A South East Asian ponerine ant of the genus *Leptogenys* (Hym., Form.) with army ant life habits*

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Summary. The emigration and raiding behavior of the SE Asian ponerine ant *Leptogenys* sp. 1, which resembles *L. mutabilis*, were observed in the field (Ulu Gombak, Malaysia). The ants formed monogynous colonies that consisted of up to 52,100 workers. The bivouac sites of this species were found in leaf litter, rotten logs, ground cavities, etc., and were rarely modified by the ants. The colonies stayed in these temporary nests for several hours to 10 days; afterwards, they moved to a new nest site. The emigration distances ranged from 5–58 m. Since nest changing takes place at irregular intervals, and pupae and larvae are always present in the nest relocations of *Leptogenys* sp. 1, the emigration behavior is not linked to a synchronized brood development. *Leptogenys* sp. 1 is a nocturnal forager; in our study, up to 42,600 workers participated in each raid. The ants move forward on a broad front; behind the swarm a fan-shaped network of foraging columns converges to form a main trunk trail. A new system of foraging trails is developed in each raid. The workers search for their prey collectively; they attach and retrieve the booty together. The diet of *Leptogenys* sp. 1 consists mainly of arthropods. Army ant behavior is characterized by (1) formation of large monogynous colonies, (2) frequent emigrations, and (3) mass raids in which all foraging activities are carried out collectively. Since *Leptogenys* sp. 1 performs these typical army ant behavior patterns, this species represents the army ant ecotype. However, this species differs considerably from army ant species that have synchronized broods and huge colonies with dichthadiiform queens.

Introduction

In the tropics of Africa and America, army ants of the subfamilies Dorylinae and Ecitoninae are faunal elements of outstanding ecological importance. They perform impressive mass raids and colony movements. Most conspicuous are the swarm-raiding epigaeic prey generalists, e.g., *Dorylus* (*Anomma*) *wilterthi* in Africa (Raignier and van Boven 1955) and *Eciton burchelli* and *Labidus praedator* in the neotropical region (Rettenmeyer 1963; Schneirla 1971).

Doryline ant species occur also in SE Asia, but the *Dorylus* species of this region are subterranean foragers, and *Aenictus* species prey mainly on various ant species (Wilson 1964). Swarm raiding epigaeic *Dorylus* species are not found in SE Asia. Gotwald (1979) hypothesized that the lack of diversity in this genus in Asia might be due to competitive exclusion by other ant species with army ant life habits that were already well established when *Dorylus* dispersed to this zoogeographical region. This idea is supported by investigations on *Aenictus gracilis* and *Aenictus laeviceps* in the Philippines (Schneirla and Reyes 1966). These species prey on a broader range of invertebrates and show transitions to swarm raiding behavior. Moffett (1984) described swarm raiding behavior also in the myrmicine ant *Pheidologeton diversus*.

During our research on migrating ants in the tropical rain forest of the Malayan Peninsula, we observed a ponerine ant species that performs spectacular mass raids and nest relocations. Here we report that this ant species indeed represents the army ant ecotype and resembles the Dorylinae and Ecitoninae in many aspects of its life history. Specimens of the species were sent for identification to B. Bolton, British Museum (Natural History), London. The species belongs to the *Leptogenys* 

* Dedicated to Professor Dr. M. Lindauer on the occasion of his 70th birthday

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processionalis species group, which is not yet revised. The species, which is morphologically close to L. mutabilis, is presumably undescribed. In the following report, this species is referred to as *Leptogenys* sp. 1.

**Methods**

All observations on colonies of *Leptogenys* sp. 1 were made in the field near the University of Malaya’s Ulu Gombak Field Studies Centre (altitude 220 m, 3°19’32” N, 101°45’16” E). The area is covered by lowland dipterocarp forest. Timber extraction has created partially open areas at various locations where bamboos have become dominant (Bishop 1973).

For observations on the nocturnal ants, torch lights and head lamps were used. Two colonies were captured. The bivouac was surrounded by a square metal frame (1.5 m × 1.5 m × 0.4 m) that was dug into the ground. A bridge connected the interior of the metal frame to a metal container (1.5 m × 1.2 m × 0.5 m) that was filled with a dense layer of bamboo, leaves, and branches. Intensive watering of the bivouac released an emergency nest relocation into the artificial nest. One of the captured colonies was killed with liquid chloroform and preserved in 80% ethanol.

