THE BIOLOGY AND BEHAVIOR OF AN ARMY ANT, ECITON RAPAX

by

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INTRODUCTION

Army ants and driver ants belong to the subfamily Dorylinae (Hymenoptera : Formicidae) and are distributed throughout most of the tropical and subtropical parts of the world. The New World Army ants, consisting of approximately 142 species, about half of which are known only by the male caste, are divided into two tribes. The rare tropical tribe Cheliomyrmicini is represented by the genus Cheliomyrmex and 5 distinctly subterranean species. The tribe Ecitonini is composed of 4 genera and 137 species, the best known of which is Eciton. Eciton is the most highly specialized group and is composed of 12 species. Members of this tropical genus are predominantly surface-adapted forest dwellers (Schneirla 1971: 10). The purpose of this study is to present the behavior and biology of a little known South American species of army ant, Eciton rapax Fr. Smith.

Eciton rapax was first discovered in northeastern Brasil by Henry W. Bates in the 1850's and was regarded as a shy and timid species whose armies were never very numerous (Bates 1863: 352). Nothing, other than casual observations, has been published on its ecology, biology or raiding behavior. Although it is one of the largest of all army ants, the majors being ±13 mm long, and is very conspicuous because of the bright yellow-orange gaster on a black body, it has never been observed in large numbers. Also, it is noted for the rapidity with which its columns vanish into the forest floor when disturbed (Mann 1916: 420). Another interesting feature of rapax is that the majors lack the long, sharp, recurved mandibles characteristic of all other species of Eciton (Fig. 1).

Willis (1967: 10) mentioned having seen antbirds occasionally at raids of rapax, which he regarded as primarily subterranean, and stated that its

behavior is a possible exception to the general rule that antbirds follow only epigaeic species of army ants.

MATERIALS AND METHODS

Colonies of Eciton rapax were most frequently encountered while walking along existing foot trails or roads in the forest and occasionally while following another colony of army ants. They were usually seen crossing or following trails and at times a raid front was encountered. Because of the large size of rapax workers, they were more easily spotted than most other species of army ants. If a column was discovered in the morning with the flow of traffic heavier in one direction, and the majority not carrying anything, the ants were probably heading away from the bivouac. In the late afternoon a single column heading again primarily in one direction, some carrying prey, was usually returning to the bivouac. These two time periods, in the morning until about 11:00 AM and late afternoon or early evening, from 6:00 to 8:30 PM, are the best times for following rapax raid columns. At other times rapax is difficult to track because of their paucity travelling along raid columns, and after 6:00 PM workers seldom raid. Emigration columns may be found outside of the two main time periods for raiding.

Upon having found a column of rapax, the first objective was to locate the bivouac. If the raid column was weak, tracking the workers for long distances was impossible, and it was best to wait until traffic increased. In the meantime it was possible to collect prey, look for the raid front, or study some other aspect of behavior.

While tracking the ants through the underbrush, string was let out from a film reel 1 to 2 m above the ground approximately along the ants' actual trail.

The string had been previously cut in sections a little over 10 m in length, and the ends tied tandem to form one continuous line. The string (1) served primarily to keep from getting hopelessly lost when evening came and the little paths chopped through the thickets and underbrush melted into the darkness; (2) served as a quick means of determining the compass direction of raid or emigration columns; (3) was used to calculate distances by counting the number of knots and multiplying by 10. It could also be easily marked with a series of dots and dashes using indelible ink in a "Rapidograph" pen to indicate the distance from the bivouac, a useful reference while recording activities occuring simultaneously along raid columns; and (4) it lasted for several weeks before rotting or being gathered by natives, which would indicate overlapping areas previously raided.

A straight-tube aspirator (Rettenmeyer 1963: 314) was the most efficient way for picking up and transferring myrmecophiles to vials without disturbing the column. Forceps 30 cm long were used for picking individual army ants carrying prey or brood out of raid or emigration columns.

