

COMPARATIVE FORAGING BY NEOTROPICAL

ARMY ANTS

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SUMMARY

The army ants (Ecitoninae) include about 150 species, and most lowland Neotropical moist forests have about 20 sympatric species. Although the most nocturnal and subterranean species are less frequently seen by people, they are probably at least as abundant as those which are active on the surface of the ground during the day. The frequency of finding common species of Ecitoninae is given for 748 colonies at one locality in Panama and one in Ecuador. Most species of army ants feed primarily on ants. Workers of army ants range from 13 mm to 1.75 mm in length, and their prey ants range up to 1.5 times the length of the largest army-ant workers. No army-ant species preys on another species of army ant. The second most important group of prey are social wasps (Vespidae: Polychaetini). A few species of army ants capture many groups of insects, other arthropods, and annelids. Among the species of potential prey with effective defenses against army ants are stingless bees, millipeds, and ticks. An average colony of *Eciton hamatum* has about 150,000 workers, a brood of 60,000 larvae, and may collect 90,000 insects per day. Based on the abundance of these ants and their high food consumption, they must have considerable effect on the prey species. The army ants do not kill colonies of social insects but only crop the colonies. Most of the adults from an attacked nest are not injured and continue the colony. Although our knowledge of the food of army ants is still very incomplete, we are convinced that there is enough prey specificity that several samples of prey from any species of Ecitoninae would be sufficient to identify a species of army ant.

RESUMEN

Comparación del abastecimiento de las hormigas guerreras neotropicales

Las hormigas guerreras (Ecitoninae) incluyen cerca de 150 especies, y la mayoría de los bosques neotropicales y húmido de baja elevación tienen cerca de 20 especies simpátricas. Aunque las especies nocturnas y subterráneas son menos visibles, son probablemente tan abundantes como las que son activas durante el día en la superficie. El número de 748 colonias en una localidad de Panamá y una de Ecuador nos da la probabilidad de encontrar especies comunes de Ecitoninae. Las mayoría de las especies de hormigas guerreras se alimentan principalmente de otras hormigas. Las obreras de hormigas guerreras miden de 13 mm a 1.75 mm de longitud, y alcanzan a capturar hormigas que tienen hasta 1.5 veces la longitud de las más grande de entre ellas. Ninguna especie de hormiga guerrera consume otra especie de hormiga guerrera. El segundo grupo más importante de presas son las avispas sociales (Vespidae : Polybiini). Unas pocas especies de hormigas guerreras capturan muchos grupos de insectos, otros artrópodos y anélidos. Entre las especies de presas potenciales con defensas efectivas son las abejas melipónidas, los milpiés y las garrapatas. Una colonia promedio de *Eciton hamatum* tiene cerca de 150,000 obreras, una cría de 60,000 larvas, y puede llegar a cazar hasta 90,000 insectos por día. Basado en la abundancia de estas hormigas y su gran consumo de alimento, se supone que deben de tener un efecto considerable sobre las especies que predan. Las hormigas guerreras no matan las colonias de insectos sociales : solamente las explotan. La mayoría de los adultos de un nido dañado no son eliminados y la colonia sobrevive. Aunque nuestro conocimiento del alimento de las hormigas guerreras es todavía muy incompleto, estamos convencidos que es bastante específico, de tal manera que varias muestras de presas de alguna especie de Ecitoninae sería suficiente para identificarla.

INTRODUCTION

Ants have the most diverse food habits of all the groups of social insects, but individual ant species may be broad or highly specialized in their diet. Although army ants are frequently described as eating everything in their path, it is obvious that army ants cannot and do not eat everything. Many entomologists, however, still believe that all army ants are extreme generalists, eating all types of insects and other small animals. Furthermore, even biologists with long experience in the tropics are surprised to learn that a tropical forest may have about 20 sympatric species of army ants. This immediately raises the question of how so many «generalist» predators are able to co-exist. In this paper we will compare the raiding behavior and diet of

sympatric army ants most of which are the same dominant species in all moist lowland tropical forests from southern Mexico to southern Brasil. Our research has been concentrated at two study sites each of which was visited several times during different years. One site is Barro Colorado Island in the center of Gatun Lake, Panama. The second site is Limoncocha, Ecuador (00° 24' S, 76° 36' W) on the western edge of the Amazon Basin at an elevation of 280 m. Both sites are lowland, moist, evergreen tropical forests. Barro Colorado has a distinct annual dry season, whereas, Limoncocha lacks a predictable and distinct dry season.