Records of the numbers of ants participating in raids or emigrations were taken by counting the incoming and outward-bound ant traffic near the nest entrance for 1 min each in 10 min intervals. For each interval, the rate of prey-retrieving workers out of 100 returning ants was determined. Since the numbers of our observations on emigrations and raids were restricted, we used the median (3) together with maxima and minima instead of the arithmetical mean (3) for the investigated parameters (Sachs 1974). For the statistical analysis of the emigration routes the Raleigh-test (Batschelet 1981) was used.

**Results**

**Nesting behavior**

*Leptogenys* sp. 1 does not exhibit any nest building activities; however, minor enlargements of the nest entrance were sometimes observed. The temporary nests (bivouacs) of *Leptogenys* sp. 1 were localized in subterranean cavities (n = 19), in or under decaying plant material, e.g., holes in fallen trees (n = 6), or in bamboo groves in hollow spaces in the layer of dead twigs and leaves that reach up to 1 m in depth (n = 14).

Examinations of emergency bivouacs that were formed after flooding (Fig. 1), as well as examinations of nests in large artificial arenas filled with plant material, plus the rapid killing of colonies in the field with liquid chloroform revealed the structure of the temporary nests. The ants did not form a distinct large cluster but instead were spread out over an area of about 1 to 1.5 m². Most of the workers were distributed over the substrate in several irregularly spaced one-layer groups. Depending on the type of nest material, one of several stories with such layers of ants were formed.

**Fig. 1.** Emergency bivouac of *Leptogenys* sp. 1 formed in a protected site after heavy rainfall (arrow: cluster consisting of workers and brood)

We also observed small clusters of ants measuring only a few centimeters in diameter. They consisted of adult and callow workers that were sitting upside-down on plant material, etc. Some of these workers held larvae in their mandibles (Fig. 2). The numerous pupae were dispersed throughout the substrate or kept in depressions in the ground where they formed several layers.

**Colony size and structure**

**Workers.** The size of our main observation colony was estimated four times during a period of 3 weeks. Each time the activities before and during nest relocations were recorded as described above. The number of workers determined by this method varied between 44700 and 52100 (x̄ = 46750). On the 50th day of our observations, the colony was captured and killed with chloroform the following day. Though a considerable number of workers escaped, we nevertheless counted 21809. From observations of the ant traffic in the emigration column and the duration of the nest-movements in four other colonies of *Leptogenys* sp. 1, we also estimated numbers of more than 30000 workers in these colonies.
Females. In 6 of the 12 emigrations of our observation colony we saw one ergatoid queen. The queen was wingless and of the same body length as the workers, but could be distinguished from the workers by her light brown cuticle, her thicker gaster, and her larger thorax (Fig. 3). During several of the observed emigrations, the queen was distinctly physogastric. In 5 emigrations of other colonies observed from beginning to end we saw only a single queen in each case. We also found a queen with strongly developed ovaries in the main observation colony that was captured.

Males. The number of males that were counted during emigrations in the main observation colony varied from 52 to 746 ($\bar{x}=150$, $n=9$). They were carried by the workers. At dusk we often observed flying males leaving their colonies. In one case we watched a male approaching the entrance of a bivouac from outside by following a foraging trail. This behavior has already been described for other Leptogenys species (Maschwitz and Mühlenberg 1973, 1975). This male may have come from an alien colony, because it was attacked by the workers; nevertheless, it went back to the trail repeatedly.

Brood. The number of pupae that were counted during the nest relocations of the main observation colony over a period of 7 weeks ranged from 6400 to 16400 ($\bar{x}=11200$, $n=12$). Since either one large larva or several small larvae or clusters of eggs were carried by a single worker, we recorded only the number of workers transporting larvae and eggs (2700–7600, $\bar{x}=3300$, $n=12$). In the captured colony we found 4580 pupae, larvae of all stages, and eggs. Only the medium-sized and large larvae ($n=3254$), not the eggs and young larvae, were counted. In 21 further nest emigrations of ten other colonies of Leptogenys sp. 1 in different years, we also observed, in random checks, that pupae and larvae were always present at the same time, and that the number of workers transporting pupae exceeded the number of workers transporting larvae. Since pupae, larvae, and eggs were always present in about the same ratio, we conclude that in Leptogenys sp. 1 the brood is produced in an acyclic way.

