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BEHAVIOR AND ECOLOGY OF THE ENIGMATIC ANT
LEPTANILLA JAPONICA BARONI URBANI
(HYMENOPTERA : FORMICIDAE : LEPTANILLINAE)

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SUMMARY

The present study of *Leptanilla japonica* has clarified for the first time the biology of the Leptanillinae. Males were obtained, which are the first specimens of the subfamily to be collected in association with workers. *L. japonica* is a totally subterranean ant. Colonies are monogynous with a dichthadiiform queen. Worker population per colony is small, usually 100-200. Development of immature individuals is strictly seasonally synchronized. Colonies often emigrate to the site of paralyzed prey (geophilomorph centipedes). For carrying larvae workers grasp peculiar structures projecting from the larval prothorax with the lower mouthparts. The final-instar larvae have a pair of specialized lateral duct organs on the 4th abdominal segment. Through these organs larval hemolymph is provided for cons'umption by adults, especially by the queen. Nutrition of the queen depends exclusively on this process. The frequency of larval hemolymph feeding by queens is abruptly elevated when the larvae mature. Owing to this the queen is able quickly to achieve full physogastry, and to lay a batch of 100-200 eggs within a few days. Emergence of new workers from pupae is synchronized with hatching of the 1st-instar larvae from the eggs. In a concluding section the lifemode of *Leptanilla* is compared with that of doryline and ecitonine army ants

. RESUME

Comportement et écologie de la Fourmi énigmatique
Leptanilla japonica **Baroni Urbani**
(Hymenoptera : Formicidae : Leptanillinae)

Le présent travail sur *Leptanilla japonica* donne pour la première fois des informations sur la biologie des Leptanillinae. Deux mâles ont été obtenus, qui sont les premiers spécimens à être recueillis en même temps que les ouvrières de la même espèce, chez les Leptanillinae. *L. japonica* est une fourmi entièrement souterraine. Ses sociétés sont monogynes, avec une reine dichthadiiforme. Le nombre d'ouvrières d'une société est faible : en général 100 à 200. La croissance du couvain est strictement synchronisée avec

la saison. Les sociétés se déplacent souvent jusqu'à l'endroit où se trouve la proie para-lysée (Chilopode géophilomorphe). Les ouvrières, pour porter les larves, saisissent avec leurs pièces buccales inférieures (labium et maxilles) la structure particulière qui fait saillie ventralement sur le prothorax larvaire. Les larves du dernier stade ont une paire d'organe canaliculaires latéraux sur le quatrième segment abdominal. Par cet organe l'hémolymphe larvaire est excrétée, pour l'alimentation des adultes, et particulièrement de la reine. La nutrition de la reine dépend exclusivement de ce processus. Quand les larves sont proches de la nymphose, la fréquence de cette activité alimentaire (appelé "LHF") augmente de manière brusque, permettant à la reine de devenir rapidement physogastre, et de fournir 100 à 200 œufs en quelques jours. L'éclosion de larves du pre-mier stade est synchronisée avec l'émergence de nouvelles ouvrières. En conclusion, le mode de vie de *Leptanilla* est comparé à celui de Fourmis nomades, Dorylinae et Ecitoninae.

INTRODUCTION

The Leptanillinae is a small ant subfamily containing about 30 named species of which 16 were described from males unassociated with conspecific workers (BARONI URBANI, 1977). It has been assumed from the adult mor-phology, especially dichthadiiform of the queens, that the leptanillines have legionary habits like those of the tropical army ants of the subfamily Dory-linae (*sens. lat.*) (WILSON, 1971). Nothing, until now, has been known of their life history. Leptanillines were initially placed as a tribe of the former subfamily Dorylinae (EMERY, 1910), but were later raised to subfamily rank (WHEELER, 1923, p. 335). This change was based mainly on several aberrant features of larval morphology (WHEELER and WHEELER, 1930). According to WHEELER and WHEELER (1965) the most notable of these are (1) the peculiar projection from the ventral surface of the prothorax; (2) the reduction of the spiracles from the usual ten pairs to a single pair located on the 3rd abdominal segment; and (3) the shape and stance of the outwardly-directed mandibles. All of these are unique to leptanillines among the Formicidae, but their functions have been totally unknown.

Five species of *Leptanilla* have been described from Japan (BARONI URBANI, 1977), but the collection of suitable material, even in that country, has been too incidental to allow detailed studies on their biology. Recently, however, I have collected eleven colonies of *Leptanilla japonica* BARONI URBANI from Cape Manazuru in southern Honshu. This material has per-mitted informative studies on the ecology and behavior of *Leptanilla*. The results of my field and laboratory observations are presented here, with discussion on the peculiar mode of life of *L. japonica*, which is apparently related to its presumed highly migratory habits.

MATERIALS AND METHODS

Leptanilla japonica is a tiny, yellow ant; the worker is about 1.2 mm long and the queen 1.8 mm long. Between July 1981 and August 1983 eleven colonies of this species were collected in the evergreen broadleaf forest at Cape Manazuru, Kanagawa Prefecture. All colonies were unexpectedly located in soil during excavation in search of other subterranean ants. Because the volumes of the nest chambers were so small colonies were easily collected in their entirety. Since the brood is rather delicate the ants were not aspirated into a vial; instead, small lumps of soil surrounding each whole colony were carefully put into a vial *in toto* and brought back to the laboratory. Of the 11 colonies collected six were cultured (at 20-25° C). Colonies were kept in rectangular clear polystyrene containers (10 × 11 × 2 cm) with a floor-cover of gypsum mixed with activated carbon powder; no brood chamber was provided. Activities were monitored through clear glass covering the tops of the containers, with the aid of a swing-arm-stereomicroscope (magnifications 10-80X). Sufficient prey was given to prevent starvation, and small geophilomorph centipedes alone were accepted by the ants (see below). The observed behavioral acts were noted using a sound recorder, or logged directly onto a portable microcomputer (Epson HC-20), for assaying time budgets. Scanning electron micrographs were taken with a J.E.O.L. JSM-25 microscope after material had been critical-point-dried with liquid CO_2 or treated with hexamethyldisilazane (NATION, 1983).

RESULTS

Nesting habits and colony composition

1. *Nesting habits*

All the nests were situated at a depth of 10-15 cm in moist well- packed earth. Ten colonies were found in the soil without covering material except leaf litter, and one was found in the soil under a large fallen dead branch.

In most cases the whole colony occupied a single, narrow, irregular space, which apparently was not excavated by the ants themselves but was a preformed crevice. In some cases, perhaps influenced by the form and distribution of the crevices, the ants were located in a few adjacent but separate chambers. The brood, if any, was cramped into a single pile without separation of eggs, larvae or pupae. When disturbed by excavation the queen and workers, whether they were alone or carrying larvae, disappeared swiftly into small cracks in the soil. This behavior is facilitated by their dorsoventrally flattened and freely movable body sections, which permit them to move easily in confined tortuous spaces in the soil. Underground tunnels were not noted at the peripheries of nest chamber.

2. Adult population

Table I shows the composition of the Cape Manazuru colonies. The collections are ordered so that they reflect the inferred seasonal cycle, regardless of individual times of collection. Queens were collected with 10 of the 11 colonies and all were monogynous. Worker population per colony is estimated to range from 100 to 200. Among the completely collected samples in the active season, however, some colonies (82-130, 82-222 and 82-314) contained many fewer workers relative to the numbers of larvae or pupae present. In these it is inferred that a large portion of workers were probably out foraging, or had expired.

3. Seasonal trend of immature development

From table I it can be seen that broods were produced in discrete generations. Furthermore, in each generation all individuals were at approximately the same stage of development in each colony, i.e., all larvae were of the same instar and size, or pupae were similarly pigmented. From the seasonal trend seen in table I, and the results of laboratory rearing (see below), the average worker-brood cycle of L. japonica is surmised as follows (fig. 1) :

    In a short period of July (late mid-summer) a batch of eggs is laid by the queen ; these hatch into larvae, at the latest by early August, and subsequently develop in concert until winter, when they hibernate, to complete development the following summer. Most larvae appear to reach the final instar before hibernation. This is suggested by the fact that there were no significant differences in head length and other morphological features examined with the SEM in comparing larvae from winter colonies (82-33 and 83-40) with those taken in summer (82-222 and 82-314). In the following July the larvae all pupate synchronously, and the queen then promptly lays the next batch of eggs. (The larvae of L. japonica do not spin cocoons prior to pupation). New adults emerge from pupae between late July and early August. The synchronization between larval hatching and adult eclosion was confirmed in the laboratory : In colony 81-173, which was collected on 11 July 1981 with about 100 eggs and 140 worker pupae, new workers emerged from most of the pupae on 26 and 27 July, while the 1st-instar larvae hatched from most of the eggs around 23 July. This result suggests that the composition of colonies 82-217 and 82-219 at collection probably indicates that hatching of larvae in nature slightly precedes eclosion of new adult workers (see table I).