Table I — Genera and number of species of Ecitoninae and Dorylinae

Tabla I — Género y número de especies de Ecitoninae y Dorylinae

Ecitoninae	No. of species	Dorylinae	No. of species
Ecitonini		Dorylini	
<i>Eciton</i>	12	<i>Dorylus</i>	54
<i>Labidus</i>	8		
<i>Nomamyrmex</i>	3	Aenictini	
<i>Neivamyrmex</i>	117	<i>Aenictus</i>	50
Cheliomyrmecini			
<i>Cheliomyrmex</i>	5		
Total	145	Total	104

Army ants are distinct from other ants in that they have huge colonies, are highly migratory, and they capture invertebrates by group raids. Although other ant species share those characteristics, none has all of them and no other ants have such regular emigrations or predatory raids. All species of army ants have usually been included in one subfamily, the Dorylinae, but it is more correct to place the Neotropical and Nearctic species in the subfamily, Ecitoninae (Table I). The following discussion will be limited to the Ecitoninae.

ARMY ANTS AS GROUP RAIDERS

All species of Ecitoninae have large colonies with a minimal size of about 25,000 and a maximum of somewhat over one million. A new colony is established only when a colony has grown large enough to produce a brood of reproductives and to divide into two daughter colonies. All species are exclusively carnivorous, with the minor exception of *Labidus* spp. which

occasionally feed on seeds or nuts high in oil. Group-raiding is considered to be an important adaptation allowing army ants to capture prey larger than themselves and also to raid social insect colonies which have considerable defensive capability (Wilson, 1958). Because of their large colony size and carnivorous habits, army ants must be migratory in order to find adequate prey near their nest. Unlike many ants which can store food such as seeds or liquids high in sugar content, army ants have no means of storing food. Consequently, large raids for food must occur almost daily for all tropical species. All worker army ants are blind but are sensitive to light. They locate their prey largely by random search, but raiding direction is heavily influenced by topographic features. A chemical trail is deposited wherever the ants run, and they are totally dependent upon that trail to find their temporary nest or bivouac. When the ants locate a good source of food, they employ a recruitment system that quickly attracts hundreds to thousands of workers to the food source (Chadab and Rettenmeyer, 1975).

Subterranean and epigaeic activity

Army ants can be classified according to the strata in which they are most active. Some species have been called epigaeic because they nest, raid, and emigrate on or above the surface of the ground. All other species have subterranean nests, but columns are often on the surface of the ground. Even the most subterranean species may occasionally be forced to have exposed columns if they encounter impenetrable soil. Highly subterranean species tend to have nocturnal columns or columns hidden under leaf litter or vegetation. When *Labidus* spp. have surface columns, the ants often cover the columns with a tunnel of loose soil. The most epigaeic raiders, especially *Eciton burchelli* and *E. hamatum*, raid to the top of the tallest canopy trees. Other species, such as *Labidus praedator*, usually stay on the ground but may go 2-3 meters up into the vegetation. The raiding strata obviously influence the kinds of prey encountered, and even when columns are restricted to the surface of the ground, subtle differences in prey may result because some army-ant species tend to go under leaf litter more than others.

The strata of activity of army ants has a large influence on their relative abundance as perceived by investigators. Studies of army ants have of necessity concentrated on the species which are most epigaeic, *Eciton* spp., and the extent of subterranean activity has been ignored or grossly underestimated. The best estimate available for the amount of subterranean activity is based on a comparison of the numbers of colonies of *Ecitoninae* found at our two study sites (Table II). These data and others for different localities in Central and South America indicate that any similar lowland moist tropical

Table II — Number of colonies of army ants found in two lowland moist tropical forests.