Most of the counts of worker ants returning to or leaving the bivouac were made 1 to 2 m from the nest entrance at 5-minute intervals. Counts were taken occasionally at different intervals along the column. Sometimes the ants would change entrances to the bivouac for no apparent reason or because of some disturbance such as frequent collecting of booty at one point along an incoming raid column. Counts were based on the number of ants passing a fixed point in one minute. When traffic was heavy, estimates were based on the number of seconds it took for 25 ants to pass the point. Later, using a conversion table, the approximate number of ants per minute was calculated.

RESULTS AND DISCUSSION

Study Site

Limoncocha (00° 24'S, 76° 36'W), Napo Province, lies on the eastern side of the Andes at an elevation of 280 m (920 ft) along the Napo River about 210 km east of Quito, Ecuador. It is located on the western periphery of the Amazon basin, the largest single lowland tropical rain forest area in the world. Limoncocha was founded in 1954 as the rural base of operations for the Summer Institute of Linguistics in Ecuador. A meteorological station consisting of a white louvered enclosure about 2 m off the ground, was set up in December, 1960, and rainfall, temperature, humidity, and cloud cover are recorded three times a day.

Limoncocha is situated on the southwestern edge of Lake Limoncocha (c. 3.5 x 1 km) an oxbow of the Napo River but now separated from it by a low forested area which periodically becomes inundated when the river floods. To the west is the Jivino River which meanders in a southeastward direction, joining the Napo about 2.5 km south of Limoncocha. The area to the north of Limoncocha is covered by continuous lowland rain forest. An airstrip 1200 m long runs east-west between the Jivino River and Lake Limoncocha.

The forest surrounding Limoncocha has been selectively logged on a number of occasions since 1954. Most of the large hardwood trees have been removed, while other large less desirable lumber trees, e.g., Ceiba and Ficus, have been spared. At the time of this study in June to August 1970, the forest understory north of Limoncocha varied from areas of dense tangled second growth to open areas of relatively little undergrowth under old canopy trees. Most of this area was covered by tall saplings, palms, and Heliconia and other low

plants. The forest was scattered with occasional dense thickets of tangled vines, saplings and scrub vegetation that had formed around fallen tree trunks, canopies and lianas, or grew up where trees had been removed. When comparing this area with a primary forest it is evident that this forest had been greatly altered from the natural primary or climax forest.

The majority of observations on E. rapax were made in the forests to the north of the airstrip within a few kilometers walking distance from the base.

The forested area south of the airstrip was interspersed with numerous interconnected clearings where Yuca, banana (Musa), and papaya (Carica) were cultivated. Small areas of the forest had been converted to pasture for cattle. Abandoned clearings no longer grazed or cultivated, quickly reverted to dense second growth tree stands and tangles. Animals suitable for food or skins had been extensively hunted by the Quichua Indians near the base.

The forest surrounding Armenia Vieja (00° 32' S, 77° 02' W, c. 300 m elevation), an area about 60 km west of Limoncocha, has been described by Grubb, et al. (1963). The structure, physiognomy and floristics of this lowland rain forest are probably very similar to those of the undisturbed forest surrounding Limoncocha. They concluded that the density of trees over 20 cm (8 in) diameter (dbh) per 930 m^2 (10,000 ft^2) in the Ecuadorian lowland forests is appreciably greater than in most other parts of the tropics, equalled only by that of the forests on the Lesser Antilles. The density of trees over 10 cm (4 in) dbh is second only to the lowland forest on Mauritius. Unfortunately, insufficient data were available at that time to indicate the extent that the high density of trees over 20 cm dbh is compensated by a low density of really big trees, i.e., trees over 90 cm (3 ft) dbh.

Precipitation at Limoncocha remained fairly constant from year to year,

from 1961 to 1970, but the month in which the greatest or least amount of rain fell each year was highly variable. Grubb, et al. (1966) pointed out that the inhabitants of Tena (00° 59' S, 77° 49' W), about 300 km southwest of Limoncocha, made no simple distinction between 'verano' or summer, and 'invierno' or winter. There is no distinct dry season at Limoncocha although there is usually a time of the year when there is less precipitation. The mean annual rainfall ranged from a high of 3288 mm (1968) to a low of 2670 mm (1969) with a mean of 2945 mm. All the mean precipitation figures are based on the 10-year period 1961 to 1970.