Nest moving behavior

The frequent colony emigrations were preceded by at least one, sometimes two raids. The new bivouac site was always located in the area that had been raided previously. The emigrations started between 2000 and 0500 hours local time, often after the retreat of the preceding raid. At the beginning of a nest relocation, the number of workers that left the nest entrance increased. Ten to 20 min later the first pupae appeared. Before the emigration column was established, single workers carrying pupae were observed in the raiding column. These
pupae were carried ventrally (Fig. 5). The ants usually moved in a single file while they were carrying brood.

The majority of the pupae were transported during the first third of the emigration; the transport of larvae began later and reached its maximum in the second third. When disturbed by heavy rain, the workers laid down the pupae in sheltered places for a while until they were able to continue with the nest relocation. After most of the brood had been transported to the new site, the number of unladen ants leaving the old nest increased. Among the “rear-guard” many callow workers were observed. As long as ants were still leaving the old bivouac site, other workers continued to return to it. Eventually the emigration column ended abruptly. The course of a typical colony emigration is documented in Fig. 4. During the emigrations we counted 12400–31000 workers ($\bar{x} = 19050$, $n = 12$) leaving the old bivouac site. These fluctuations seemed to be due mainly to the fact that many raiding workers did not return to the previous nesting site, but instead joined the emigration column to the new bivouac.

Fig. 4. *Leptogenys* sp. 1: above: numbers of workers and brood leaving from and returning to the former bivouac during a nest relocation (incl. end of the preceding raid); □ workers out; □ workers in; □ workers carrying pupae; ■ workers carrying larvae; below: □ rate of prey-laden workers

Fig. 5. Emigration column passing a group of guarding workers (arrow: ptiliid beetle)

The queen was not protected by workers when she followed the emigration trail. However, at a distance of some meters from each other, we observed several large groups of up to 100 workers that guarded the emigration trail at both sides. They remained motionless with their heads turned towards the worker column and their mandibles opened (Fig. 5). The passing ants were checked with the antennae.
Table 1. Emigrations of Leptogenys sp. 1. Colony 1, during a 7 week period: start, duration, and distance of colony movements, and the location of the new bivouac. Three short range site shifts (<3 m) along the rotten log were observed between nights 13-23.

| Night | No. | Start(b) | Duration(min) | Distance(m) | Nest site |
|-------|-----|----------|---------------|-------------|-----------|
| 1     | 1   | 3        | 0300          | ?           | leaf litter |
| 4     | 2   | 1        | 0120          | 161         | 49        |
| 5     | 3   | 5        | 2230          | 230         | 6         |
| 10    | 4   | 3        | 0310          | 170         | 30        |
| 13    | 5   | 10       | 0100          | 167         | 38        |
| 23    | 6   | 4        | 2150          | 213         | 11        |
| 27    | 7   | 4        | 2010          | 159         | 24        |
| 31    | 8   | 6        | 0020          | 165         | 19        |
| 37    | 9   | 0        | 0350          | 153         | 58        |
| 39    | 11  | 2        | 0500          | ?           | 9         |
| 40    | 12  | 1        | 0020          | 173         | 27 |
| 41    | 13  | 0        | 2220          | 124         | 15        |
| 42    | 14  | 1        | 0320          | 175         | 5         |
| 43    | 15  | 1        | 0230          | 171         | 19        |
| 44    | 16  | 1        | 2110          | 170         | 11        |
| 47    | 18  | 3        | 0300          | ?           | 29        |
| 47    | 19  | ?        | 0330          | ?           | ?         |

n = 18
\( \bar{x} = 1.5 \)

\( n = 12 \)
\( \bar{x} = 166 \)
\( \bar{x} = 19 \)

Frequency of colony emigrations. From the beginning of our observations in 1973, we found that the colonies usually left their nesting sites within 1 to 3 days. This indicates a frequent relocation of nesting sites. For 7 weeks we observed the emigration behavior of one colony of Leptogenys sp. 1. During this period, the whole colony moved 19 times over longer distances (>3 m). The colony stayed in one site up to 10 days (\( \bar{x} = 1.5 \) days, \( n = 18 \)). During the 10-day stay, the ants shifted their nesting site three times over short distances (<3 m). However, in the 37th, 39th and 40th night, the ants abandoned their new bivouac already after a few hours. In each of these nights, therefore, we observed two emigrations. More details are given in Table 1.