Tabla II — Número de colonias de hormigas guerreras encontradas en selvas tropicales de áreas bajas y húmedas.

	Panama		Ecuador	
	No.	%	No.	%
<i>Eciton</i> spp. total	137	63.7	216	40.5
<i>burchelli</i>	23	10.7	27	5.1
<i>hamatum</i>	49	23.8	51	9.6
<i>drepanophorum</i>			2	0.4
<i>lucanoides</i>			35	6.6
<i>dulcius</i>	13	6.0	10	1.9
<i>vagans</i>	15	7.0	27	5.1
<i>mexicanum</i>	37	17.2	32	6.0
<i>rapax</i>			32	6.0
<i>Labidus</i> spp. total	43	20.0	224	42.0
<i>praedator</i>	34	15.8	108	20.3
<i>coecus</i> + sp. 1	9	4.2	116	21.8
<i>Nomamymex</i> total	15	7.0	33	6.2
<i>Neivamymex</i> total	20	9.3	60	11.3
Total	215	100	533	100

forest can be expected to have about 20 sympatric species of army ants. The species, *Eciton burchelli*, *E. hamatum*, and *E. lucanoides* typically emigrate, raid, and bivouac on or above the surface of the ground. Those most epigaeic species comprise 21-35 % of the army ant colonies found (Table II). Although all other species have subterranean nests, raid and emigration columns of all *Eciton* species are typically epigaeic. The *Eciton* species have the most conspicuous columns partly because the ants are the largest, ranging from 3-13 mm in body length, they carry the largest prey, and columns are sometimes 5-8 ants wide. Most workers in the other genera range from 6 mm, down to 1.75 mm in body length, and narrow columns 1-3 ants wide are typically partially or completely hidden by litter or vegetation.

Although we have found no exclusively subterranean workers in Central America or Ecuador, in the United States several species of *Neivamymex* are known whose workers are apparently exclusively subterranean in all activities. Nests or columns of some very common species have never been found. The ants are known to be abundant because clusters of ants can be found under stones, and males frequently fly to lights. Since there are also about 25 more species of male *Ecitoninae* described than there are workers for which no male is known, these unassociated males probably belong to highly subterranean species.

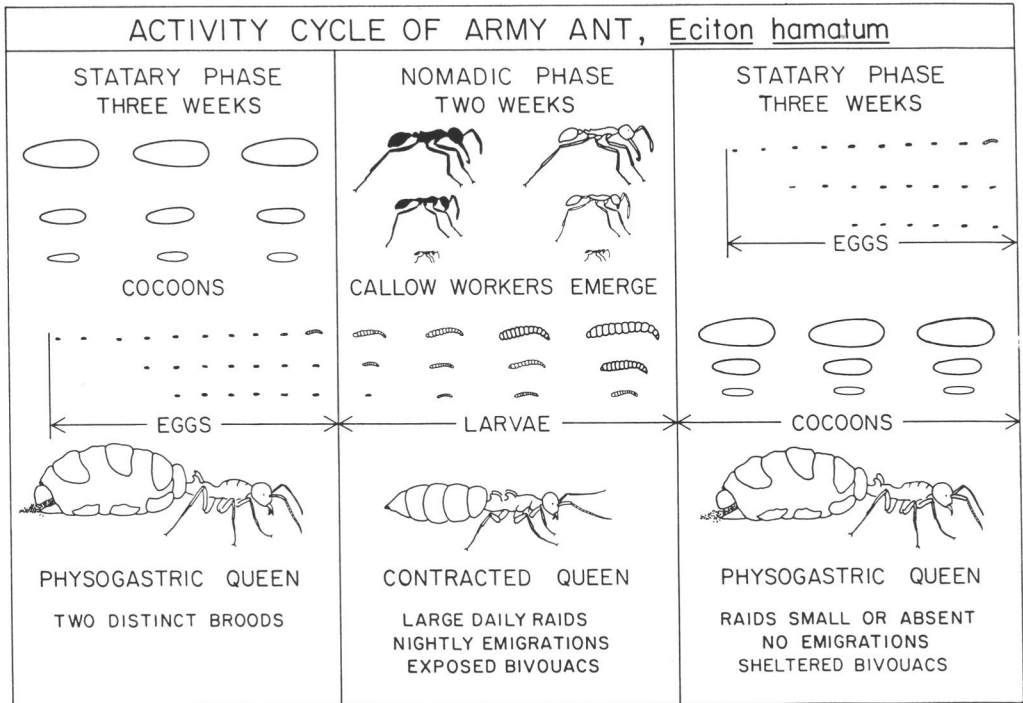
All species of *Labidus* probably do much raiding underground ; and even when they raid on the surface, their columns connecting to the bivouac are subterranean. Both raid and emigration columns sometimes were found extending only 10-100 cm on the surface. Thus, Table II is essentially a summary of epigaeic activity seen and not an accurate measure of the numbers of colonies present in those habitats. Nonetheless, the abundance of *Labidus* colonies ranged from 20-42 % and *Neivamyrmex* and *Nomamyrmex* together ranged from 16-18 % despite the fact that we also were more active on the surface of the ground during the day. Therefore, we conclude that colonies of *Labidus*, *Nomamyrmex*, and *Neivamyrmex* are at least twice as abundant as indicated in Table II, and comprise 60-76 % of all army-ant colonies.