As is the case with the larvae of most ant species, there is no information on the number of larval instars in L. japonica. However, their hatching in July and attainment of the final instar by mid November, at latest, in the same year, suggest rapid larval growth in this species. (Most subterranean ant species at Manazuru forest cease their extranidal activities in mid November when the soil temperature at 15 cm deep falls below 15° C ; MASUKO, unpubl.). In all colonies where pupae were found a small number of individuals remained as larvae (5-10 % of total, see table I). These larvae seemed from their size to be of the same generation as the pupae.

Table I. — Field data on 11 colonies of *Leptanilla japonica*.

Tableau I. — Données recueillies sur le terrain pour la population de 11 sociétés de *L. japonica*.

Colony no.	Date of collection	Queen	Workers	Male	Eggs	Hatch-lings	Final-instar larvae	Pupae worker	Pupae male
83-14	16.i.83	1	135	0	0	0	138	0	0
83-40	20.ii.83	0	25	0	0	0	31	0	0
82-33	7.iii.82	1	127	0	0	0	86	0	0
82-130	19.v.82	1	29	0	0	0	c. 200	0	0
81-173	11.vii.81	1[a]	100	0	c. 100	0	9	136	1[b]
82-217	14.vii.82	1	c. 80	0	0	⎱ c. 150	10	c. 200	0
82-219	14.vii.82	1	c. 70	1	⎱ c. 50	⎰	15	c. 200	0
82-222	14.vii.82	1	31	0	c. 130	0	18	220	0
83-97	3.viii.83	1	49	0	9	4	6	116	0
83-105	3.viii.83	1	42	0	1	1	4	81	0
82-314	17.viii.82	1	15	0	0	0	198	0	0

[a] When collected in the field, only this queen was slightly physogastric while the others were not at all.

[b] This male pupa emerged as an adult later in the laboratory.

[a] Au moment de la récolte dans la nature, seule cette reine était légèrement physogastre ; les autres pas du tout.

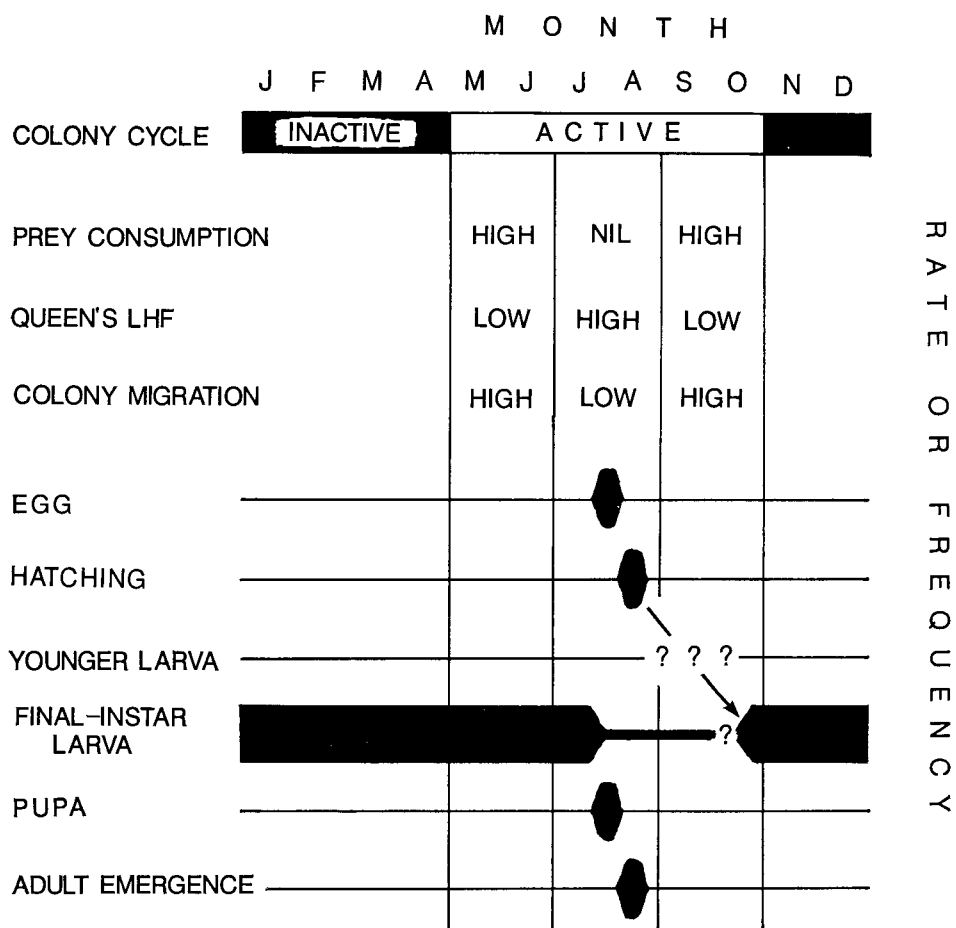[b] Cette nymphe a fourni un mâle adulte, au laboratoire, un peu plus tard.

Fig. 1. — Seasonal cycle of colony functions of *Leptanilla japonica*. For explanation see text.

Fig. 1. — Cycle saisonnier des différentes fonctions sociales de *L. japonica*. Pour les explications, voir le texte.

4. Production of sexuals

The characteristics of sexual production of *L. japonica* remain poorly known, since the material obtained in this study is scanty. A male-pupa and an adult male were collected in the field with colonies 81-173 and 82-219, respectively (*table I*). These are the first male specimens in the Leptanillinae to

have been collected from a colony, and confidently associated with workers. They will be described elsewhere (OGATA, TERAYAMA and MASUKO, in prep.). Absence of gyne-pupae, and the extremely small number of males, suggest that they were produced irregularly in this case. At the time of collection the worker-pupae of colony 81-173 were not at all pigmented ; the male-pupa had, however, already darkened to some extent. A male ultimately emerged earlier than workers in the laboratory. The male of colony 82-219 had already emerged in the field at a time when worker-brood was still at the pupal stage.

Laboratory observations

Six colonies were observed in the laboratory for varying periods. Four of them (colonies 81-173, 82-217, 82-219 and 82-222) which included pupae when collected perished within 1-3 weeks of the beginning of culture, because of fungus infection. The other 2 colonies (82-33 and 83-14) were both collected with larvae, in winter. Their longer period of survival (43 days for colony 82-33 and 103 days for colony 83-14) permitted the study of details of larval development up to pupation, and of activities of the queens and workers. Descriptions in this section are based chiefly on observations on these colonies. When larvae of colonies 82-33 and 83-14 attained their full growth, with swollen bodies, the queen abruptly entered physogastry and prey consumption by the colony was terminated. To facilitate discussion the colony stage before this change is referred to below as the "larval-growing stage" and the stage thereafter the "egg-laying stage". Similar, if not homologous, changes in colony behavior are well known between the alternating "nomadic" and "statary phases" of some tropical army ants (SCHNEIRLA, 1971). The temporal use of nest sites in the field (discussed above), the convergence to army ants in adult (especially queen) morphology, and the frequent colony migrations observed in the laboratory (see below) suggest strongly that *L. japonica* is a highly migratory ant. The terminology used to describe the behavioral cycles of army ants has not been followed here, however, in the absence of direct field evidence of colony migration correlated with changes in the brood composition of colonies of this species.