Distances and directions of colony emigrations. In Fig. 6 a map of the movements of this colony during the 7 weeks is given. The distance covered by a single emigration varied from 5 to 58.7 m (\( \bar{x} = 19 \) m, \( n = 17 \)). The statistical analysis (Raleigh-test, Batschelet 1981) of the directions of the emigrations shows that the choice of a new nest site is not made at random. The direction from the old to the new site deviated 28° on average from the direction chosen in the previous emigration, even if the 90° turns (bivouacs 2, 13, 18), which were obviously induced by hitting an obstacle (stream, road, forest border), are included (\( r = 0.70, n = 17, P < 0.001 \)).

Guests
Like the colonies of Dorylinae and Ecitoninae, Leptogenys sp. 1 was accompanied by a large
number of guests. Their number varied from colony to colony. Many species of guests followed the emigration trail during or shortly after the nest relocation. We observed at least two species of staphilinid beetles (see Note added in proof); a lepismatid, which was sometimes transported on pupae; a reddish spider (Oonopidae); white collembo- 

Several guest species are carried on different stages of the brood apparently depending on their special residence site in the colony. Exalloniscus maschwitzi, an isopod species that is greatly adapted to its myrmecophilous life (Ferrara et al. 1987), often clings to the end of a pupa and is thereby carried to the new bivouac. We observed up to four individuals of a tiny pilid beetle on top of a pupa and also observed mites riding on pupae. On the larvae we found a larger dark pilid beetle, a whitish beetle with partly reduced wings, and several mites. A mite species was also observed on the workers.

**Foraging behavior**

*Leptogenys* sp. 1 forages nocturnally. The raids began at dusk and ended before or shortly after dawn. During the observation period, 1–3 raids per night ($\bar{x} = 2$, $n = 7$) were conducted. In every raid a new trail system was developed (Fig. 8). We registered up to 38,400 participants in each raid (16,700–38,400, $\bar{x} = 27,200$, $n = 11$). Three raid phases were distinguished: the exodus, the main raiding phase, and the retreat (Fig. 7).

**Exodas.** The forays started after sunset between 1920 and 1945 hours. The first activities that could be seen outside the bivouac were groups or columns of workers moving beneath the leaves. From there they expanded rapidly in several directions into the leaf litter around the bivouac. They advanced by forming pseudopodia-like formations, which consisted of hundreds of workers, or narrow columns. The main trail on which the mass exodus occurred was established within 20–60 min ($n = 5$). During the exodus, the outgoing traffic dominated
the principal trail. Increasing numbers of workers left the bivouac; at the height of the exodus, sometimes more than 1000 workers per min, i.e., up to 13 rows abreast, travelled at the base of the trunk trail. A few workers walked in the opposite direction towards the bivouac dragging their gasters over the ground, presumably laying pheromone trails. We regarded an exodus as completed when in two successive measurings less than 50 workers per min were recorded leaving the bivouac.

Main raiding phase. The foray reached its height during the main raiding phase, which varied in length from a few minutes to several hours (10-400 min, \( \bar{x} = 170 \) min, \( n = 17 \)). During the main raiding phase, there was low level traffic on the trunk trail in both directions, whereas many thousands of foragers were involved in the big swarm raid. Up to 88% of the returning ants were carrying prey to the bivouac. More details are given in Table 2 and Fig. 9.

Retreat. The period of balanced traffic to and from the bivouac was followed by the retreat, which continued for 30-150 min (\( \bar{x} = 105 \) min, \( n = 16 \)). When the homebound traffic started to prevail (> 50 workers per min), the percentage of burdened workers rapidly decreased to less than 10%. We observed the beginning of the retreat as a nearly synchronous turn of the ants at the forefront of the swarm. The wave of return moved along the fan of columns behind the swarm and finally reached the bivouac. Outgoing ants turned after frequent collisions with nestmates that were returning to the nest; nevertheless, there were still some workers leaving the nest entrance until the end of the foray. Frequently, a new exodus or an emigration already began while the last workers from the previous raid were still returning to the bivouac.

