

Larval hemolymph feeding: a nondestructive parental cannibalism in the primitive ant *Amblyopone silvestrii* Wheeler (Hymenoptera: Formicidae)

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Summary. The queens of larger colonies of the primitive ant *Amblyopone silvestrii* are exclusively dependent on the hemolymph of their own larvae as a nutrient, even when prey feeding is possible. On the other hand, the foundresses suppress larval hemolymph feeding (LHF) when prey is available, allowing them to rear the first workers more swiftly. The nondestructive form of cannibalism can be regarded as a nutritive adaptation related to: (1) the lack of social food transfer in this species, and (2) its specialized predation on large sporadic prey (centipedes). LHF similar to that in *Amblyopone* was found in *Proceratium* and another type of LHF, with a larval specialized exudatory organ, in *Leptanilla*.

Introduction

Apart from a few secondarily workerless parasites, all known species of ants are eusocial, with an apterous worker caste (Wilson 1971). The ubiquity of eusociality among ants restricts comparative studies of their early social evolution, compared to those on wasps and bees. It is useful, however, to research the biology of archaic genera, such as *Amblyopone*, *Nothomyrmecia*, and *Myrmecia*, in order to determine the primitiveness of their habits and extrapolate to the social life of ancestral ants.

I report here on what appears to be a primitive form of social food transfer, termed *larval hemolymph feeding* (LHF) in the Japanese *Amblyopone silvestrii* Wheeler, and discuss its adaptive significance. Although this phenomenon has been fragmentarily observed in some species of *Amblyopone* (Haskins 1928; Haskins and Haskins 1951; Gotwald and Léviéux 1972; Traniello 1982) and in *Myrmecia* (Haskins 1970), this has been the first

study to investigate its details, paying special attention to its significance to the social life of the ants.

Methods

Amblyopone silvestrii is a medium-sized ant, 4–5 mm long, reddish-brown in color, and subterranean during both nesting and foraging. All colonies for this study were collected in the evergreen, broadleaved forest at Cape Manazuru, central Japan (35° 8' N, 139° 10' E).

In the laboratory, colonies were housed in styrene observation nests measuring either 10 × 11 × 2 cm or 10 × 19 × 2 cm, depending on the size of the housed population; the bottom of each was covered with the plaster of Paris mixed with activated carbon powder. Brood chambers had been excavated in the center of the plaster floor, and the tops of the terraria and brood chambers were covered with clear glass. The ants were easily reared on prey such as small-sized mealworms or field-collected centipedes. Observation nests were kept in a constant temperature chamber (at 20°–25° C), while the behavior of ants was observed outside the chambers at room temperature (usually 19°–27° C). Most observations were made with a stereomicroscope attached to a swing arm. Notes on their behavior were recorded on tapes during an early stage of the study. Thereafter, the behavioral time budget of queens was recorded with the aid of a portable microcomputer (Epson HC-20); for each queen, the behavior was assayed by the focal animal sampling method (Altmann 1974) over a total of more than 10 h made up of periods 0.5–2.5 h long, repeated within 2 weeks (exceptionally 17 days were taken for one queen). A video tape recorder (VTR) was also used for continuous observations extending for several days.

Results

Description of larval hemolymph feeding (LHF)

As established by my laboratory observations, LHF of *A. silvestrii* is a behavior in which adult ants pierce the dorsal integument of the upper abdomen of older larvae by pinching with their sharpened mandibular tips, and then feed upon hemolymph leaking from the puncture (Fig. 1). The larvae are most often pinched at the two intersegmen-



Fig. 1. *Amblyopone silvestrii* queen drinking hemolymph from a puncture on the dorsum of a 5th-instar larva