In general, January and February tend to be the driest months of the year with a mean rainfall of 189 mm and 171 mm respectively. March was the most unpredictable month with a mean of 239 mm and a range of 395 mm between the mean wettest (445 mm) and driest (128 mm) years. The time of the year of greatest precipitation, referred to as 'invierno' in the American tropics, is most likely to occur from April to July at Limoncocha. April and May were the wettest months with a mean of 330 mm and 329 mm respectively while June was 3rd with 293 mm. August and September (215 mm and 202 mm) tend to be noticeably drier than the preceeding months, so that there is a minor dry season before the sharp increase in precipitation in October (270 mm). November appeared to be the most stable month in terms of rainfall with a mean of 225 mm and a range of 146 mm.

Limoncocha thus appears to have two short relatively dry periods each year (January-February and August-September) although this is not always true every year. Richards (1952) stated that seasonal distribution of rainfall in the tropics is a function of latitude and that at the equator, evenly distributed and high rainfall occurs throughout the year, "though there are probably no land surfaces within the tropics with a completely non-seasonal rainfall".

The mean monthly temperatures at Limoncocha are quite uniform, but the wet months, April through July, tend to be the cool ones because of high precipitation and cloud cover. The coolest day of the year is likely to occur at almost any time. Monthly maximum temperatures varied between 30.6°C (87°F) and 35.6°C (96°F) while monthly minimum temperatures ranged from 15.6°C (60°F) to 21.1°C (70°F). The highest recorded temperature at Limoncocha for the 10-year period was 36.7°C (98°F) (November 1967) while the coldest was 14.4°C (57.9°F) (August 1965). There is little variation among the maximum monthly temperatures and among the minimum monthly temperatures. In both cases the range seldom exceeded 18°C (10°F) and usually fell within 4.5 to 12.4°C (2.5 to 6.9°F). The difference between the mean of the maximum monthly temperatures and the mean of the minimum monthly temperatures for each year over 7 years, ranged from 45.1 to 50.7°C (25.0 to 28.2°F).

In summary, the climate at Limoncocha is wet with a tendency for some seasonal variation in precipitation. Annual temperatures are uniformly high with slight contrasts between the warmest and coldest months. On a cool, damp, rainy night the air can become uncomfortably chilly, usually requiring one or two light blankets for sleeping.

Distribution

Schneirla (1971) published a distribution map for the genus Eciton and 4 other common genera of dorylines. The tribe Ecitonini extends from the central portion of the United States including parts of Nebraska and Iowa south to southern Argentina. The two species of Eciton with the greatest range are E. vagans and E. mexicanum whose colonies can be found from southern Mexico south to the 46th parallel in southern Argentina. E. rapax is found

approximately in the central portion of the total range of Eciton.

Kempf (1970) stated that rapax is restricted to the Amazon basin of South America. It has never been collected in northern Colombia, in the Orinoco basin, or the Guianas. E. rapax has been collected at 30 localities in Colombia, Ecuador, Peru, Bolivia, and Brasil. It has been reported as far north as Paraiso, Colombia and as far south as Corumbá, Brasil. The eastern limit is Belém, at the mouth of the Amazon river, and the most western record is Putuimi, Ecuador. A list of all localities is given in Table 1. The records by Portocarrero, Willis (pers. com.) and Kazan have not been published. Localities with known coordinates are plotted by numbered points on the map (Fig. 2). The highest reported elevation for rapax is 1,000 m, and relatively low mountains seem to be effective barriers to its dispersal.

Males have never been collected with workers. Borgmeier (1955: 212, 270) reported that E. jansoni Forel, known only from males, is probably the male of rapax. However, Rettenmeyer (1963: 403) stated that distribution records for jansoni show it is sympatric with rapax only in Ecuador and Colombia and that it extends further north into Central America. Since workers of Eciton are more commonly collected than males, it is unlikely that rapax occurs in Panama or Central America where it has never been collected. Based on color and distribution, it is more probable that E. setigaster is the male of rapax.