Activities of workers and development of larvae

1. *Brood pile and guard ants*

When laboratory rearing began the number of living larvae had reduced to only 12 in colony 82-33 and to about 100 in colony 83-14, because of injuries sustained in collection and transportation. The transfer of the ants to laboratory nests at first greatly disturbed them, and resulted in their being scattered over the plaser floor for a short time. By the next day, however, they were normally aggregated and all the larvae had been gathered into a
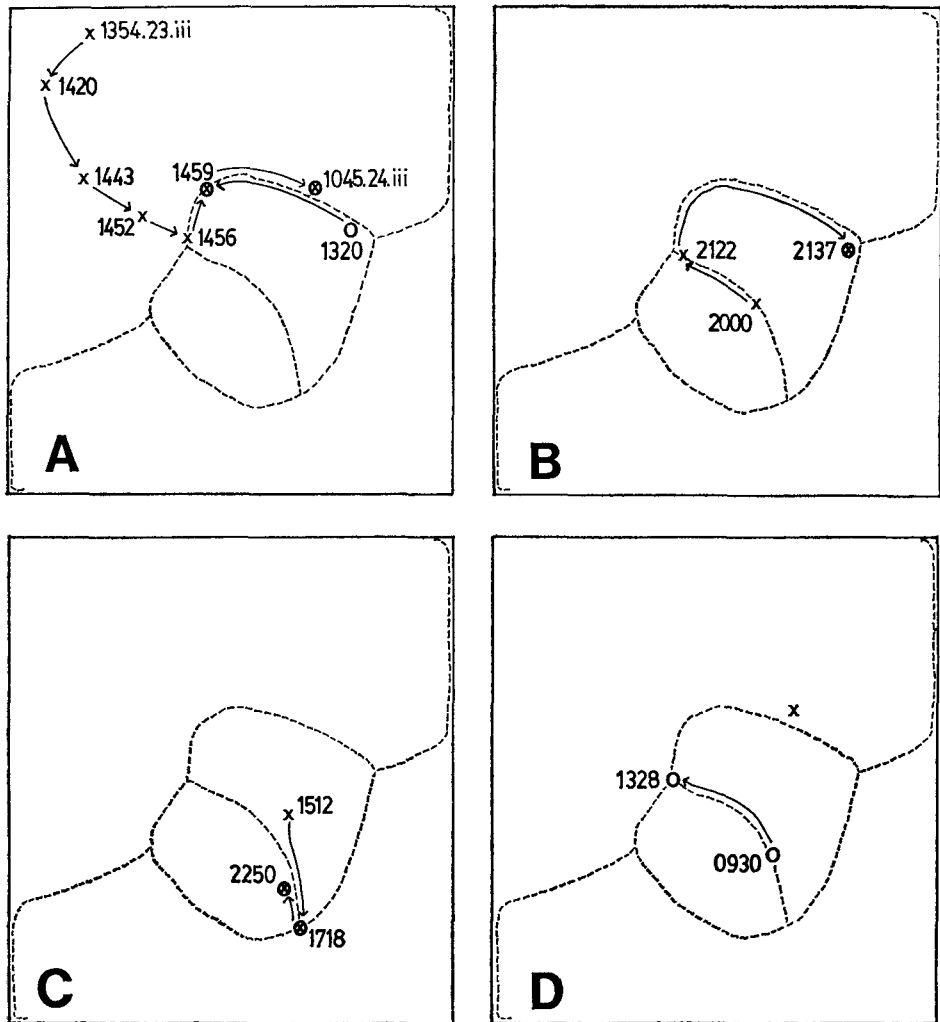
Fig. 2. — Diagrams of a trail system of *Leptanilla japonica*, observed in a laboratory colony. The courses of trails (broken line) were persistent during the culture. The outer rectangles represent the confines of an artificial nest (10 × 11 cm). Trajectories of prey transport and colony migration are shown for three cases of predation (A-C) and one case of colony movement without prey consumption (D). X = site of retrieved prey; O = colony site where the queen and brood existed; (x) = site of prey feeding by colony. Of a series of x's in each figure, the first one represents the position where the prey was first recognized as completely immobilized. Each symbol is accompanied with hour of day when the locations were recorded. A : March 23-24, 1982. B : March 26, 1982. The colony remained at the same place, while the prey was moved from the site of its complete paralysis at 2000. C : March 29, 1982. The prey completely immobilized at 1512 reached the colony site at 1718 ; then the ants, together with the prey, moved along a trail to the

single pile. This was flat, loosely organized, and attended by some dozens of workers, while others engaged in foraging activity. Interestingly, the queens spent most of their time on the brood pile. Half, or more, of the workers at the pile stood at its periphery. They were apparently guard ants, since most of them faced outward and took a characteristic posture, with the anterior half of the body raised, the forelegs suspended in the air, and the mandibles open. They frequently rushed to approaching objects such as nestmates. Such guards also gathered around the spot where larvae were feeding on retrieved prey. Other workers present at the brood pile engaged mostly in larval care or nestmate-grooming.

2. *Trail system*

Throughout the period of laboratory life a conspicuous trail system, on which the ants travelled, was observed on the floor of the nest chamber (*fig. 2*). The course of the pathways often changed with time. Even when undisturbed the movements of workers along the trails were not organized: each worker came and went from the brood pile area independently, so that there was no apparently organized movement in groups. Some workers departed from the trails to stray singly, and apparently randomly, over the interior of the containers.

When the queens and unladen workers moved on the trails their abdomens were lowered, apparently causing the ventral surface to touch the substrate. In the case of workers it appeared that the sting was not protruded on the trails at this time. This suggests that a sternal gland secretion partici-

place recorded at 2250. D : April 2, 1982. Colony migration occurred between 930 and 1328 on April 2 and the ants remained at the place recorded at 1328 until 20 April when their rearing was terminated. The prey given at 2251 on 3 April was found paralyzed at x at 2358 on the same day but it remained intact until 20 April.

Fig. 2. — Diagramme du système de pistes de *L. japonica*, observé au laboratoire (société 82-33). Les pistes (lignes tiretées) ont persisté durant l'élevage. Le contour rectangulaire extérieur représente les limites du nid artificiel (10 × 11 cm). Les trajets suivis pour le transport de la proie et pour le déplacement de la société sont représentés pour 3 cas de chasse (A, B, C) et un cas (D) de déplacement de la société sans qu'il y ait eu consommation de proie. X = position de la proie ; O = position de la société ; (x) = lieu de consommation de la proie par la société. Dans une série d'x, le premier indique l'endroit où la proie a été immobilisée. L'heure est indiquée à côté de chaque symbole. A : 23-24 mars 1982. B : 26 mars 1982. La société ne s'est pas déplacée, tandis que la proie, paralysée à 20 h., a été amenée jusqu'à la société. C : 29 mars 1982. Paralysée à 15 h. 12, la proie a atteint la société à 17 h. 18 ; ensuite les Fourmis, traînant la proie, se sont déplacées le long d'une piste, jusqu'à l'emplacement enregistré à 22 h. 50. D : 2 avril 1982. La société s'est déplacée entre 9 h. 30 et 13 h. 28, le 2 avril et elle est restée à l'endroit enregistré à 13 h. 28, jusqu'à la fin de l'élevage (20 avril). La proie, donnée à 22 h. 51, le 3 avril, a été trouvée à 23 h. 58 en x, paralysée ; mais elle est restée là, intacte, jusqu'au 20 avril.

pates in formation of the trails, as in the case of *Onychomyrmex*, an Australian army ant genus related to *Amblyopone* (HÖLLDOBLER and TAYLOR, 1982). The results of histological investigations on the exocrine glands of *L. japonica* will be published elsewhere (HÖLLDOBLER, PALMER, MASUKO and BROWN, in press).

3. *Prey capture*

No field data was obtained on the feeding habits of *L. japonica*. Instead, different soil invertebrates were given to laboratory colonies to test food preferences in the larval-growing stage (as defined above).

Although organisms such as an annelid (ca. 5 mm long), a nematode (ca. 5 mm long), a campodeid (ca. 3 mm long), *Isotoma* collembolans (ca. 1.5 mm long), and ant larvae (*Oligomyrmex sauteri* Forel) were totally ignored (tested once for each), geophilomorph centipedes of small size (body length ranging 10-20 mm) were invariably stung, paralyzed and ultimately consumed. The centipedes were given to the ants either in an intact condition or, if active enough to disturb the culture, in an injured state. During 22 days of its larval-growing stage colony 82-33 hunted and consumed 7 intact geophilomorphs (10-15 mm long; mainly nymphs of *Prolamnonyx holstii* (Pocock)), and fed partly on a cryptopid (13 mm long), but rejected the chopped body (5 mm long) of a *Strigamia* species and a segmented piece (15 mm long) of an undetermined larger geophilomorph. During its 52-day larval-growing stage colony 83-14 consumed 14 intact or injured geophilomorphs (12-20 mm long; mainly *Prolamnonyx holstii* nymphs), 3 pieces of chopped portions (each 5 mm long) of unidentified larger species, and a cryptopid (15 mm long).

