibrations through the substrate. When excited by such passing prey, workers immediately rush to or pursue over a short distance the prey while raising the head and opening the mandibles to the full extent (70°–80°). When prey remains still or is moving slowly, workers often take a way around the prey to approach its lateral side in a cautious manner. Reaching within a striking range, the mandibles are fully opened and the head is rotated so that the plane of mandibular movements becomes orthogonal to the long axis of the prey. In a single snap, the ant then grips around the prey body trunk (Fig. 3A). In this instance, a pair of long hairs projecting forward from the clypeus (Fig. 2, arrows) serves as the tactile trigger. If a centipedes is relatively large and thus its escape reaction is forceful, the ant is dragged about in the foraging arena for a while. The centipede, during this flight, frequently bites at the clinging ant and tries to pull it apart, but this counterattack is usually ineffective and almost harmless to *A. silvestrii*. Subsequently, the ant, seizing an opportunity, cautiously hugs the prey body by its fore and middle legs, and loosens the mandibular grip only slightly, to move forward along the prey trunk over several segments (Fig. 3B).

This procedure is repeated several times over the whole length of the prey until it completely loses the locomotor ability due to paralysis. Eventually, the ant releases the prey and begins self-grooming by the side.

This skillful hunting seunee is obviously an adaptation to linear-shaped prey organisms such as geophilomorph centipedes. Usually, single workers required several to a dozen minutes to completely paralyze geophilomorphs 1.5–2.5cm in length. It was once observed that a worker subdued a 4cm-long geophilomorph (*Queenslandphilus vividicans*) in 21 minutes from the first seizure. After paralysis, the body surface of prey is licked eagerly by the huntress on the spot (Fig. 3D). Concurrently she may, using the mandibles, lightly grip the prey trunk at several points, probably to

The ant grips again and delivers another sting (Fig. 3C).

confirm paralysis; because the portions responding actively to this treatment are again stung.

4. Prey retrieval

With the prey completely paralyzed, the retrieval starts. The huntress first leaves the prey and conducts an orientation trip in order to check the position of the nest entrance. Then she returns to the prey and drags it over several centimeters. Again she releases it and proceeds singly to the nest. Such orientation and prey dragging are repeated alternately until the prey is brought in the nest (Fig. 3E). Although the whole process of this transport can be completed by only the huntress despite large prey size, other workers in the arena are sooner or later attracted to the prey, and join the transport. In such cases, the original huntress often deserts further execution, which is taken over by the newcomers. When the huntress on the way of an orientation trip enters the nest chamber, other workers often show vibration displays to her, who may also respond similarly with the same behavior. Furthermore, nearby workers carefully examine her body with the antennae, and some of them may even become aggressive and nudge the huntress with the mandibles open. This aggression is provoked probably by prey odor attached to her surface. Following this, some of such aroused workers may leave the nest, but in the present study no guiding behavior has been noticed in the original huntress. There is therefore no indication of recruitment to food source in *A. silvestrii*.



Fig. 2. Head of *A. silvestrii* worker. Dorsal view. Arrows indicate a pair of hairs protruding from the anterior margin of the clypeus. Scale=0.25mm