Colony Phases

Statary Phase

The exact length of a statary period for E. rapax is not known. The best approximation is 27 days, computed for colony E-720, bivouacked in an Atta cephalotes nest from 2 to 29 July 1970. The colony was first observed entering

Table 1.--Locality records for Eciton rapax Fr. Smith[a]

Locality	Coordinates	Elev. (m)	Citations
BOLIVIA			
1. Rio Beni			Mann 1926
Departamento del Beni:			
2. Cachuela Esperanza	(10°32'S, 65°38'W)		Mann, 1926
3. S. Antonio			Borgmeier 1955
Departamento de Cochabamba:			
4. Chaparé	(16°30'S, 65°30'W)		Borgmeier 1955
BRASIL			
Estado do Amazonas:			
5. Amazonas			Emery 1894
6. Alto Purús			Borgmeier 1955, 1961
7. Ponte Alegre	(08°57'S, 67°50'W)		Borgmeier 1961
8. Santo Antonio do Içá	(03°05'S, 67°57'W)		Borgmeier 1955
9. Tefé (Ega)	(03°22'S, 64°42'W)		Smith 1858
Estado do Mato Grosso:			
10. Corumbá	(19°01'S, 57°39'W)		Borgmeier 1955
11. Mato Grosso (estado)			Emery 1894
12. Barra do Tapirapé			Borgmeier 1955 Malkin 1962[b]
Estado do Pará:			
13. Belém	(01°27'S, 48°29'W)		Emery 1894 (Para) Smith 1855, 1858 Borgmeier 1955 Willis 1971[c]
14. Itaituba	(04°17'S, 55°59'W)		Borgmeier 1955
15. Santarém	(02°26'S, 54°42'W)		Smith 1855, 1858 Borgmeier 1955
Territorio de Rondônia			
16. Camp 41[d]			Mann 1916
17. Pôrto Velho	(08°46'S, 63°54'W)		Mann 1916

Table 1. continued

Locality	Coordinates	Elev. (m)	Citations
COLOMBIA			
Comisaría del Putumayo:			
18. Putumayo	(00°07'N, 75°52'W)		Borgmeier 1955
19. Umbria	(00°34'N, 76°34'W)[e]		Borgmeier 1955, 1961 Reichensperger 1933 Willis 1971[c]
Intendencia del Caquetá:			
20. Paraiso	(01°45'N, 75°43'W)[e]	750	Willis 1971[c]
21. Tres Esquinas	(00°44'N, 75°15'W)[e]		Willis 1971[c]
ECUADOR			
Provincia del Morona Santiago:			
22. Putuimi	(02°39'S, 77°28'W)[e]		Willis 1971[c]
Provincia del Napo:			
23. Limoncocha	(00°24'S, 76°36'W)	280	Kazan[b]
PERU			
24. Rio Aguaytía			Borgmeier 1955
25. Rio Ucayali			Borgmeier 1955
26. Valle Chanchamayo			Borgmeier 1955
27. Departamento de Loreto			Borgmeier 1955
Departamento de Huánuco:			
28. Tingo Maria	(09°09'S, 75°56'W)	760	Borgmeier 1955
Departamento de Junin:			
29. Santa Beatriz	(10°57'S, 75°12'W)	1000	Portocarrero 1965
30. Satipo	(11°16'S, 74°37'W)		Borgmeier 1955

[a]Coordinates taken from U.S. Board on Geographical Names unless specified otherwise.

[b]Collector

[c]Personal communication.

[d]306 km from Pôrto Velho along Madeira-Mamore R.R.

[e]Coordinate given by Willis

the Atta nest about 1:30 PM and last seen there on the 29th when the colony emigrated.