Such predation on small geophilomorphs, and the characteristic mode of larval feeding on these organisms (see below), suggest that *L. japonica* preys chiefly or exclusively on these centipedes in nature. Recently, a single colony of an undescribed species of *Leptanilla* was collected on Formosa. Its larvae, when discovered, were found clustered on a captured geophilomorph (OGATA, TERAYAMA and MASUKO, in prep.).

Under laboratory observation workers which came upon centipedes instantly attacked them. The ants tenaciously seized and stung the prey until it was completely paralyzed (*fig. 3*). In most cases the centipedes were immobilized within 10 minutes of their introduction and attack by only several workers was sufficient to accomplish this paralysis, which is expressed as an inhibition of motor activity. I observed once, during the egg-laying stage of colony 82-33, that a geophilomorph (15 mm long) which had been paralyzed but was thereafter ignored by the ants, remained alive, moving its appendages for 17 days, until it was preserved for study (see *fig. 2D*).

4. *Larval and prey transport*

Soon after a centipede is paralyzed nearby workers begin to drag it towards the brood pile. There is often a concurrent migration of the whole

colony in the direction of the prey. On rare occasions the colonies moved to the prey, which was not transported from the site of paralysis (*table II*). Whether or how *L. japonica* workers recruit nestmates during prey transport could not be investigated in the present study. This is partly because of the small size of the artificial nests used, in which violent escape reactions of prey seized by foraging ants immediately attracted nearby workers directly before possible recruitment could begin. In any case, larval feeding
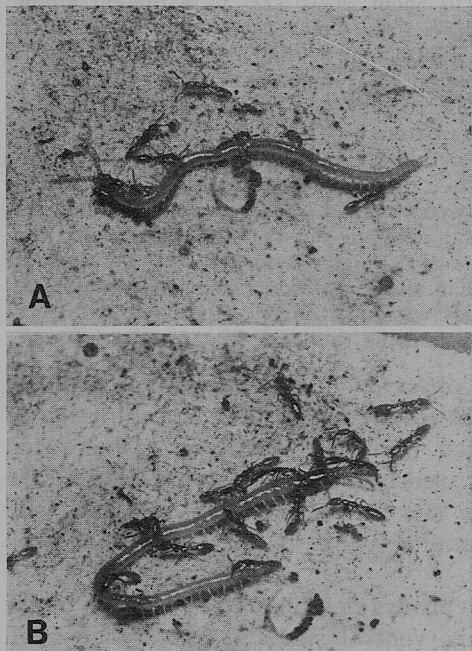
Fig. 3. — Prey capture of *Leptanilla japonica*. Workers attacking a geophilomorph centipede (15 mm in length). B : Paralysis of the prey 15 min after the scene of A.

Fig. 3. — Capture de la proie de *L. japonica*. A : Ouvrières attaquant un Géophilomorphe (15 mm de long). B : Paralysie de la proie, 15 minutes après la situation A.

Table II. — Occurrence of prey retrieval to nests and colony migration to prey site in 14 cases of prey capture followed by larval feeding in *Leptanilla japonica*. Records from two laboratory colonies (82-33 and 83-14) were combined.

Tableau II. — Apparition d'un transport de la proie, ou d'un déplacement de la société vers la proie, dans 14 cas de chasse ayant abouti à la consommation de la proie par les larves. Données établies à partir de 2 sociétés (82-33 et 83-14) élevées au laboratoire.

	Prey retrieval	
	occurred	did not occur
Colony emigration		
occurred	4	3
did not occur	7	—

on prey usually began within an hour of capture. The following is an episode
of larval transportation to the prey site observed in colony 82-33 (*fig. 2A*),
whose composition at the time included a queen, approximately 100 workers
and 11 larvae :

At 13 h 20 on the 23rd of March 1982 an intact geophilomorph (body length ca.
15 mm) was admitted to the nest. At 13 h 34 a worker first succeeded in stinging the
prey, which it had seized with its mandibles. At 13 h 54 12 workers were counted
attacking the centipede at a point directly 7.5 cm from the brood pile. The prey was
already almost completely paralyzed. At 14 h 07 about 30 workers were present around
the victim, which had not been moved since 13 h 54. A few workers were then first observed
to drag the prey towards the brood pile, though most others simply chewed and licked its
surface. At 14 h 43 the centipede had been dragged to a point 6 cm from the brood pile.
At this point the first larval transport towards the prey by a worker occurred, but the
transporting worker turned back with the larva to the brood pile when about halfway to
the prey. At 14 h 48 the queen first departed the brood pile and moved all the way to the
prey, but soon returned to the brood pile. After that she repeated similar lone shuttles
between the brood pile and prey site 3 times. At 14 h 56 a worker carrying a larva first
arrived at the prey, now 4 cm from the brood pile, but did not settle there. Between
14 h 59 and 15 h 01 workers carried larvae one after another along a trail between the
brood pile and prey site, with the result that all larvae were ultimately transferred.
On the following day (at 10 h 45), the prey body was found largely consumed, with most
of the larvae attached to it, at a different point on the trail (*fig. 2A*).

Two other cases of prey transport observed in this colony are depicted
in *figures 2B* and *2C*. Prey feeding by the colony ceased after consumption of
the geophilomorph hunted on 29 March (*fig. 2C*). Afterwards, the queen
swiftly entered physogastry, which was clearly discernible by 31 March. On
2 April the colony emigrated to a new site on the trail (*fig. 2D* ; the site
recorded at 1328) where it remained stationary until 20 April, by which time
the last worker had died.

Larvae being carried by workers are always held in a fixed posture under
the transporter and along its body axis, ventral side uppermost and head
forwards (*fig. 4*). Workers, remarkably, do not use their mandibles to grasp
transported larvae. Instead, they use the lower mouthparts (the labio-
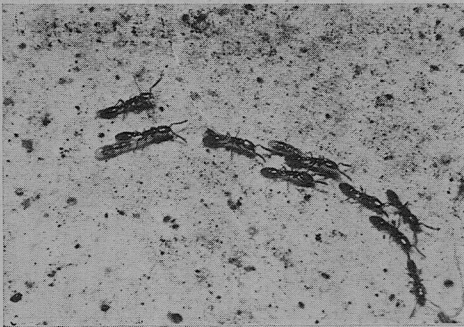maxillary complex) to seize the peculiar structures which project from the

Fig. 4. — Larval transport by *Leptanilla
japonica* workers along a trail. They
use the labio-maxillary complex to
grasp the specialized structure on
the prothorax of the larvae.

Fig. 4. — Ouvrières de *L. japonica* trans-
portant des larves le long d'une
piste. Elles utilisent les maxilles et
le labium pour saisir la structure
spécialisée du prothorax des larves.

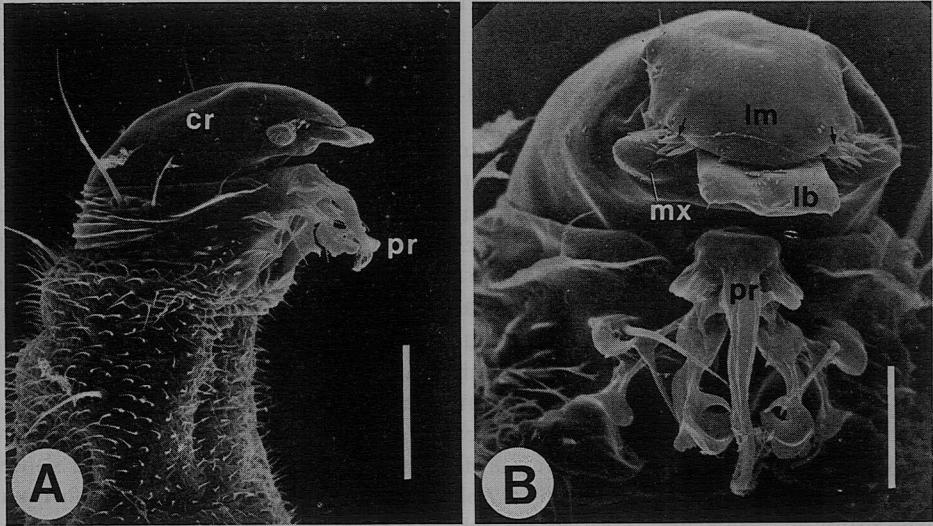Fig. 5. — Scanning electron micrographs of the prothoracic structure of *Leptanilla japonica* final-instar larva. A : Lateral view, scale = 50 μm. B : Ventral view, scale = 20 μm, *cr* = cranium ; *lb* = labium ; *lm* = labrum ; *mx* = right maxilla ; *pr* = prothoracic structure. Arrows indicate the laterally pointed teeth of the mandibles.