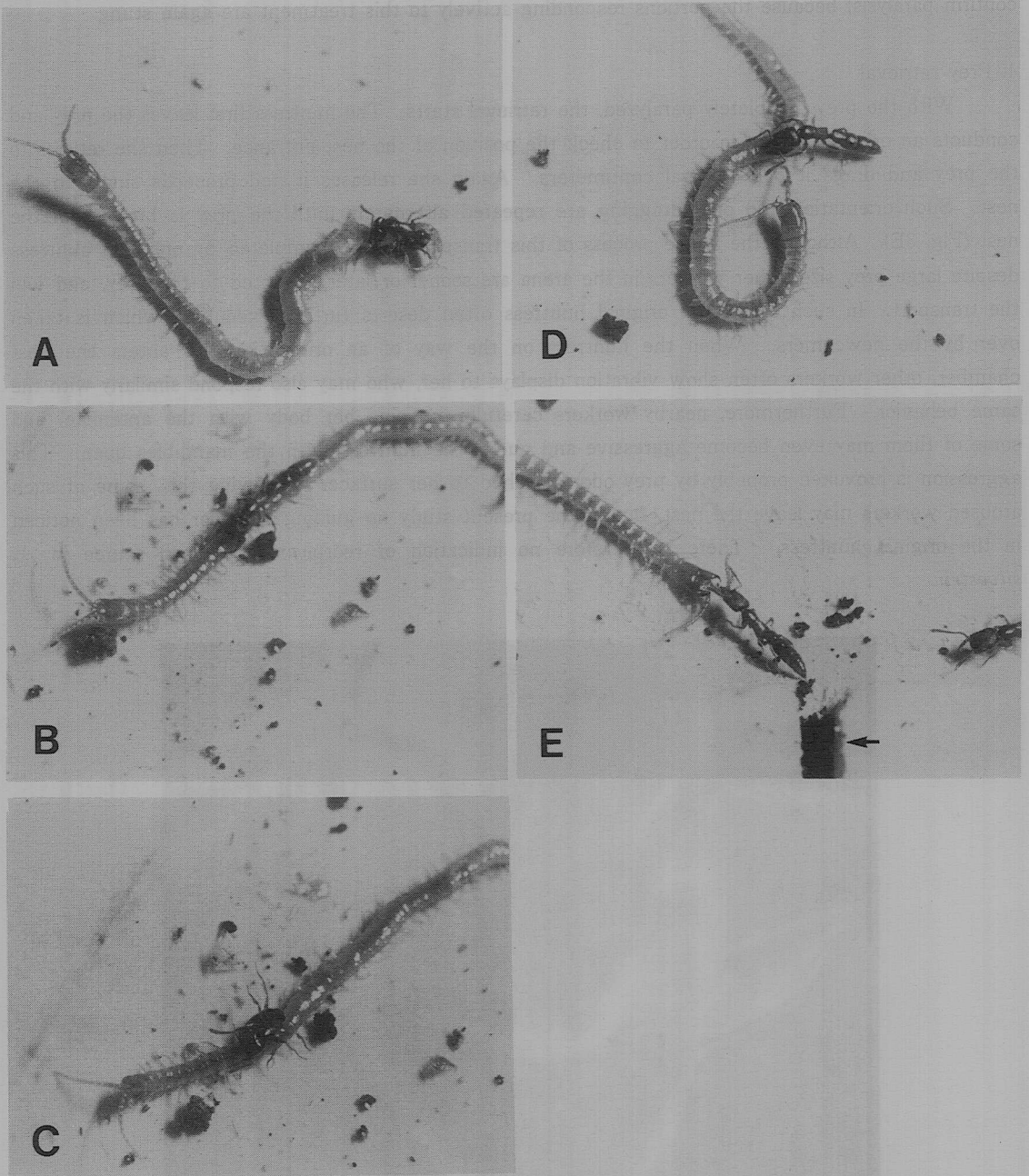


Fig. 3. Sequence of prey capture by *A. silvestrii* worker. The prey is a geophilomorph centipede. A. Early phase of hunting event where a worker is holding the posterior part of a centipede in her mandibles and stinging it. B. The worker cautiously proceeds along the prey body. Note that the ant's mandibular grip is loosened but the prey body is maintained between the mandibles. C. The worker again stings a newly gripped part of the prey. D. She licks the body surface of the paralyzed prey. E. Finally, the worker is about to drag the centipede into the entrance hole (arrow) of the nest chamber.

Discussion

The field data on captured prey revealed that *A. silvestrii* largely attacks geophilomorph centipedes as prey. Although diet specialization on chilopods or other linear-shaped arthropods (e.g. beetle larvae) has long been known for the Amblyoponini (Wheeler 1900, 1933; Haskins 1928; Brown 1960; Gotwald and Lévieux 1972; Traniello 1982), the evidence has been fragmentary. Since the members of the Amblyoponini commonly hunt large, thus difficult arthropods which live in closed spaces in rotting logs or in the soil, such capture of big prey in a confined space which is contiguous to their nests, has an interesting consequence to the biology of the amblyoponines. Researchers have often found at the time of field collection of *Amblyopone* and *Myopopone* that small isolated groups of workers and larvae were clustered around freshly hunted prey (Wilson 1958; Brown 1960). As amblyoponines lack the habit of dismembering prey before provision for larvae, these observations suggest that workers move larvae temporarily to the site of hunted prey because of some difficulty arising during its retrieval. This temporary displacement of larvae in relation to predation is suggestive for understanding of the evolutionary origin of the legionary behavior in army ants (Wilson 1958 and 1971). In fact, the amblyoponini contains a legionary member, *Onychomyrmex* (Wheeler 1916; Brown 1960). Information on the frequency and details of this emigration process has been, however, much incomplete for any amblyoponine species due to their hypogaecic behavior. In the case of *A. silvestrii*, such an isolated feeding spot was encountered in the field on one occasion: On 20 April 1982, during excavation of a one square-meter quadrat, 14 larvae (four 4th-instar and ten 5th-instar) were located in the soil; they were accompanied with 2 workers and feeding on a geophilomorph centipede, but no nest-like structure was recognized there. The nest was located about 25cm from this site. In the laboratory, when transport of prey was prevented, colony members of *A. silvestrii* readily emigrated, in part or in whole, to the food source. In this migration, without exception, workers first moved the larger individuals of the 5th-instar larvae, followed by younger larvae. Sometimes even eggs were carried out of the nest chamber and placed near the prey, and also the queen left the chamber, usually shortly after the replacement of eggs. After prey consumption, the brood was returned to the nest chamber.

The genus *Apomyrma* had been placed in the Amblyoponini until recently Bolton (1990) transferred it to a different subfamily, Leptanillinae. Limited circumstantial evidence suggests that *Apomyrma* predates on geophilomorph centipedes and is a highly migratory ant (Brown et al. 1970). On the other hand, the authentic leptanilline genus *Leptanilla* has been recently shown to be the ants feeding especially on geophilomorph centipedes and having a highly migratory habit (Masuko 1989 and 1990). The Leptanillinae was formerly linked with the army ant subfamilies Dorylinae and Ecitoninae, but, based on new morphological evidence, Bolton (1990) presently considers it to be a sister group of the Ponerinae. This view is interesting because, as described above, the ants specialized in centipedes and showing nomadic behavior are found in both of the Leptanillinae (*Leptanilla* and probably also *Apomyrma*) and the Ponerinae (the Amblyoponini). Moreover, an aberrant form of nutrient exchange, hemolymph feeding, was found both in *Leptanilla* (Masuko 1989) and in the Amblyoponini (*Amblyopone* [Masuko 1986] and *Mystrium* [Wheeler and Wheeler 1988]). (Furthermore, species of a non-amblyoponine genus, *Proceratium*, have this behavior, too; Masuko 1986.) Whether these behavioral characteristics apparently common in the leptanillines and the

amblyoponines in particular, are synapomorphies or not remains unsettled, but it is an appealing problem deserving future comparative study.

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