**Swarm raid.** In the “amoeba-like” structure that was formed by the workers spreading out from the bivouac after sunset, one of the “pseudopodia” became very attractive. The ants accumulated at this point and, as the mass advanced, the swarm became an organized unit. The workers at the forefront explored the area by slowly moving about and palpatating the substrate, investigating leaf litter, subterranean cavities, and rotten logs. They also ascended the vegetation up to 5 m. As the swarm moved forward, a fan-shaped network of columns developed behind it. The trail system converged in the back forming a main trunk trail that permanently connected the swarm to the temporary nest (Fig. 9). Narrow columns developed at the flanks of the swarm and in the direction of its advance.
Fig. 9. Structure of a raid exemplified by a section of a developing swarm (s = swarm front; f = fan-shaped network of trails)

In the following description the data for swarm and fan are combined, because a reliable discrimination between the formations was not always possible. The swarm and fan covered up to 10.5 m in width (3.1–10.5 m, \(\bar{x} = 6.8\) m, \(n = 17\)) and 15.5 m in depth (4.6–15.5 m, \(\bar{x} = 9.5\) m, \(n = 16\)). Its area ranged from 16 to 58 m² (\(\bar{x} = 37.5\) m², \(n = 14\)). The advancing swarm kept a main direction of progress. The maximum distance covered by the forays was 56 m (7.3–56 m, \(\bar{x} = 24\) m, \(n = 13\)). The course and advance of one swarm raid is documented in Fig. 10. Further details are given in Table 3.

We estimated that an area of approximately 300 m² was raided by the swarm every night (ex-pansions on the flanks and in vertical directions were not considered). A detailed analysis of swarm raiding behavior will be given in a forthcoming study.

Diet

The diet of *Leptogenys* sp. 1 consists mainly of adult and immature arthropods, but also includes to a limited extent other invertebrates like planarians, snails, and earthworms. The largest arthropod prey individual was a scolopender (12 cm long). Vertebrates usually escaped by running away when they got in contact with the biting and stinging ants. The only vertebrate victims were a frog (5 cm long) and a snake (15 cm long), which presumably got cornered in inadequate retreats. Non-animal food did not seem to play any role in the natural diet of *Leptogenys* sp. 1, although three times the ants retrieved fresh papaya seeds that were presented to them. Carbohydrate foods (bread, cookies, fruit) were not collected by the workers. Artificially offered mantids, phasmsids, cicadas, diptera, and bees were taken, as well as the meat of fish or canned dog food. The ants did not attack big *Achatina* snails but preyed on them if the shell was destroyed.
Table 3. *Leprogenys* sp. 1. Size, maximum distance from bivouac, and velocity of advance of swarm raids (the data for swarm and fan area are given in combination, because a reliable distinction between these formations is not possible in each case)

| Night | Raid | Time (h) | Depth (m) | Width (m) | Area (m²) | Distance bivouac forefront (m) | Velocity of advance (cm min⁻¹) |
|-------|------|----------|-----------|-----------|-----------|-------------------------------|-------------------------------|
| 4     | 1    | 0200     | ?         | ?         | ?         | 49.0                          | 12.3                          |
| 7     | 1    | 2200     | 13.5      | 6.0       | 53        | 13.5                          | 9.0                           |
| 2     | 2    | 0100     | 7.3       | 3.2       | 16        | 7.3                           | ?                             |
| 3     | 3    | 0300     | 11.0      | 3.1       | 25        | 11.0                          | ?                             |
| 8     | 1    | 0000     | 13.5      | 5.7       | 42        | 13.5                          | 5.1                           |
| 2     | 2    | 0600     | 9.0       | 6.6       | 30        | 24.0                          | 11.7                          |
| 9     | 1    | 2320     | 15.5      | 9.8       | 58        | 8.2                           | ?                             |
| 1     | 2    | 0250     | 9.0       | 10.5      | 54        | 34.0                          | 8.8                           |
| 10    | 1    | 2200     | 15.5      | 5.0       | 46        | 13.0                          | ?                             |
| 1     | 1    | 2330     | 8.7       | 8.0       | >29       | 4.4                           | ?                             |
| 2     | 1    | 0100     | 8.7       | 8.0       | >45       | 30.4                          | 8.2                           |
| 1     | 1    | 0230     | 4.6       | 6.0       | >16       | 3.5                           | ?                             |
| 14    | 1    | 2315     | 9.9       | 5.2       | 28        | 10.9                          | 5.2                           |
| 2     | 2    | 0300     | 7.8       | 6.8       | 28        | 11.7                          | ?                             |
| 17    | 1    | 0550     | 6.0       | 7.1       | 28        | 32.5                          | 8.8                           |
| 18    | 1    | 2310     | 10.1      | 6.2       | 35        | 4.8                           | ?                             |
| 2     | 1    | 0150     | 9.0       | 8.0       | 40        | 33.0                          | 14.3                          |
| 5     | 2    | 0000     | 12.5      | 7.3       | 48        | 20.5                          | 11.4                          |

\[ n = 16 \quad \bar{x} = 9.5 \]
\[ n = 17 \quad \bar{x} = 6.8 \]
\[ n = 14 \quad \bar{x} = 37.5 \]
\[ n = 12 \quad \bar{x} = 22.25 \]
\[ n = 16 \quad \bar{x} = 8.8 \]