Fig. 5. — Photographie au microscope à balayage de la structure prothoracique des larvae du dernier stade de *L. japonica*. A : Vue latérale ; échelle = 50 μm. B : Vue ventrale ; échelle = 20 μm. *cr* = capsule céphalique ; *lb* = labium ; *lm* = labre ; *mx* = maxille droit ; *pr* = structure prothoracique. Les flèches indiquent les dents des mandibules, qui font saillie latéralement.

ventral surface of the larval prothorax (*fig. 5*). The fact that the mandibles were not involved was easily observed through the stereomicroscope, but the use of the lower mouthparts to grasp the larval projections could not be observed directly from above. However, a worker grasping a larva was found in the preserved material, and stereomicroscopic examination confirmed that the prothoracic structures of the larva were closely set into the worker's lower mouthparts. This connection was unfortunately broken in the course of treatment for planned SEM illustration, but it can be concluded that the larval structures form a coupling mechanism for rransportation of larvae by workers using their labio-maxillary mouthparts. No other functions for the larval prothoracic structures have been suggested by the present study. The peculiar and complex form of these projections likely correspond with the related structures of the worker's mouthparts, as between a key and a lock, but details remain unknown. It was occasionally observed, however, that workers, when greatly disturbed, grasped larvae with their mandibles around the region a little behind the head and dragged them in a less structured manner. In suche cases, the larvae were often dorsal or lateral side up,

under the bodies of transporting workers, and were not aligned with the body axes of the transporters.

5. *Feeding characteristics of larvae and workers*

Workers do not dismember captured centipedes for larval feeding, but the larvae are carried and attached to the prey. They cut through the pleura (the softest part of the prey) unassisted by workers, and finally consume the tissue within, ultimately leaving shriveled and almost completely depleted exoskeletal remains. *Leptanilla* larvae have a peculiar, slender body form, classified as "leptanilloid" by WHEELER and WHEELER (1976). This is characterized by the small size of the cranium relative to the whole body length, and by the thorax and the first abdominal segment being cylindrical, in contrast to the remaining posterior segments which are laterally extended (*fig. 6*). These morphological characteristics can be collectively termed "microcephaly", and can be regarded as an adaptation related to larval feeding in some ant groups (MASUKO, unpubl.). Microcephaly must facilitate group-feeding by a large number of larvae upon a single, whole prey item (*fig. 7*). Also of interest is the morphology of the larval mandibles, as described by WHEELER and WHEELER (1965). They are directed outwardly, and only their apices and outer borders are furnished with major sharply pointed teeth. Without assistance from workers *L. japonica* larvae are able to thrust their heads and thoraxes deeply into the bodies of prey centipedes. It is suggested that the mandibular abduction might tear and dig the prey tissues, much as do the actions of the forelegs of fossorial animals, assisting in this process.

Larvae often moved actively around the prey, usually wriggling dorsoventrally. Their bodies can be bent completely double in both dorsal and
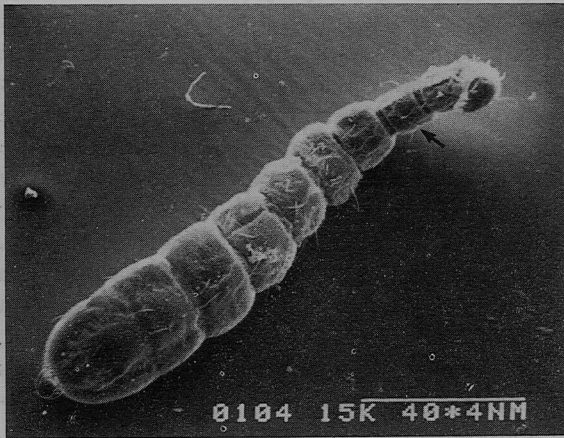

Fig. 6. — Whole, ventrolateral view of a final-instar larva of *Leptanilla japonica*. Arrow indicates the first abdominal segment. Scale = 0.4 mm.

Fig. 6. —Vue générale (ventrolatérale) d'une larve du dernier stade de *L. japonica*. La flèche indique le premier segment abdominal. Echelle = 0.4 mm.

Fig. 7. — About one hundred larvae of *Leptanilla japonica* clustered on a prey, geophi-
lomorph centipede. Arrow at lower left indicates the queen standing with the
abdomen raised obliquely.

Fig. 7. — Larves de *L. japonica* (une centaine environ) rassemblées sur la proie, et autour
(il s'agit d'un Chilopode géophilomorphe). La flèche indique la reine, qui se tient
avec l'abdomen dressé obliquement.

ventral directions. By such movements they are able to crawl and reach the
prey. This behavior seems, however, to be rather more haphazard than
directed.

Workers take nutrients directly from prey, mostly by feeding at openings
created by larvae. It is also peculiar that whenever workers attached their
mouthparts to prey their antennae were pulled posteriorly in a V-shaped
configuration. Such an antennal position was also taken when workers can-
nibalized immature individuals, but was not observed during larval hemo-
lymph feeding by workers. Larval fecal masses discharged during the
process of pupation may be also consumed by workers, as is known in
some other ants (LE MASNE, 1953 ; see below). Oral trophallaxis is evidently
absent in this species, since it was never observed.

6. *Development of larvae, pupation, and oviposition by queens*

The descriptions in this section are based principally on observations
on colony 83-14, where brood rearing was most successful, and where many
larvae completed pupal ecdysis. However, the colony was ultimately infested
by mites which destroyed all the pupae before emergence.

When culture of this colony began on 17 January the gaster of the queen

was totally contracted, with a maximum width of about 0.35 mm. On 23 January (up to which time the colony had consumed 2 geophilomorphs and one cryptopid) her gaster was first noticed to be slightly, but obviously, inflated, especially dorsoventrally, with a diameter of about 0.50 mm. From that time 14 centipedes were consumed by the colony and the larvae increased in size without ecdysis. On 8 March the queen remained partly physogastric. When observed on 10 March (no observation was made on the 9 th), however, her gaster had markedly expanded. Its intersegmental membranes were greatly extended, so that the whole gaster looked like a balloon, with a diameter of about 0.65 mm. This enlarged gaster, and sometimes also the head and thorax of the queen, strongly attracted workers. During her physogastry, several workers usually clung motionless to the surface of her gaster in a peculiar stance, with either their middle or hind legs, or both pairs, suspended in the air, even while the queen was moving actively (figs. 8, 10). The mouthparts of such clinging workers were attached to the intersegmental membranes of the queen's gaster. Licking movements were not observed but the workers occasionally seized or lightly pulled the intersegmental membranes with their mandibles. On this day (10 March) two larvae were found whose thoraxes had swollen into a spheroidal shape, with the intersegmental grooves obliterated, indicating the initiation of pupation. These changes in the queen and the larvae indicate the point of progression from the larval-growing stage to the egg-laying stage in L. japonica colonies.

The queen's gaster continued to enlarge until 15 March when it reached about 1.10 mm in diameter, the maximum size observed for this individual (fig. 8) (note that the body length of a contracted queen is about 1.8 mm). On the same day approximately 80 % of the existing larvae had spheroidal thoraxes. The queen began to lay eggs on 16 March, only about one week after the first signs of her physogastry. Eggs appeared uninterruptedly at the tip of her abdomen like a beaded string. Workers sometimes assisted

Fig. 8. — A fully physogastric queen of Leptanilla japonica.