Observations on this one colony indicate that most of the ants participating in the day's raid leave early. After that, only a few workers exit, although unladen workers may be seen travelling sporadically back and forth along the column in the morning. Raiding terminated early in the evening during the last 10 days of the statary period, and all rapax workers were back at the bivouac before 9:00 PM. Termination times fluctuated between 7:50 and 8:50 PM. All raids observed during the first 17 days, except on the 2nd day when the raid continued into the following morning, terminated by 8:15 PM.

The period when one is most likely to find rapax travelling in columns along the forest floor is in the morning when they leave, and in the evening when they return to the bivouac with the day's spoils.

During the statary period there was no way of predicting whether the ants were going to raid on a particular day or not. Also, it was impossible to predict the direction in which they would raid. Constant surveillance was necessary, since at certain times of the day, there was no traffic along the raid column.

Nomadic Phase

The time required for rapax to complete its nomadic phase is not known. Colony E-720 was followed from 29 July after completing its statary phase until 5 August 1970 when observations were terminated. That colony emigrated six times during the nomadic phase with an average distance of 119 m between bivouacs. The longest emigration, recorded during the 6th nomadic day, covered 180 m, while the shortest emigration covered 60 m on the 7th nomadic day.

On the 2nd and 5th nomadic days, the colony did not emigrate.

Colony E-720 raided every day during the nomadic phase. During that period, it emigrated in a westerly direction following the raid columns and bivouacking along them.

Raiding Behavior

Army ants are considered either column or swarm raiders and search out prey beneath, on the surface of, or in vegetation above the ground. E. rapax is a surface-adapted column raider whose colonies start raiding after dawn and end shortly after dusk. During the statary phase they generally send out only one trail system from the bivouac. Contact with the bivouac, in the form of a continuous raid column between the raid front and the bivouac, is sometimes interrupted for a period of several hours. Chemical trails are laid down by advancing foraging workers and are most likely composed of hind gut products, as indicated by Blum and Portocarrero (1964) for Eciton species. Raiding is generally heaviest and the ants most excitable during the nomadic phase. This species is carnivorous and raids soft-bodied arthropods, taking a much more limited variety of prey species compared with E. burchelli, E. hamatum or Labidus praedator.

Initiating Raids

Many species of army ants do not raid every day during the statary period, and E. rapax is no exception. It usually began raiding between 6 and 9 AM. Sometimes a raid began during the middle of the day, but it had a shorter duration than a regular raid. Commencement of raiding was observed on only a few occasions. The few times I arrived at daybreak (6:15 AM) the ants

unfortunately did not raid.

During the statary phase workers of colony E-720 began their raids by first clustering together inside the subterranean nest entrance. Later a few ants, acting as scouts, made short exploratory excursions around the nest entrance, but eventually all returned to the nest. If they were using the same entrance and trail as the day before, they took less time scouting than if they were using a different entrance or heading in a different direction. As more ants left the bivouac, others gathered just within the entrance and soon there was a pile-up of workers. Some of the workers groomed themselves while others stood around, but in general, the ants' restless behavior seemed to force them outward. The first excursions became longer and longer until one column or as many as three short ones were formed in different directions. The fronts of these emergent columns were composed of as many as 12 ants, but no one individual was the leader as shown by the constant exchange of ants at the head of the column. The ants that were once in the lead turned around and returned in the direction of the nest, while other workers took their place at the raid front. Each time, the lead ant would venture ahead a little further than her predecessor, antennating the ground. Each lead ant touched the tip of her abdomen to the substrate before retreating presumably contributing her share of trail substance. The constant exchange of workers at the front serves to lay down a strong, persistent, and continuous chemical trail connecting the ants in the lead with the rest of the colony. The ribbon of excited ants built in intensity and at its peak more than 275 workers left the nest in one minute, sometimes by way of more than one exit. There were always a few ants travelling in the opposite direction of the main flow of traffic even at the peak of the exodus.

The departing raid column ranged in width from 1 to 6 ants. As they traveled further from the nest, the column narrowed down to 1 to 3 ants in width, depending upon whether the ants were travelling predominately in one or two directions. Large workers were often seen passing or running over the smaller, slower workers.