Effect of activity cycle on raiding

The most extensively studied tropical army ants are *Eciton hamatum* and *E. burchelli* both of which have precise activity cycles first described by Schneirla (1933, 1973) (Fig. 1). Raiding is directly correlated with these cycles. During the statary phase lasting about three weeks, the colony remains in one bivouac, and the queen becomes physogastric and lays a huge brood of 25,000 to 100,000 eggs. Since the previous brood is in the pupal stage, enclosed in cocoons, there are no larvae requiring food. Consequently raids during the statary phase are short in distance and duration, and the food collected indicates the basal consumption rate to sustain the adult population under minimal activity levels.

The young callow workers emerge from their cocoons during 24-48 hours at the same time the eggs of the next brood are starting to hatch. The stimulation from those young adults is thought to be the primary trigger initiating the nomadic phase in which the colony emigrates nightly for a 2-week period. Throughout the nomadic phase the colony has greatly increasing requirements because the larvae, synchronized in age, consume more as they grow. In addition, the old adults must eat more to sustain their higher level of activity, and the brood of 25,000 to 100,000 young adults eat but do not participate in collecting prey during the first half of the nomadic phase. At the onset of the nomadic phase, raids typically start about 6:00 A.M. and end between 3:00 and 6:00 P.M. as the emigration begins. At the end of the nomadic phase, raids start at about the same time but continue until 6:00 to 10:00 P.M., with prey being carried to the new bivouac for several hours after the emigration has begun.

Considering the amount of prey brought into the nest, it is surprising to find so little food when bivouacs are sampled or examined. The insect prey

Fig. 1 — Activity cycle in *Eciton hamatum*Fig. 1 — Ciclos de actividad en *Eciton hamatum*

is not stored, and most is consumed within a few hours so it is not transported to the next bivouac. During the nomadic phase *Eciton hamatum* typically has three base raid columns radiating from its bivouac (Fig. 2), and one of these becomes the emigration route. From counts of ant traffic on these columns it is possible to estimate the amount of prey collected during the day. When the emigration starts, prey seen coming out the emigration column from the old bivouac includes mostly prey that just came in on the other two raid columns. Prey numbers can also be estimated from the prey carriers on the emigration column near the new bivouac, but care must be taken to distinguish between prey ant larvae and the larval brood of the army ants carried in

the same manner. Fortunately, army-ant larvae can usually be recognized by their elongate shape in contrast to the more plump shape and frequently larger size of the prey species. Estimates of daily prey intake by this method are further complicated because much of the prey is not brought directly back to the day's bivouac but deposited in the prey caches along the raid columns. Each temporary cache may contain over 1,000 pieces of booty guarded by workers and soldiers. It saves the ants considerable energy to deposit prey in caches, partly because that prey in caches near the new bivouac need only be carried a relatively short distance in the emigration and partly because the raiding ants can go back immediately for additional prey.