Fig. 8. — Reine complètement physogastre de L. japonica.

egg deposition by pulling eggs from the queen's cloaca with their mandibles. A total of about 20 eggs were found in the larval pile. Eggs were ellipsoidal with long axis 0.26 ± 0.01 mm and short axis 0.18 ± 0.01 mm (mean ± S.E.; n = 10; measured on preserved material at 160X).

On 17 March eggs numbered about 50 and most larvae had begun to purge their digestive tracts. Workers assisted them to discharge fecal masses and at times fed on the material so produced. On 19 March prepupae totaled about 40 and the number of eggs had reached about 100 (although about 20 % of them were collapsed, for an unknown reason, and workers were seen attaching their mouthparts to some of the eggs). Around this time the number of ants at the brood pile crearly increased, despite reduction in the total worker population (in which 50-60 workers now survived). This indicates that, in the egg-laying stage, most of the colony worker force is involved in brood care, while foraging is inactivated.

Oviposition by the queen lasted for a week after 16 March, and was not observed on 24 March when her gaster was still slightly distended, with a diameter of about 0.50 mm. By then the number of eggs had reduced to about 30. On 27 March there were about 30 prepupae and 30 worker-pupae, but all eggs had disappeared without producing hatchlings. There remained also 9 larvae, one of which had a swollen thorax. On 29 March the queen's gaster had completely contracted to its initial state, and by 30 March nearly all the prepupae had pupated. Workers were observed to help them shed the last larval skin. Most pupae had become pale-yellow on 18 April. Four geophilomorph centipedes and one cryptopid were paralyzed but then ignored by the ants between 9 March and 18 April, during the period of queen physogastry.

From 20 April the ants began again to consume newly introduced and captured centipedes. On 27 April all pupae had been destroyed by mites, so that laboratory rearing was terminated and the surviving members (the queen, 27 workers, and 5 larvae) were fixed for other studies.

Activities of newly emerged workers are precocious, since, in colony 81-173 where about 70 new workers successfully eclosed, such unpigmented workers, only one or two days after emergence, were observed to travel along the trails in the same manner as old workers.

The relationships between larval growth, egg production, predatory activity and colony migration in *L. japonica* colonies may be summarized as follows (see also *fig. 1*). In the larval-growing stage intensive predation on geophilomorph centipedes occurs repeatedly; the larvae consume this prey and grow in synchrony, while the queen remains with a contracted abdomen. Colony migration is frequent, in response to prey acquisition. When the larvae mature colonies enter the egg-laying stage. The larvae pupate synchronously; prey is no longer hunted; and the queen swiftly accomplishes physogastry, to lay a batch of eggs. Colonies at this stage become stationary,

perhaps because no more food is required, and because the workers are ineffiicent in carrying eggs and pupae, as opposed to larvae. When new adults emerge larvae of the next generation hatch in concert and another larval-growing stage begins. Closely related to the queen's rapid ovarian development is the intensity of her hemolymph feeding from larvae. The rate of this behavior was observed to increase abruptly in the egg-laying stage (see below).

7. Ovarian development

In comparison with the ecitonine army ants (SCHNEIRLA, 1971) the mass oviposition by *L. japonica* queens is on a small scale. It is probable that queens lay a single batch of eggs maximally numbering around 200 each year. The number of eggs produced must be related to the number of ovarioles. Dissections were made on 3 freshly-killed contracted queens. The numbers of their right and left ovarioles were 15-17, 15-17, and 17-14, respectively. As seen in *figure 9* the shape of the ovary at this stage is nearly spherical, suggesting that the balloon-like appearance in physogastry is produced by all the ovarioles filling with a number of eggs being matured synchronously. No ovarioles were found in dissections of 5 freshly-killed workers.

Behavior of the queen

In order to understand the role of reproductive females in the functional cycle of *Leptanilla* colonies much attention was paid to the activities of queens apart from egg-laying. For this purpose behavioral time budgets were
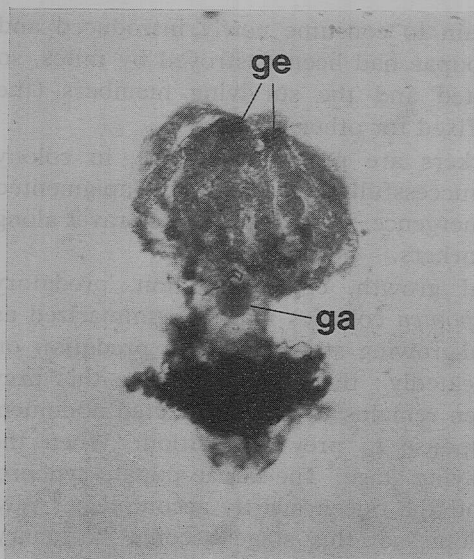

Fig. 9. — Whole ovary dissected out from a freshly-killed, contracted queen of *Leptanilla japonica*. *ga* = last abdominal ganglion ; *ge* = germarium.

Fig. 9. — Vue générale de l'ovaire d'une reine de *L. japonica* à abdomen contracté, fraîchement tuée. *ga* = dernier ganglion abdominal ; *ge* = germarium.

constructed on the queens of both colonies 82-33 and 83-14. On the basis of the preliminary data on queens 82-33 more systematic observations were made on queen 83-14, whose data are summarized in *table III* and discussed below.

1. *Rest*

In the larval-growing stage the contracted queens spent most time resting, usually standing motionless on the larval pile *(table III)*. It is curious that queens at rest invariably keep their gasters raised obliquely, at angles ranging from about 20° to 70° (mostly 50° - 60°), from the horizontal *(fig. 7, arrow)*. The function of this posture is not clear. Furthermore, small but obvious gastral pulsations occurred at regular intervals of 10 - 15 seconds. These movements might be linked to functioning of the aorta. The queens rarely descended from the brood pile, except when large numbers of larvae were placed on the prey, at which times the brood pile usually became diffuse. For defecation the queens regularly left brood pile to excrete a milky droplet (nearly as large as an egg), usually about 5 mm from the periphery of the pile. Such excreta remaining at the abdominal tip of a queen were observed once to attract several workers which attached their moutparts to it in turn, and finally ingested it.

Disturbance by the observer caused queens to leave the pile and to travel along the foraging trails. Workers encountering such a queen were totally indifferent, and passed without response of the kind which would be expected during colony emergency in other ant species.

From this rather inactive condition the queens entered an almost "restless" state which developed over a period of only a few days ; the time proportions of active and resting periods were thus completely reversed *(table III)*, with the active periods being occupied by larval hemolymph feeding.

2. *Larval hemolymph feeding (LHF)*

The term "larval hemolymph feeding (LHF)" was first coined for the primitive ponerine ant *Amblyopone silvestrii*, to denote an aberrant form of feeding in which adult ants (generally queens) pierce the dorsal integument of the abdomen of older larvae by pinching with the mandibular tips, and then feed on hemolymph oozing from the single resulting puncture (MASUKO, 1986). Although LHF in *Leptanilla* is functionally very similar to that in *Amblyopone* there is an important difference. *Leptanilla* queens imbibe hemolymph from a pair of specialized duct organs placed bilaterally on the 4th larval abdominal segment, without damaging the integument *(figs. 10 and 11* ; MASUKO, 1989). These organs were previously regarded as spiracles (WHEELER and WHEELER, 1965). My behavioral and histological studies have confirmed that they are duct organs tapping the larval body cavity to the

Table III. — Comparison of percentage time spent on each behavior by the queen of colony 83-14 of *Leptanilla japonica* between her contracted and physogastric conditions. The behavior was recorded continuously for 90 minutes or more on each observation day. For each behavior, the means of percentage time during 22-24 January and 11-13 March were calculated and statistically analyzed for equality by two-tailed *t*-test after arc-sine transformation. In spite of the small sample size (n = 3), the mean differences are significant for *rest* (P < 0.05), *LHF* (P < 0.05), and *being licked by worker* (P < 0.01).

Tableau III. — Pourcentage de temps consacré à chaque type de comportement par la reine de la société 83-14 de *L. japonica*. Comparaison entre les périodes où la reine a l'abdomen contracté, ou bien est physogastre. Le comportement a été enregistré de manière continue pendant 90 minutes ou plus, chaque jour d'observation. Pour chaque type de comportement, les moyennes des pourcentages de temps, du 22 au 24 janvier et du 11 au 13 mars, ont été calculées et soumises à l'analyse statistique par le test de Student, après transformation en arc-sinus. Malgré la taille réduite de l'échantillon (n = 3), les différences entre les moyennes sont significatives pour *repos* (P < 0.05), *LHF* (P < 0.05), et *léchage par des ouvrières* (P < 0.01).