Raid Fronts

The head of the advancing raid column, where ants spread out over a wide area, is called the raid front and searching and raiding are concentrated within this area. E. rapax raid fronts varied in width of from a few centimeters to 4 m. The front was not a solid wall of ants advancing evenly, but a dynamic and constantly changing mass of advancing and retreating ants with a resultant forward advance. In general, the front made advances at one end and then at the other, in short alternate waves. Often one front divided into two or three smaller raid fronts.

At the front there was seemingly much confusion and turmoil among the ants. Workers combed the ground searching out prey under leaves, twigs, piles of organic matter, holes in the ground, rotten logs, etc. When encountering entangled areas, they almost invariably headed upwards. Slippery or waxy plant surfaces were seldom scaled. This was especially true of Heliconia and Anthurium plants, the leaves of which are commonly used by different species of polistine wasps as nesting sites. When these plants are close to other vegetation, rapax is able to bridge the gap, and then usually only nests near holes in the leaf are vulnerable to the army ants.

Spiny palm trees were ascended more often than any other tree. E. rapax readily scaled the trunk and palm fronds touching the ground and headed

directly to the crown, where there was usually a great accumulation of dead leaves and branches. Part of the raiding column remained on the ground, scurrying around in the debris beneath the palm. The ants usually seemed quite excited, and at the height of a surge up the tree, as many as 150 ants passed a given point in a minute. The crown of these palms at times was 10 to 15 m above the ground. Once the ants reached the top, they infiltrated the debris and disappeared from sight. The ascending column usually dwindled in numbers so that there was no continuous column between the crown and the ground. The amount of time they spent in the crown depended upon whether or not prey was located. One time rapax was still coming down a spiny palm 100 minutes after they first ascended.

Directly behind the raid front was a network of anastomosing trails separated by 2 to 30 cm. As the front advanced, these trails elongated and merged with adjacent trails until a single base column led to the bivouac. The front was an impressive network of thousands of ants running in all directions while 50 to 100 cm behind, the ants confined themselves to the anastomosing chemical trails.

At the raid front at the end of the days raiding, the ants grouped together on a number of occasions before they headed back to the bivouac together. The ants poured out of those clusters at a steady pace, head to tail, much like pulling the center strand out of a ball of twine until only a shell of outer string is left. This remaining shell of ants quickly disbanded, fell into formation, and disappeared from the area in less than 60 seconds.

At the end of a raid at a raid front, workers would often cluster together in small groups and groom themselves or eat part of the prey they had recently caught. Most of those not carrying prey back along the raid column

towards the bivouac continued raiding a short time later.

Few ant nests were actually seen being raided. On three occasions Dolichoderus rugosus was observed to be raided. These ants fled their subterranean nest, filing out one after another carrying pupae, larvae or egg brood between their mandibles as they headed up the nearest tree, vine or shrub. Such precision was observed that it looked as though they had rehearsed it many times. After reaching between 0.5 to 2 m above the ground, they turned off the main stems and headed for the extremities of the plant, where they stood on top of the leaves or hung beneath them until the danger had passed. Once they went at least 9 m up a tree (20 cm dbh) before I lost sight of them. The attacked ants remained out of their nest for over 30 minutes.

E. rapax was observed one time leaving a nest of Dolichoderus attelaboides carrying pupae and eggs. Most of the attelaboides escaped before rapax was able to trap them within their nest. Sometimes rapax followed attelaboides along the escape route, but the army ants were not too adept at capturing the vigilant adults. It was quite amusing to watch them "play hide and seek" on the ends of leaves, where rapax probably reacted to the leaf movement and vibrations caused by the moving prey rather than to the visual stimulus of the prey.

Odontomachus adults were collected on a few occasions standing on leaves, sometimes carrying brood, while rapax raided nearby.

Gigantiops destructor also fled their subterranean nests carrying brood between their mandibles as they ascended nearby vegetation to escape rapax. Gigantiops, the most agile of ants, was able to escape by jumping from leaf to leaf, quickly outdistancing their pursuers.