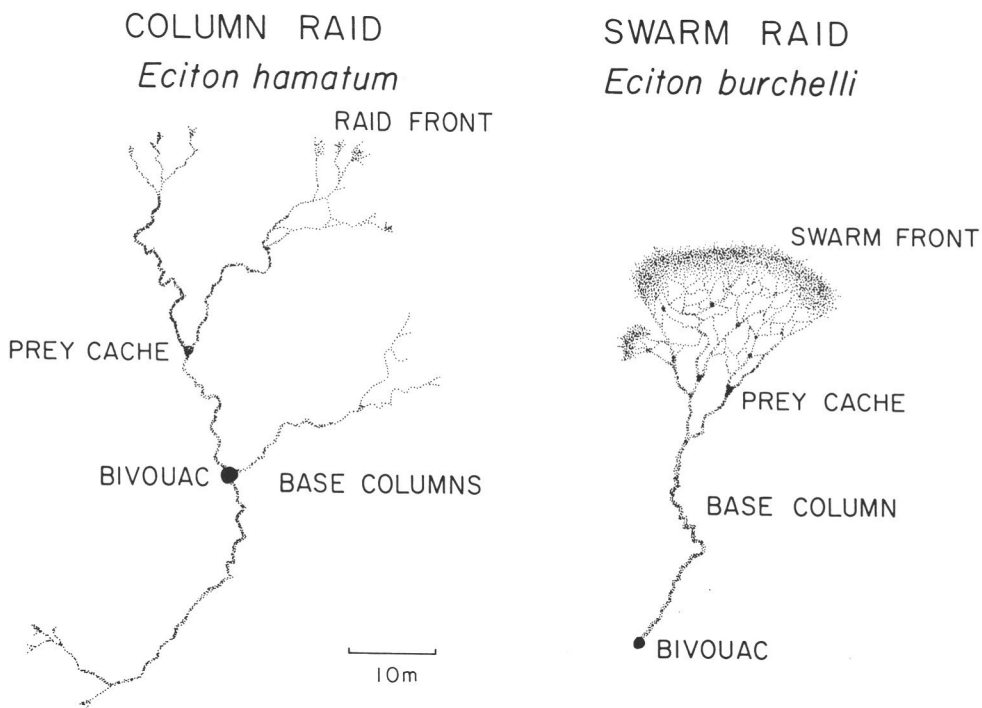


Fig. 2 — Structure of the raids of two species of *Eciton*.

Fig. 2 — Estructuras de las correrías en dos especies de *Eciton*.

During emigrations of *E. hamatum* the rate of ant traffic flow may be 25-50 ants per second. That is too fast for accurate counts, especially when

prey carriers must be distinguished from those carrying brood, and unladden ants going in both directions must also be counted. The best technique we have used consists of filming the column with a 16 mm camera at 48-64 frames-per-second, for 5-sec intervals every 30 min (or sometimes more frequently when there is great fluctuation in traffic). Accurate counts can then be made when these films are projected at a reduced speed. In order to obtain the most complete coverage of the colony including estimates of prey brought to the new nest, it is essential to film within a few meters of the new bivouac as soon as it is possible to locate it. Although the technique sounds simple, there are so many practical problems that we have only obtained good records for eight emigrations and partial records for 14 others.