Condition of queen	Contracted			Fully physogastric			t_s
Date in 1983	22 Jan	23 Jan	24 Jan	11 Mar	12 Mar	13 Mar	
Behavioral acts							
Rest	75.1	69.5	51.6	38.1	38.2	21.3	3.53
LHF	7.1	10.8	13.0	28.2	20.7	18.2	3.62
Hold worker	0	1.3	0	0	0	0.3	ns
Self-groom	0.5	1.3	0.9	1.1	1.7	10.7	ns
Be licked by worker	5.0	1.1	9.7	19.0	27.6	22.9	4.91
Other activities							
on brood pile	11.6	14.9	21.7	13.5	11.7	24.7	ns
on substratum	0.6	1.1	2.9	0	0	2.0	ns
Total	99.9	100.0	99.9	99.9	99.9	100.1	
Sample time (min)	90	92	92	100	100	100	

ns : Not significant.

Fig. 10. — A partly physogastric queen of *Leptanilla japonica* drinking hemolymph of a final-instar larva. Arrow points the queen's head. Note that some workers and larvae are attached to the queen's abdomen, particularly, its exposed intersegmental membranes.

Fig. 10. — Reine partiellement physogastre de *L. japonica,* absorbant l'hémolymphe d'une larve de dernier stade. La flèche indique la tête de la reine. Noter que des ouvrières et des larves s'agrippent à l'abdomen de la reine, et particulièrement à ses membranes intersegmentaires.
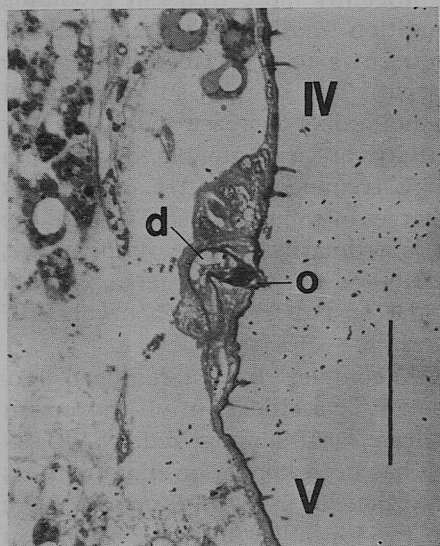
Fig. 11. — Longitudinal section (1μm) through the region of the larval hemolymph tap at the posterior end of the 4th abdominal segment. The duct (*d*) is sectioned along the nearly full length. *O* = position of the outlet. *IV* = 4th abdominal segment. *V* = 5th abdominal segment. Scale = 50 μm.

Fig. 11. — Section longitudinale (1 μm) de la région de l'organe canaliculaire larvaire au bout postérieur du quatrième segment abdominal. Le canalicule (*d*) est sectionné sur la presque totalité de sa longueur. *O* = position du débouché du canalicule. *IV* = quatrième segment abdominal. *V* = cinquième segment abdominal. Echelle = 50 μm.

exterior of the body. These organs were thus termed the "larval hemolymph taps" (MASUKO, 1989). In addition, the true spiracles have now been located, placed as usual, on 10 segments, from the mesothoracic to the 8th abdominal (MASUKO, unpubl.).

Despite their bulk, physogastric queens were very active. For LHF they used almost all larvae within their reach, and secured larvae being licked or carried by workers. The relative time spent in LHF by queen 83-14 was doubled from the larval-growing stage to the egg-laying stage of colony life, and, on average, the number of larvae handled for LHF per hour increased from 7.5 when she was contracted to 21.2. About half of the larvae handled by this queen were released without hemolymph being imbibed (58 % and

47 % in her physogastric and contracted conditions, respectively). The mean duration of a single bout of hemolymph feeding from the duct organs was not significantly different between the two conditions of gastral inflation— 101 sec. when physogastric (S.D. = 66, n = 17) *versus* 116 sec. when contracted (S.D. = 85, n = 7) (one-way ANOVA, $F_{1,22}$ = 0.23). Furthermore, workers facilitated the queen's LHF by placing larvae near her. Queens sometimes treated a nearby worker almost like a larva. They held its trunk with their legs, nipping along its length. The worker remained immobile with the body lowered during this manipulation, and was always released after a few seconds.

3. Grooming

The queen in physogastry received significantly more frequent grooming by workers than when in a contracted condition (*table III*). (The actions of workers applying their mouthparts to the queen gaster, described above, have not been regarded as grooming in this context.) This increase in grooming of the queen could be related chiefly to the noticeable increase in soil on her body surface due to her high level of activity, or to accumulated refuse in her infrabuccal cavity, related to her high frequnecy of LHF. *Leptanilla* queens have not been observed to discharge infrabuccal pellets onto the substrate following each bout of LHF, as is ordinarily seen in *Amblyopone*, whose queens discharge one or two white filtered dregs of hemolymph from the infrabuccal cavity onto the floor of the nest after each bout of LHF (MASUKO, 1986).

Insect self-grooming behavior involves complex but stereotyped movements. This stereotypy permits systematic classification of movement patterns. Formicoid grooming repertoires have been summarized by WILSON (1962) and FARISH (1972). However, nothing has been known on these matters for the Leptanillinae. The characteristic movements used by *L. japonica* are described below, mainly with reference to the formulae provided by FARISH (1972).

(*a*) *Antennal grooming: Leptanilla* is unusual, in that the funiculi and scapes are separately groomed using different movements of the forelegs (L1). (*i*) *L1-funiculus grooming*: The antennal cleaner (the strigils of the tibial spur) of L1 is moved swiftly distad along the funiculi. Two methods were observed: 1) use of ipsilateral L1; 2) use of both L1, simultaneously on the same antenna. In the first method the funiculi of the same side are usually groomed 2 or more times in succession before transfer to the other side. This simple grooming is combined with other unit movements to form a composite of grooming movements, though it also frequently appears in isolation, in the course of other activities such as walking. (*ii*) *L1-scape grooming*: The scape of one antenna is quickly wiped with the ipsilateral L1. This movement occurs ordinarily in combination with both of L1-mouthparts grooming and head grooming.

(*b*) *L1-mouthparts grooming*: While the mandibles are open, the tarsi and distal parts of the tibiae of L1 first quickly wiped forward the ipsilateral surface of the lower

mouthparts, and then immediately are drawn back in the space between the maxilla and the labium. In this process, detritus attached to the fore tarsus is transferred to the infrabuccal chamber, as described by WILSON (1962).

(c) *Head grooming* : The sides of the head and the outer surface of the mandibles, while open, are wiped by a forward stroke of the ipsilateral L1, followed immediately by L1-mouthparts grooming. Additionally, wiping of the antennal scapes is usually combined with this series, forming the most complex grooming movement in *L. japonica.*

(d) *Thorax grooming :* (i) *Dorsum by L1* : The frontal corners of the prothorax are quickly wiped by the tarsi of L1, which movement progressively changes to head grooming. (ii) *Pleuron by L1* : Both L1 are reflexed back in an awkward manner, being folded at the femoral-tibial joint, and groom the pleura of the thorax in a sawing motion. The dorsal parts of the coxae of middle (L2) and hind (L3) legs also appear to be groomed with this movement.

(e) *L3-abdomen grooming* : The sides and the venter of the abdomen are wiped by the tarsi of the ipsilateral L3, each side being groomed alternately. During this movement, the abdomen is somewhat bent towards the leg being used. Usually, this movement is performed concurrently with the other grooming which use L1, but it also occurs independently while walking.

(f) *L1-L1 grooming* : One L1 is passed through the antennal cleaner of the opposite L1 alternately, both legs being raised off the floor. This grooming is remarkably frequent in *L. japonica,* punctuating most sequences of other grooming movements.

(g) *L1-L1-L2 grooming* : Both L1 are lifted in the air and wipe the tarsus of a single L2, but usually the ipsilateral L1 hardly reaches the L2 because of postural difficulty.

(h) *L1-L1-L2-L3 grooming* : This is essentially the same as L1-L1-L2 grooming, except that L3 on the same side as L2 is also incorporated.