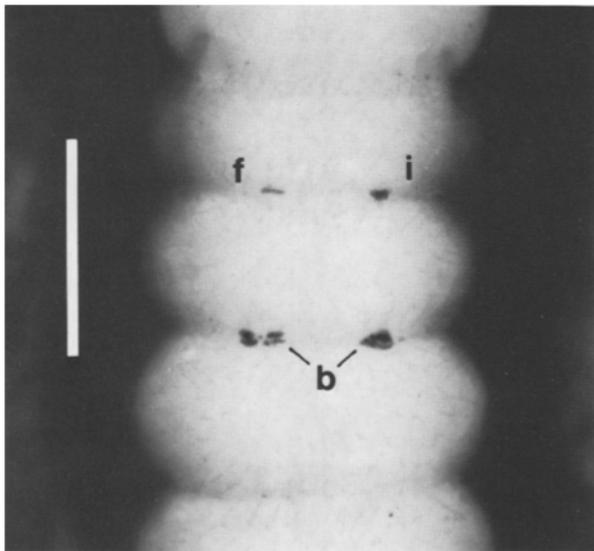


Fig. 2. Scars from LHF on the dorsum of a 5th-instar larva (prepupa). Four points of scars are seen at two intersegmental grooves between the 2nd and 4th abdominal segments. In each bout of LHF, queens use a puncture, which is usually reopened at one of preexisting scars. Presence of multiple bold scars indicates that the larva has been exploited repeatedly. Degrees of scar are classified into three arbitrary classes: "faint" (*f*), "intermediate" (*i*), and "bold" (*b*). Scale, 0.5 mm

tal grooves between the 2nd and the 4th abdominal segments (Fig. 2). In general, queens (inseminated females) perform LHF; except when the colony is starved, it is seldom seen in workers and dealate, uninseminated females. The latter castes instead feed directly on prey, the cuticle of which has been opened either by larvae or adults. Uninseminated females, which are often encountered in field-col-

lected mature nests, are ordinarily observed to labor in a workerlike manner. Queens start each bout of LHF by active antennal stroking and handling of a larva, and then pinch it from either side. Invariably, after several pinchings, the mandibular tip applied to the larval dorsum punctures its integument, and a droplet of hemolymph flows from the wound. The queen at once attaches her lower mouthparts to the puncture to lick the droplet. She then "freezes" motionless for several minutes, during which time the lapping movement of her lower mouthparts, still attached to the puncture, usually ceases, indicating that she is imbibing hemolymph from the larval body cavity using her pharyngeal pump. Each bout of LHF usually involves a single larva. Following LHF the queen ordinarily discharges one or two pure white infra-buccal pellets onto the nest floor, probably the filtered dregs of hemolymph. Queens at this time are often groomed at the mouthparts by workers, which remove the pellet and usually discard it outside the brood chamber.

LHF by queens of developed colonies

LHF is not only performed solely by queens, but it is a queen's only way of obtaining nutrients. Table 1A shows the feeding time budget of three queens observed in laboratory colonies that were monogynous and mature, i.e., including more than 20 workers (the field data suggest that *A. silvestrii* colonies become mature, that is, start production of sexuals, when their worker population exceeds about 10). All three queens indulged in LHF to the exclusion of other modes of feeding, even though captured prey items (centipedes or mealworms) were available in the brood chamber throughout the observation period. To confirm this again and to ascertain the time intervals between bouts of LHF, two further queens of monogynous mature colonies were observed with a VTR. One, who was observed continuously for 5 days at $27 \pm 1^\circ \text{C}$ under constant light (LL), repeated LHF at intervals of $5.3 \pm 0.7 \text{ h}$ (mean \pm SE). The other queen was observed under both LL and DD (constant dark), each for 3 days, at $22 \pm 1^\circ \text{C}$; these periods were preceded by 3-day light and dark adaptation periods, respectively (an infrared light was used for observation in darkness). The difference between mean intervals of LHF by this queen under LL and DD was not statistically significant (ANOVA, $F_{1,11} = 0.508$), so the data were combined to yield an interval of $9.1 \pm 1.8 \text{ h}$ (mean \pm SE). Also in this VTR study, it was noted that the queens obtained their nutrients exclusively by LHF despite

Table 1. Percentage of time spent in each mode of feeding by *Amblyopone silvestrii* queens

Feeding mode	A Queen of developed colony			B Foundress		
	82-4	82-12	82-406	82-299	84-40	81-96
Larval hemolymph feeding (LHF)	4.07	4.95	3.45	0.96	0	0
Feed on prey	0	0	0	9.61	2.47	0.69
Cannibalize immature	0	0	0	0	0	0.45
Rumination ^a	0	0.13	0	0.86	0	0.62
Sample time (h)	11.3	20.3	26.0	14.9	19.7	10.1
Prey availability (%) ^b	100	100	100	100	100	20

^a Rumination is a behavior in which ants lick again or feed on the pellets put out of their own infrabuccal chambers

^b Percentage of time in which prey was present in the brood chamber compared to the total sample time

continuous accessibility to prey. It is thus confirmed that nearby prey remains are ignored by *A. silvestrii* queens, while they repeat LHF at intervals of several hours.