Raid Columns

Eciton rapax raid columns were formed of worker ants travelling along chemical trails connecting the bivouac with the distal raid front. The column varied in width depending upon the time of day, and the distance from the bivouac or raid front. The length of a raid column varies according to army ant species and colony phase.

The peak activity period for these raid columns was in the morning when the ants were leaving the bivouac and in the evening when the ants were returning after the day's raid. Between these peak hours there was usually a noticeable lull in incoming and outgoing traffic at the bivouac and periods when there were no ants travelling along the trail. There was a lapse of activity for 135 minutes on one occasion. When the ants returned to the bivouac in the late afternoon or early evening, they paraded in single file, head to tail, and at a fairly steady pace. Although the column initially meandered through the forest, the ants tended to slowly straighten out the curves. They generally continued true to the compass direction in which the day's raid began.

Army ant columns are subject to a variety of natural disturbances, such as insects and other animals crossing the column, rain striking the ants or washing substrate away. Many species when alarmed, send majors or soldiers to the site. E. rapax on the other hand, usually retreated when disturbed and hid until the danger had passed. A limited number of majors, not carrying anything, usually were attracted to the area. Apparently an alarm pheromone was released at the site of the disturbance, and the ants converging on that area would not pass this chemical barrier. The majority of ants, however, never reached the point of alarm, because as the ants doubled back

they alerted others, and those ants also immediately turned around. Some of the workers, nevertheless, did not get the message and barreled right through the disturbed area. The column responded like a sock being pulled inside out, for the ants travelling along the trail turned outwards, peeling back along each side of the column. They continued retreating, sometimes as far as 10 to 15 m, until they found a convenient place to hide in the ground litter. With an even greater stimulus they scattered in all directions, causing even greater confusion and also an increase in the speed with which they retreated. Under those conditions, the ants laid down more alarm substance over a greater area, and more majors converged on the site.

During the afternoon of statary days, the first workers usually returned to the bivouac without prey between 5 and 6 PM. The greatest number of ants arrived between 6:45 and 8:00 PM. Prey usually arrived about 6:00 PM, with the greatest concentration between 6:30 and 7:30 PM. These figures were based on data collected during the last 10 days of the statary period.

Near the end of the raid column, the ants came along in waves of from 2 to 15 ants with individual ants arriving intermittently. The raid column almost always ended abruptly within a 5-minute period when not disturbed. Near the end of the raid column, a series of workers usually carried other conspecific workers who were tired, injured or missing limbs. As many as 15 to 20 workers being carried were counted in half an hour.

Selected graphs (Figs. 3-5) depict the proportion of rapax (E-720) leaving and returning to the bivouac during three of the last five days during the statary phase. Each graph includes: (1) the number of unladen ants leaving the bivouac per minute; (2) the number of unladen ants returning to the bivouac per minute; and (3) the number of ants carrying prey returning

to the bivouac per minute. From these and other graphs a number of trends can be seen: (1) there is usually a lull in the movement of ants travelling between the bivouac and the raid front during the late morning to afternoon, with only an occasional ant sometimes being seen; (2) the booty being brought in is usually concentrated in a specific area of the column and most of it arrives within a limited time period toward the end of the raid; (3) there is a peak in the number of ants returning without prey near the end of the raid after most of the prey is brought in; (4) the incoming raid column stops abruptly, usually within 30 to 45 minutes after most of the prey has arrived; (5) all workers were back at the bivouac before 9 PM; and (6) the greatest concentration of army ants returning to the bivouac occurs between the hours of 6:30 and 8:00 PM. Also at this time there is a minimal flow of workers leaving the nest.

Booty Caches

While army ants are raiding, much of the prey is temporarily deposited in areas called booty or prey caches along the raid columns. These were usually small and on the ground beneath leaves, palm fronds, within hollow palm fruits, and once within a decomposed log. Six booty caches were sampled from three rapax colonies. Approximately 60% of the 256 pieces of prey collected from these caches contained ants of the genus Odontomachus. Gigantiops was the second most abundant genus collected, comprising 26% of the prey, while Neoponera was third with 8.6%. Dolichoderus, Camponotus, and Pachycondyla together formed the remaining 5.7%. The largest booty cache contained 66 prey items. The average number of items per cache was 43. Most caches are probably much smaller since these represented the largest caches found.