FOOD OF ARMY ANTS

Prey of *Eciton hamatum*

E. hamatum feeds almost exclusively on ant brood, but the species attacked in Panama vary from those attacked in Ecuador even when the same or similar species are present at both locations. Although attines are common in both localities, these ants were rarely raided in Ecuador but commonly raided in Panama. Formicinae, followed by Dolichoderinae, make up the largest biomass of prey in Ecuador. The formicines *Gigantiops destructor* and *Camponotus* spp. were represented in 54 % and 64 % respectively of 154 samples of prey of *E. hamatum* in Ecuador. In these same samples the dolichoderines *Hypoclinea* and *Dolichoderus* were found in 87 % and 45 % respectively and the myrmicine *Pheidole* in 48 % of the samples. Ponerines are less commonly raided than the previous three subfamilies, and the genera raided most commonly are *Pachycondyla* (= *Neoponera*) and *Anochoetus*. *E. hamatum* usually only captures a portion of an ant colony that is attacked. When the army ants attack, workers of the attacked species typically rush out of the nest carrying their brood. These ants may disperse over many meters, often going into the canopy of trees where they usually escape capture. After the army ants depart, the escapees return to their nest with the brood they carried out and continue colony activity. For at least one species, *Dolichoderus rugosus*, the odor of one crushed worker of *E. hamatum* is enough to cause a mass evacuation. *E. hamatum* seldom brings back adult ants to its bivouac. These not only resist or evade capture but are difficult for both the army-ant adults and larvae to eat, and many pieces of adults are discarded uneaten on refuse deposits. We have even seen a worker of *hamatum* carry an adult ant out of a nest in a stem and drop the ant before going back inside

the nest, presumably to obtain some brood. Along with the ant brood, the army ants bring in Membracidae which are tended by *Pheidole*, but we do not know whether the army ants eat the Homoptera. Although a few other parasites or myrmecophiles show up in samples, all these nonsocial insects make up less than 0.01 % of the prey.

Next to ants, social wasps (Vespidae : Polybiini) are the second most important food source for *E. hamatum*. Most adults escape when the ants attack, but any remaining in or on the nest are captured. The odor of army ants is detected by some of the wasps and directly or indirectly triggers evacuation of the nest before numerous ants can overwhelm the colony (Chadab, 1980). Although social wasps make up only about 0.5 % of the pieces of prey brought in by *E. hamatum*, in biomass dry weight the wasps are 2-10 % of the total prey. As a result of the escape behavior of both ants and wasps, army ants do not eliminate colonies but interrupt their growth.

Prey of other *Eciton* species

E. lucanoides, which morphologically is the column-raider most closely related to *E. hamatum*, also has the most similar prey. Likewise, the two closely related species *E. dulcius* and *E. vagans* have great overlap in prey species. Both the latter species concentrate to a high degree on Ponerinae, especially *Odontomachus* spp., which appear to be avoided by *E. hamatum*. The smallest of the *Eciton* species, *E. mexicanum*, also seems to concentrate on Ponerinae, especially *Ectatomma* spp.

The workers of *Eciton rapax* are the largest of any Ecitonine (13 mm) and the only species of *Eciton* which does not have a distinct soldier caste. All soldiers of the other *Eciton* spp. have huge hook-like mandibles used for defense but not for capturing nor carrying prey. The largest workers of *E. rapax*, however, are not restricted to colony defense but actively participate in all aspects of raiding and emigrating. *E. rapax* preys primarily on large species of Ponerinae including *Pachycondyla crassinoda*, the largest ant we have seen regularly captured by any army ant. *P. crassinoda* is 18 mm long or 5 mm longer than the longest *E. rapax* workers, and it has a bigger sting and larger mandibles than the army ants. We do not know if it can ever successfully defend its colonies against *E. rapax*.

The last *Eciton* species we studied, *E. burchelli*, is completely different from the other species in its raiding behavior. It has swarm raids in one direction from the bivouac (Fig. 2). That type of raid covers the surface of the ground and much of the vegetation more thoroughly than a column raid. As a consequence the ants flush out a tremendous diversity of invertebrate and vertebrate animals. The advancing swarm is more efficient at capturing

grasshoppers, crickets, spiders, and other active arthropods. Although *E. burchelli* captures arthropods as large or larger than the smallest workers and on rare occasions will even kill a small vertebrate such as a lizard, ants and social wasps still make up about 50 % of its diet. Since identification of the prey of *E. burchelli* is tantamount to identifying all the species of large arthropods in a tropical forest, analysis of *E. burchelli* has not progressed far. It is perhaps more fruitful to mention a few of the species avoided by *E. burchelli*.