Scarred larvae

Larvae subjected to LHF were always mature or near-mature individuals of the 5th instar, which is the final instar for both female and male larvae in this ant (the larval instars of *A. silvestrii* are easily determined based on the body size and the chaetotaxy). Usually several members of the 5th-instar population are pinched repeatedly, which causes their scars to become increasingly evident (Fig. 2). These observations are confirmed by field-collected material (Fig. 3): 149 5th-instar larvae belonging to eight winter nests were collected at Manazuru during December 1982 and April 1983. Their body size, which was measured when alive as the width of the 4th abdominal segment with an ocular micrometer accurate to 0.025 mm, ranged from 0.475–0.800 mm, with a mean of 0.647 mm. Those with scars thought to have been made during the preceding active season, and characteristic of LHF, were all in the size class above 0.625 mm. Figure 3 shows that among 106 larvae of this class, only 44 (41.5%) had scars: seven (15.9%) had only “faint” scars, 19 (43.2%) had “faint” to “intermediate” scars, and 18 (40.9%) had at least one “bold” scar (for classification of scar degrees see Fig. 2).

The punctures close shortly after LHF by hemolymph coagulation and scarred larvae do not die from their wounds nor are they cannibalized, as would generally be the case with damaged larvae of higher ants. In well-fed laboratory colonies most scarred larvae were observed to continue feeding and to succeed in pupation. However, if these colonies are starved, larvae most exploited for LHF

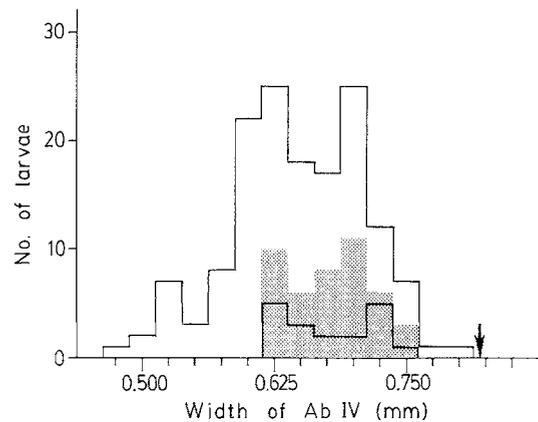


Fig. 3. Size of 5th-instar larvae with scars from winter population, measured as the width of the 4th abdominal segment. Open histogram represents the total ($n=149$). Stippled histogram represents individuals having scars characteristic of LHF, among which those framed have “bold” scars. Arrow indicates the average size at which six matured worker larvae started spinning for metamorphosis in laboratory

and hence the most debilitated were devoured and consumed before the same-sized but unscarred or weakly scarred larvae.

Among 169 larvae contained in cocoons collected in the field during 1981 and 1984, 125 (74.0%) had scars characteristic of LHF. These facts suggest that, even under natural conditions, the potentially destructive effect of LHF on the larval population is not profound. It is still probable, however, that LHF has some unfavorable effects on its recipients, e.g., causes delay in their development or lowers their rates of survival, especially in colonies with few larvae.

LHF by foundresses

The possibility of LHF by foundresses (colony-founding queens) is of interest. Since the appearance of the first workers is crucial to subsequent

colony survival, it is expected that foundresses will show a low rate of LHF compared to queens in developed colonies, in order to rear the first workers as quickly as possible. Unlike the foundresses of higher ants, which maintain their first brood on nutrients regurgitated while claustral, *Amblyopone* foundresses forage alone outside the nest (Wheeler 1933; Haskins and Haskins 1951; Haskins 1970).

Table 1B shows the feeding time budget of three haplometrotic (singly colony-founding) queens, each of which was collected with her immatures and later observed in the laboratory. Foundress 82-299 showed both LHF and prey feeding, but she spent much more time at the latter. Only prey feeding was observed in the case of foundress 84-40. Prey availability was experimentally lowered during observation of foundress 81-96. In her case only prey feeding and cannibalism of the pupae were recorded during the studied 10-h period. Outside this period, however, she was observed to perform LHF on some particular larvae, which were later cannibalized. Thus, as predicted, their feeding characteristics differed greatly from those of queens in mature colonies, when prey was available.

Survey of LHF among Japanese lower ants

A preliminary qualitative survey of the presence or absence of LHF was conducted on several Japanese species, primarily ponerines (Table 2). LHF was judged to be present when LHF-characteristic scars were found on the integument of mature larvae or prepupae. LHF similar to that in *Amblyopone* was found only in the genus *Proceratium*; monopoly and persistence of LHF by the queens were also confirmed with behavioral observations for one species (*P. itoi*). Moreover, another type of LHF has been found in a nonponerine genus, *Leptanilla*. In this second type of LHF, the queens take the hemolymph from specialized duct organs at the 3rd abdominal segment of the larvae, without harming their integument. Table 2 also contains the information available at present on food habits and the ability of food exchange in these species. The relationships between these habits and LHF are discussed below.