Predatory behavior

When a worker got in contact with prey, it was able to recruit hundreds of nestmates within a few minutes, and a mass attack followed. Victims were bitten and stung. Soon the prey's movements weakened; the prey was pinned down, torn apart by oppositely pulling groups of workers, and subsequently slowly divided into small pieces that were carried back to the bivouac. Legs and wings of even small prey were cut off. Usually the prey was cut into pieces that could be carried by one forager; larger prey pieces were rarely carried cooperatively.

Discussion

The ecotype "army ant" is characterized by typical behavioral patterns:

1. Army ants form large colonies consisting of many thousands of workers but usually only a single queen.

2. Army ants change their nest sites frequently. Their temporary nests (bivouacs) are modified only slightly. Sometimes the species do not perform any nest building activities at all.

3. Army ants are mass-raiding predators. The exodus begins before prey is localized by scout ants. All foraging activities, i.e., search, attack, and retrieval, are conducted collectively. A new trail system is developed in each raid. The raiding groups are connected to the bivouac by at least one continuous column. The raids are coordinated by communication, based on mass recruitment (Chadab and Rettenmeyer 1975; Topoff et al. 1980).

Besides the Ectinoninae and Dorylinae, which possess all of these characteristics, there are other ants that possess only some of them. Frequent nest relocations seem to be more common in ants than hitherto reported (Smallwood and Culver 1979; Smallwood 1982; Tsuji 1987), particularly in ant species with unspecific nesting demands, like *Monomorium pharaonis* (Wilson 1971), and in species living in unstable habitats such as the leaf litter stratum. Because of the high air humidity at the ground layer of tropical rainforests, nesting in this environment is possible even in unsheltered sites, as frequently observed in bivouac-nesting species. In this habitat, even obligatorily migrating ants can be found that are not migrating hunters like the army ants but true "nomads", e.g., *Dolichoderus cuspitatus* (Maschwitz and Hänel 1985).

*Leptanilla* was considered to be an army ant because its apterous queens are highly physogastric from time to time. Because of the small colony size in this genus, the term army ant should not be applied to *Leptanilla*. Masuko (1987) gives a
convincing explanation for the brood synchronization in *L. japonica*.

The term "army ant", as was introduced by Wilson (1958), includes a number of ant species that live in temporary nests and attack and retrieve the prey co-operatively, e.g., *Leptogenys diminuta*. In this species, however, scout ants search for food solitarily and recruit a group of workers from the nest to the place where prey has been localized. The raiding workers form a distinct group that is not connected to the bivouac by a continuous column of workers (Attygalle et al. 1988). Since the search for food is done solitarily, the foraging behavior of *L. diminuta* differs from the hunting strategy of real army ants in an important feature (Fletcher 1973).

*Leptogenys* sp. 1 performs the typical army ant behavior patterns:

1. The monogynous colonies consist of several ten thousands of individuals.
2. The raids of *Leptogenys* sp. 1 are coordinated interactions of many thousands of workers that are not directed to specific food sources by successful scouts.
3. The colonies stay in the same site for only a few days. The ants do not build a fixed nest and modify the substrate only very little to a low extent.

Ant species like *Leptogenys* sp. 1 that do not spend much energy on nest building activities may abandon their nest sites frequently. However, for monogynous species nest relocations are linked with the risk of losing the single reproductive female, and the energy costs for emigrations are high for large colonies (Smallwood 1982). The frequent nest relocations in army ants are considered to be advantageous because the colonies are often migrating to new feeding sites (Schneirla 1971; Wilson 1971). Topoff and Mirenda (1980) demonstrated that the food supply may even have a direct influence on the emigration frequency of army ants.

Franks and Fletcher (1983) analyzed the emigration behavior in *Eciton burchelli*. They demonstrated that similar to *Leptogenys* sp. 1, the choice of a new bivouac site is not made at random. The emigrating *Eciton burchelli* colonies follow a certain geometrical pattern that increases the amount of unraided foraging area.