Arthropods not captured by *Eciton* spp.

All ticks and millipeds are apparently adequately protected by their defensive secretions. However, the defensive chemicals of Hemiptera usually are not effective, and Reduviidae, Pentatomidae, and others are captured by *E. burchelli*. Many caterpillars are protected if they are covered with dense or long hairs. Phalangida have such thin legs that the ants have difficulty climbing them. If an ant gets on a leg, the daddylonglegs shakes it off, sometimes standing on fewer and fewer legs until it gets down to three when it will run off. Spiders can escape by dropping on a strand of silk which the army ants will not descend. Some beetles such as Scarabaeidae are so armored that they cannot be dissected by *E. burchelli* even in several hours of intensive effort. Some beetles are greatly incapacitated by the army ants since the legs may be injured or tarsi removed so the beetle has difficulty walking. We have never seen a butterfly captured by *E. burchelli*, but some fast-flying insects that would seem to be immune have been killed. For example, adult flies and even dragonflies are sometimes caught by the ants. Termites which are so well represented in tropical forests would seem to be an excellent source of food for army ants, but we know of no common species that raids them. All the *Eciton* species we have seen encounter *Nasutitermes* and a few other termites have been repelled by the termites' defensive secretions or odors. The other main group of tropical social insects, the Meliponini or stingless bees are also not raided. We have seen *Eciton* spp. approach colonies of *Trigona* and *Melipona* and occasionally run into the entrance tubes of the bees. The bees attack the ants and daub them with sticky propolis. The army ants in every case were able to capture only one to a few adult bees.

Prey of *Labidus* spp.

Labidus praedator has swarm raids which resemble those of *E. burchelli* except that the ants are smaller (workers 2-7 mm in comparison to 3-10 mm) and capture smaller prey. *L. praedator* can also capture prey many times its

size such as cockroaches, but the majority of prey are much smaller such as Homoptera. *L. praedator* is highly subterranean and raids extensively under litter where it captures many isopods and amphipods. Other species of *Labidus* are more subterranean than *L. praedator*, and we know less about their prey. They do capture beetle larvae that would not be found by *E. burchelli* because the larvae live in litter or soil.

Prey of *Nomamyrmex* spp.

Nomamyrmex esenbecki has been considered most closely related to *Labidus* on morphological grounds, and those two genera have the most similar guests living within their colonies. From the standpoint of its raiding, *N. esenbecki*, is similar to an *Eciton* species because it has epigaeic column raids and attacks similar prey. Although it raids many kinds of ants and occasionally social wasps, it seems to concentrate more than any other army ant on raiding *Odontomachus*. A spectacular subterranean raid by *Nomamyrmex esenbecki* on *Atta mexicana* was incidentally observed and filmed in February 1970 in Ajijic, a locality on the northern border of Chapala Lake, Jalisco, Mexico. The leaf-cutter nest had been excavated to a maximum depth of 3.5 meters to permit filming of the nest interior and during the course of the filming the *Nomamyrmex* attacked at a depth of 1-2 meters. The army ants carried off many thousands of larvae, pupae, and callow workers and killed many adult ants including the queen. No army ants were active on the surface of the ground, and the entire raid would not have been detected if the excavation had not been dug in order to film the leaf-cutters. (The film «Les Fourmis Tropicales» was shown as part of this symposium, and Dr Pierre Jaisson, one of the observers, kindly provided additional information).

We have not been able to find workers of the other two species of *Nomamyrmex*, but it is noteworthy that there are two records of *N. hartigi* feeding on termites in Panama and Brasil (Rettenmeyer, 1963). The ants were found raiding up covered termite tunnels on tree trunks and bringing down termites. That is the only Neotropical army ant suspected of specializing on raiding termites, but some North American *Neivamyrmex* regularly eat them as well (Pullen, 1963).

Prey of *Neivamyrmex* spp.