Discussion

Two traits in the biology of *A. silvestrii* may be involved in the adaptive basis of this aberrant form of feeding. First, food transfer by regurgitation be-

tween adults is totally absent, as is often the case in lower ants. In *A. pluto*, however, Gotwald and Léviéux (1972) and Léviéux (1972) reported that they observed food exchange from mouth to mouth between workers, but only rarely. In my observations on *A. silvestrii*, adults after prey feeding sometimes put out the pellet from their own infrabuccal chamber and again lick or feed on it at the tip of their lower mouthparts; I have called this behavior "rumination", distinguishing it from "regurgitation" from the crop. Such pellets often attract nearby nestmates, which bring their mouthparts into contact with those of the ruminating ant, to take the pellet away and often finally ingest it. This kind of food transfer is, however, a haphazard event with only a trivial function. It suggests that the food exchange observed in *A. pluto* possibly entailed not true regurgitation but rather mere transfer of the ruminated pellets.

Second, as in other amblyoponine species (Brown 1960; Gotwald and Léviéux 1972) and based on field data, predation by *A. silvestrii* is largely restricted to geophilomorph centipedes, which provide about 80% of the prey at Manazuru. Stenophagy on such relatively large predaceous animals presumably causes the hunting success rate of this ant to be lower or more sporadic than in the case of an omnivorous species or a species specializing in prey types with small size and high density (e.g., dacetine ants specialized on Collembola; Brown and Wilson 1959; Masuko 1984). This presumed sporadicity in prey hunting may be increased by the small colony size of this species, which limits the ants to fielding relatively small foraging forces. Thus the number of workers per colony of *A. silvestrii* was 17.9 ± 15.2 (mean \pm SD) for 30 colonies collected in inactive seasons (November to April, when there are no or few foragers) during 1981 and 1984 at Manazuru.

When field colonies become starved owing to prey shortage, *Amblyopone* queens, in the absence of regurgitation by the workers, are able to obtain nutrient only from immatures. In such cases irrevocable loss of brood by destructive cannibalism would be selected against, as long as the possibility remained of obtaining prey within a short time. This would favor the evolution of nondestructive cannibalism, such as LHF. The nondestructive nature of LHF would be equally or more important in the colony-founding stage when there are few larvae as in the later stages with many. Furthermore, the productivity of *A. silvestrii* queens is very low: they lay on average only one or two eggs per day, and 5th-instar larvae are present in the nest year round. Therefore, LHF is accessible to

Table 2. Relationships between larval hemolymph feeding (LHF), food transfer by regurgitation, and food habits of 12 ponerine and 1 leptanilline ant species distributed in Japan. Presence of LHF and regurgitation is indicated by "X." LHF was judged to be present when LHF-characteristic scars were found on the integument of larvae. Abbreviations for food habits are: Cs, specialist carnivore (specialized prey animals are indicated in parentheses); Cg, generalist carnivore; G, gramnivore

Ants	LHF	Regurgitation between adults	Food habits confirmed in nature for the species	Reference	Food habits confirmed in nature for congeneric other species	Reference
Ponerinae						
Amblyoponini						
<i>Amblyopone silvestrii</i>	X ^a		Cs (centipede)	The present study	Cs (centipede, coleopteran larva)	Brown 1960; Gotwald and Lévieux 1972; Traniello 1982
Ectatomini						
<i>Proceratium watasei</i>	X		Cs (arthropod egg)	Kubota 1980; Masuko, unpubl.	Cs (arthropod egg)	Brown 1957, 1979
<i>Proceratium itoi</i>	X ^a		Cs (arthropod egg)	Masuko, unpubl.		
<i>Proceratium japonicum</i>	X		Cs (arthropod egg)	Masuko, unpubl.		
<i>Discothyrea sauteri</i>	^d		Cs (arthropod egg)	Masuko, unpubl.	Cs (arthropod egg)	Brown 1957
Ceraphachyini						
<i>Cerapachys humicola</i>	^d		?		Cs (immature of ant)	Brown 1975; Hölldobler 1982
Ponerini						
<i>Hypoponera excoecata</i> ^b		(X ^c)	?		Cs (collembolan)	Lévieux 1982
<i>Ponera japonica</i>			?			
<i>Ponera scabra</i>			?			
<i>Cryptopone sauteri</i>	^d		Cs? (soft-bodied insect larva in rotting wood)	Masuko, unpubl.		
<i>Brachyponera chinensis</i>		X ^e	?		Cs (termite), Cg, G	Wheeler 1936; Lévieux and Diamonde 1976
<i>Trachymesopus pilosior</i>			Cs? (isopod)	Masuko, unpubl.		
Leptanillinae						
<i>Leptanilla japonica</i>	X ^{a, f}		Cs (centipede) ^g	Masuko, unpubl.	Cs (centipede)	Terayama, unpubl.