(i) *L3-L3 grooming* : This involves the reciprocal movement of one L3 stroking the other beneath the abdomen, which is raised slightly.

The movements *a/i/1*, and *g/h/i* were recorded only from workers, and not from the queen. This may be due to the short observation period and does not necessarily indicate their absence from the queen's repertoire.

DISCUSSION

Although many details of the biology of *L. japonica* are far from verified, the dorsoventrally flattened body form of both adults and larvae, and the predation on soil-inhabiting centipedes, indicate that this ant is highly adapted for a totally subterranean life, involving movement through narrow preformed crevices. Its small colony size contrasts notably with that of the army ants. Colonies of dorylines and ecitonines are huge, and capture a broad spectrum of terrestrial arthropods, often including other social insects (GOTWALD, 1982). A physogastric queen of *L. japonica* lays a batch of 100-200 eggs within a few days. The estimated numbers of eggs delivered within the same period by *Eciton hamatum* and *E. burchelli* queens amount to 50,000 - 200,000 (RETTENMEYER, 1963 ; FRANKS, 1985). The total number of observed

ovarioles of an *L. japonica* queen was only 31-32, while a queen of *E. burchelli* may have a total of about 2,600 ovarioles (HAGAN, 1954). In *E. hamatum* the queen, which is about 20 mm long when contracted (SCHNEIRLA and BROWN, 1952), lays eggs of 0.3 mm diameter (SCHNEIRLA, 1971 ; his *figure 8.8*). Eggs of almost the same size (0.26 mm in the length) are produced by the much smaller *L. japonica* queen, which is only 1.8 mm long when contracted. Since the egg/queen size ratios are 0.015 in *E. hamatum* and 0.14 in *L. japonica*, the relative egg weight is probably approximately a thousand times greater in the latter. *E. hamatum* queens, however, produce about a thousand times as many eggs as *L. japonica*, so that egg production is fairly comparable in relative scale. Stated another way, army ant egg production is characterized by egg dwarfism, which is also evident in social bees and wasps (IWATA and SAKAGAMI, 1966). The multiplication of ovarioles is also widely observed in social Hymenoptera, especially in ant queens (IWATA and SAKAGAMI, 1966). Indubitably, these traits have evolved in relation to increase in the queen's fecundity, and, among ants, both are embodied in the reproduction of army ants.

Although details of predatory behavior of *L. japonica* remain unknown, the present study suggests that this ant is a specialist predator of geophilomorph centipedes and forage using a trail system. Considering the small body size and nest population of workers, it is probable that the trails in nature are short, probably no more than one meter in length. In nature the prey would be encountered and captured on or around the trails along which it is retrieved to the nest site, or, conversely (or often concurrently) all colony members migrate to the place of prey capture, as observed in my laboratory studies. In addition, the precocity of callow workers, impermanent use of nests, as suggested by field observations, the dichthadiiform queen with strong legs, and the larval structures forming a coupling mechanism for transportation, all indicate that *L. japonica* is a highly migratory ant. Considering the nature of the prey, however, daily nest relocation, as in army ant colonies during the nomadic phase, is improbable. Colony migration to a prey site, as observed in the laboratory, suggests that most migrations of *L. japonica* colonies occur at irregular intervals in response to successful prey capture, or as a result of prolonged food shortage, or some other environmental disturbance.

There is little information on sexual brood production and mating behavior in *L. japonica*. It seems probable that males move between nests in flight, seeking virgin females which do not leave their parent colonies to mate. If, as seems very probable, *L. japonica* is univoltine, coincidence between numbers of workers and mature larvae or pupae present in a colony would indicate that the adult life span of workers is normally one year, or a little more, and thus that yearly renewal of the total worker population occurs in colonies of this species. If this is the case, males and queens are

likely produced in normal broods along with workers, because entirely repro-
ductive broods without workers, as reported for army ants (SCHNEIRLA and
BROWN, 1952), would interrupt worker production for almost 2 years. Sexual
dimorphism in *L. japonica* is greatly different from that known in army ants.
Unlike the peculiarly large and robust males of army ants (FRANKS and
HÖLLDOBLER, 1987), the male of *L.japonica* is small and slightly-built com-
pared to conspecific queens, as is general in the sexual dimorphism of ants
(OGATA, TERAYAMA and MASUKO, in prep.). Lone males assigned by previous
authors to the Leptanillinae have been caught in traps or by sweeping
(PETERSEN, 1968 ; OGATA, pers. comm.), suggesting that the males leave the
nests for mating. Judging from the apterous condition of the queens it is
probable that new colonies are established by colony fission, as in army ants.

Larval hemolymph feeding by *Leptanilla* appears to be an adaptation to
unstable food conditions affecting this specialist predator of relatively large
prey, as in the apparent case in *Amblyopone silvestrii* (MASUKO, 1986, 1989).
Both species lack the habit of regurgitation, so that, when food is depleted
in a colony, the adults, especially the queens, can obtain nutrients only by
cannibalizing brood. To feed on worker trophic eggs is also impossible for
these ants. In *Amblyopone* the queen completely inhibits ovarian development
in workers (probably through social dominance ; MASUKO, 1987). In
Leptanilla, the worker caste has no ovaries. Nondestructive use of brood as
food, if it is possible, would be much more advantageous than cannibalism,
and this could explain the evolution of LHF. Furthermore, for ants which
produce broods cyclically, another plausible advantage is that LHF readily
secures synchronization between larval maturation and oviposition by the
queen (MASUKO, 1989). LHF or LHF-like feeding, utilizating mature larvae,
possibly occurs also in army ants, however little is known about the nutrition
of their queens (e.g. RETTENMEYER, 1963 ; SCHNEIRLA, 1971 ; GOTWALD, 1982).
The larval hemolymph tap, which is unique to *Leptanilla*, may have evolved
in order both to lessen the damage resulting from intensive LHF on a re-
latively small number of larvae, and to raise the efficiency of hemolymph
transfer necessitated by the queen's rapid ovarian development, which is
important in the strictly synchronous production of the brood (MASUKO,
1989).

L. japonica overwinters larvae. Production of new adults from posthi-
bernating larvae is rather common both in ant species found in Manazuru
forest (MASUKO, unpubl.) and in temperate species in general (ICHINOSE,
1987). In *L. japonica*, the brood event over a year is inevitable from the
synchronization of pupation and oviposition. On the other hand, *Cerapachys
humicola*, which is found in Manazuru forest and whose larvae develop and
mature in synchrony, produces adults from eggs laid in the same year without
overwintering (MASUKO, unpubl.). This brood production pattern may be

viewed as coincident with the observation that this species lacks the habit of LHF, which mediates pupation and oviposition in *L. japonica.*

In discussing the characteristics of army ant behavior WILSON (1958) took account only of colony migration ("nomadism") and group-predation. He did not emphasize cyclical brood production (or, more accurately, cyclical production of synchronously developing brood). In fact, the function of this phenomenon is rather obscure, although it is conceivable that the migration cycle has evolved to synchronize with the presence of the life stage requiring the greatest food supply (WILSON, 1971). When comparison is limited to tropical army ants, brood production is generally more cyclical in epigaeic species than in hypogaeic ones (GOTWALD, 1982). Apart from the army ants and *Leptanilla,* synchronous brood development is known in some other legionary or group-predatory ponerines such as *Onychomyrmex* (TAYLOR, cited in SCHNEIRLA, 1971, p. 167) and *Cerapachys* (HÖLLDOBLER, 1982). On the other hand, the tropical dolichoderine ant *Dolichoderus cuspidatus,* which is truly "nomadic" (i.e. migrating with the symbiotic coccids with which it lives), produces broods acyclically (MASCHWITZ and HANEL, 1985). Similar noncyclical brood production is exhibited also by a temperate, queenless migratory myrmicine, *Pristomyrmex pungens* (TSUJI, pers. comm.). Since both species largely or exclusively depend on homopteran honeydew as nutrient, the nature of the food could be important in determining the brood production patterns of migratory ants. Yet brood production is acyclical in the tropical, carnivorous legionary ponerine *Leptogenys* sp. 1 near *mutabilis* (MASCHWITZ, STEGHAUS-KOVAC, GAUBE and HANEL, in prep.). Much more information is needed to illuminate the evolution and function(s) of cyclical brood production in migratory ants.

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