The genus *Neivamyrmex* includes 117 species, but each *Neivamyrmex* species has a more limited geographical range than the common species in the three genera of army ants discussed above. We have few prey records, but these suggest that *Neivamyrmex* species concentrate on small species of ants.

N. pilosus, for example, repeatedly has been found raiding *Crematogaster*, a genus of myrmicine ants which seems to be avoided by *Eciton* species. Two species, *N. pseudops* in Panama and *N. diana* in Ecuador, raid *Pseudomyrmex*. All army ants raid species of ants which range from the size of the smallest army ant workers of the species up to 1.5 times the length of the largest workers. Thus, there is a general correspondence between the size of the prey and the size of the predator. One of the primary advantages of the extreme polymorphism exhibited by many army ant species is that the different size of ants are adapted to handle different sizes of prey. Although army ants capture some ants considerably smaller than themselves, such as *E. hamatum* preying upon *Strumigenys*, it is rare that they do so. We assume that most *Neivamyrmex* species specialize on small ants, a conclusion substantiated by 15 tropical species and three species of *Neivamyrmex* we have observed in Kansas. ●

PREY SIZE AND BIOMASS AND INTERACTIONS BETWEEN PREDATOR AND PREY

It appears that for every species of ant known in a tropical forest there exists an army-ant species of appropriate size to raid it with one exception. The largest ponerine in Panama and Ecuador, *Paraponera clavata*, does not seem to have an effective army-ant predator (unfortunately !). That ponerine is common at both localities, and we have seen *E. burchelli* workers fight with *Paraponera* workers for hours, but the army ants were not successful in raiding the nests. Only one major subfamily of ants is never raided by army ants and that is the Ecitoninae. Regardless of the size relationships, no army ant of any species has been seen to injure or capture another army ant although whenever two species of army ants come in contact considerable innocuous nipping back and forth may occur. The amount of prey collected by a colony of army ants is directly related to both the size of the colony and the stage of larval brood present in the colony. All species have considerable variation in colony size, but atypically small colonies seem to be unable to maintain the raiding-emigrating behavior and probably cannot exist for more than a few months. Colonies of *E. hamatum* range from 50,000 to 250,000 adults and have an average size of about 150,000 with a brood of 60,000 larvae. Brood production is so high that adult mortality must also be high. Most of the mortality we believe is due to three factors : (1) mortality or severe injury when fighting with ants or wasps, (2) separation from chemical trails, or (3) exposure to high temperatures or severe rain during raiding or emigrating.

Estimates of prey numbers and biomass (dry weight) are given in Table III. These data show that the average strong raid brings in 15,000 to

40,000 prey per day. Maximum raids for *hamatum* may yield about 90,000 insects, including many minute ant eggs and larvae and few adults.

Table III — Estimates of prey carriers, numbers of prey, and prey biomass for *E. hamatum*

Tabla III — Estimación de hormigas transportadoras de presas, del número de presas, y de la biomasa de presas en *E. hamatum*.

Colony phase	Raid strength	Daily number prey carriers	number	Total prey biomass (mg)	number	Wasp prey biomass (mg)
statory	weak	2,000-5,000	3,000-7,600	1,070-2,680	18-46	130-330
statory	strong	10,000-35,000	15,200-53,200	5,400-19,000	91-319	650-2,280
nomadic	weak	5,000-10,000	7,600-15,200	2,700-5,400	46-91	330-650
nomadic [Ⓢ]	strong	25,000-60,000	38,000-91,000	13,400-32,200	228-547	1,630-3,920

The army ants must have a considerable effect on the prey species and may prolong the length of time for an ant or wasp colony to reach an adequate size to produce reproductives. Since the army ants do not kill ant or wasp colonies they are ecologically analogous to grazing animals. The army ants crop their social insect prey, leaving the adults to continue the colony and produce more brood for the next army-ant colony to collect. Although our knowledge of the food of army ants is still very incomplete, we are convinced that prey specificity is such that several samples of prey from any species of Ecitoninae would be sufficient to identify a species of army ant.

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