^a Confirmed also by behavioral observation in the laboratory

^b This species is formally still placed under the genus *Ponera* (see Onoyama 1980), but it most likely belongs to *Hypoponera*

^c Observed in a European species, *H. eduardi*, by Le Masne (1952)

^d Prey feeding by the queen was also observed in a developed laboratory colony

^e Confirmed by Kôriba (1963)

^f Second type of LHF, with a larval specialized exudatory organ

^g Based on the laboratory study

queens all the time, and could sustain their low fecundity despite unstable food conditions. In a literal sense, the larvae serve as "food reservoirs" for colonies. The larval hemolymph is also probably assimilated by queens more efficiently than prey flesh, which might explain why queens of developed colonies persist with LHF even when prey is available.

A more elaborate form of nutrient transfer from larvae to adults has been known in vespine

wasps: Maschwitz (1966) showed that the stomodeal secretions of the larvae contain carbohydrates, which, he suggested, sustain the activities of adults, especially foragers. He also reported that in the ant *Tetramorium caespitum* the larval stomodeal secretions have higher concentrations of amino acids than the hemolymph. Ant larvae also produce a clear droplet from the anus. Such droplets are known to be imbibed by workers from time to time in some ant genera (Wheeler 1918; Le

Masne 1953). However, no information exists on the function of both kinds of fluids in ant colonies. *A. silvestrii* larvae, especially shortly after feeding, also readily excrete a transparent droplet from the mouth or proctodeum when under a strong contact stimulus, or while being pinched during LHF. Although such droplets are often licked up by nearby adults, this kind of nutrient(?) transfer is not systematic and presumably has only a minor function in colony life. It is, however, possible that LHF is a primitive evolutionary grade which might have led to more elaborate larval trophallaxis.

To test the proposed adaptive basis of LHF, field data on the rate of hunting success are obligatory; such data are, however, extremely difficult to collect in totally subterranean species like *A. silvestrii*. Another kind of test may come from comparisons between species, paying attention to LHF, food habits, and the ability to exchange food. Both *Proceratium* and *Leptanilla* lack the ability to regurgitate food. *Proceratium* are specialized predators of arthropod eggs (Brown 1957; Masuko, unpublished data). *Leptanilla* are also most likely, along with *Amblyopone*, specialist hunters of geophilomorphans. The rate of foraging success is, however, unknown for both.

Information on food habits of the other species in which LHF was not found is also rather incomplete. However, an interesting contrast between *Proceratium* and *Discothyrea* can be noted. The latter genus does not show LHF, despite being phylogenetically close to the former (Brown 1958) and also consists of egg predators (Brown 1957; Masuko, unpublished data). There are, however, as yet very few data in this comparative study than can be used to test the hypothesis.

Despite these considerations, the queen's monopoly of LHF remains unexplained. However, it may be related to her dominance in the colony. For example, two interesting phenomena have been observed on LHF by workers. First, *A. silvestrii* workers were, when starved, often observed to take larvae outside the brood chamber (i.e., probably away from the queen) to perform their own LHF. Second, when the queen was removed from laboratory colonies, the workers soon formed dominance hierarchies in connection with the laying of eggs. The hierarchies were marked by displays of aggression and subordination. In such colonies, only the highest-ranking workers show LHF with any frequency even when prey was available. These observations suggest that in an ordinary colony situation, the queens suppress the occurrence of LHF by workers in an unknown way.

Are there any effects of having hemolymph ex-

tracted during the larval stage on the caste or size at maturation of the individuals subjected to LHF? At present, little is known of the dwarfing effect of LHF or the relationships between LHF and caste differentiation in *Amblyopone* and *Proceratium*. The mechanism of caste differentiation in modern ants (possibly including *Amblyopone*) has probably evolved to a more elaborate and effective stage (Brian 1980). However, in the more advanced myrmicine genus *Myrmica*, Brian (1973, 1974) showed that in the presence of queens, workers attack gyne-potential larvae by biting their heads or ventral thoracic areas and possibly also by applying a glandular secretion that causes such larvae to metamorphose precociously into workers. Although it is unknown whether *Myrmica* workers take some hemolymph while biting larvae, the apparent similarity between this behavior and LHF in *Amblyopone* deserves closer attention.

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