In *Leptogenys* sp. 1 the emigration distances are similar to the raid distances. Since we never observed that the colonies returned to their previous nest site, we can conclude that a considerable shift of their trophophoric field is achieved by the nest relocations. The migratory behavior presumably prevents the area close to the nest site from food depletion.

In spite of the similarities there also are differences between the behavior of *Leptogenys* sp. 1 and the lifestyle of the ecitonine and doryline swarm raiders. Synchronized broods and correlated regular changes between migratory and stationary phases, which are lacking in *Leptogenys* sp. 1, are often considered to be typical for army ants. But we have to point out that the brood cycle of some ecitonine species is not as regular as in *Eciton burchelli* and *E. hamatum* (Rettenmeyer 1963). The ecitonine swarm raider *Labidus praedator* sometimes has nonsynchronous broods, and several bivouacs of this species were observed in the same site for months (Rettenmeyer 1963). Also in African driver ants (*Dorylus* (*Anomma*) spp.), emigrations are irregular (Raignier and van Boven 1955) and not correlated to the brood condition (Gotwald 1978).

The colony size of *Leptogenys* sp. 1 is large, but does not reach the numbers of several hundred thousands or more workers that are attained in species of the Ecitontinae and the Dorylinae (Wilson 1971).

The queen is primarily wingless in all army ants as well as in *Leptogenys* sp. 1. The morphological differences between the workers and the queen are not very pronounced in *Leptogenys* sp. 1, whereas in the colonies of Dorylinae and Ecitontinae, these differences between the workers and the dichthaudiform queens, which have a huge gaster, are enormous. Workers that guard the queen during emigrations (Schneirla 1971) are not found in *Leptogenys* sp. 1. While the workers of most ecitonine and doryline species are polymorphic, *Leptogenys* sp. 1 workers are monomorphic. A narrow range of size is also found in the dorylines of the genus *Anenictus* (Schneirla and Reyes 1966).

Recent field studies (Franks 1982; Franks and Fletcher 1983) and the data collected by Willis (1967) permit a comparison between the *E. burchelli* average swarm raid and the average foray in *Leptogenys* sp. 1. The raid of *Leptogenys* sp. 1 attains a similar width, but is much shorter and advances much slower than the foray of *E. burchelli*. The swarm raid of this ponerine ant species contains only about one-fifth of the workers that may be involved in the raids of *E. burchelli*.

Whereas *E. burchelli* colonies generally produce one swarm per day, the colonies of *Leptogenys* sp. 1 often conduct two or more raids each night. The nightly raids of a colony of *Leptogenys* sp. 1 cover
an area of approximately half the size of the daily foraging area of *E. burchelli*.

**Comparison with other Leptogenys species**

We began our studies on this genus with *Leptogenys processionalis* (*L. ocellifera*) from Sri Lanka (Maschwitz and Mühlenberg 1973, 1975). This species as well has many army-ant-like habits, but also some distinct specialized characteristics. The colony size is similar to that of *Leptogenys* sp. 1. The ants may change their nest frequently; however, one colony was observed at the same site for at least ten weeks. In contrast to the characterization of army ant behavior already mentioned, the raiding ants leave the temporary nest to deepened trunk trails that may be used for several weeks.

In the area where our studies on *Leptogenys* sp. 1 were conducted, we found a total of twelve *Leptogenys* species, five of which have army ant characteristics. Besides *Leptogenys* sp. 1, these species are *L. mutabilis, L. birmana, L. crassicornis*, and *Leptogenys* sp. 2 (undescribed and possibly undescribed species resembling *L. borneensis*). Though we have not yet finished our studies on the behavior of these species, differences in their ecology are obvious. *L. mutabilis* is an epigaeic mass raider, but contrary to *Leptogenys* sp. 1, the workers forage mainly beneath the leaf litter. *L. crassicornis* is hypogaeic, but parts of the raid columns of this small species sometimes were discovered above ground, at night.

The seven species that are not army ants in the sense already mentioned search for prey solitarily. After encountering the prey, they either recruit a group of nestmates, e.g., *L. diminuta*, or even attack and retrieve their prey solitarily, e.g., *L. peuqueti*.

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Note added in proof:
Kistner (Chico, Calif.) is describing the two Zyrasini species as *Maschwitzia ulrichi* and *Togpelenys gigantea* (new species and new genera) (in preparation).