Prey Species

Eciton rapax preyed upon a number of species of ants and wasps within the tropical rain forest. The prey examined was taken from raid columns, emigration columns, booty caches, and bivouacs. The columns were sampled by picking up workers along with their prey. Small pieces of prey, not as easily seen as large ones, were probably not sampled as often. On some occasions the column was sampled only to get an idea of what was being raided. No sample is considered to be a totally random assortment of prey, but must be judged only as a collection of what rapax was raiding on that particular day, and at that, may not include all of the species raided. Booty caches probably contain more of a random assortment of prey than columns since they accumulate prey over a period of hours, and many of the collections from columns were biased toward large prey.

Ant pupae were by far the most common form of prey rapax carried to its bivouac. No estimates were made of the number of individuals in an attacked colony that were killed or captured, eaten on the spot, ignored or abandoned. Cocoons containing pupae were identified when possible.

At Limoncocha 21 different colonies of rapax were found during 1967 (7), 1970 (12), and 1971 (2). Data from 1967 and 1971 were obtained from Rettenmeyer and Naumann. Prey was collected, at least once, from 16 of the 21 colonies.

The major part of the diet consisted of ants belonging to the subfamilies Ponerinae, Formicinae, and Dolichoderinae, in order of decreasing abundance. A total of 1151 ants belonging to the subfamily Ponerinae, representing a minimum of 15 species, were collected on 139 separate occasions. From the subfamily Formicinae, there were 490 ants collected on 55 occasions represent-

ing 20 species. Two species from the subfamily Dolichoderinae totaled 119 individuals.

Three of the 5 genera of Ponerinae raided made up the bulk of the samples. In order of decreasing abundance, they were: Odontomachus, sampled on 81 occasions; Neoponera, sampled 35 times; Pachycondyla, collected on 16 occasions; Ectatomma, collected 4 times; and Paraponera, collected on 3 occasions. The next most important subfamily, Formicinae, was represented by 2 genera; Gigantiops, collected on 20 separate occasions; and Camponotus, collected on 35 occasions. The remaining subfamily, Dolichoderinae, is represented by the single genus, Dolichoderus, sampled on 29 occasions.

The only other important prey were wasps belonging to the family Vespidae, subfamily Polistinae. They were taken in relatively large numbers on three occasions, and collected individually from raid columns from time to time.

The most common genera of prey are discussed in approximate order of decreasing frequency. Within each genus, the species are discussed alphabetically.

Formicidae : Ponerinae

Odontomachus. Of all the insects preyed upon, Odontomachus was by far the genus most frequently raided. A total of 8 species were identified, 2 of which are possibly undescribed. In all, 225 adults, 503 pupae, and 109 larvae were sampled from 16 rapax colonies. Of these, 215 adults, 20 pupae, and 1 larva were identified to species. Males were collected but could not be identified. Approximately 140 pieces of adult Odontomachus were pinned from prey samples but were not identifiable. Thus a total of 989 Odontomachus prey items were collected, including males. Of the total number of Odontomachus

collected, only 28% were identifiable.

Odontomachus bauri, common to the forests of Costa Rica, Panama, Venezuela, and Colombia, was raided by only one colony of rapax (E-720). All 15 adults were identified from 6 of the 23 raid columns sampled. This was one of the least frequently raided species of Odontomachus.

O. bauri, as far as is known, is mainly a terrestrial species, nesting in the leaf mold at the base of large forest trees, especially buttressed ones, and under rotten logs (Brown, pers. com.).

Odontomachus haematodus adults (n=47) were collected from 50% of the rapax colonies sampled. O. haematodus, the most frequently raided prey species, was collected on 21 occasions, 18 of which were from raid columns. Prey samples from colony E-720 contained haematodus in 12 of 23 raids sampled or approximately 52% of the time.

This ponerine is essentially a ground-nester living under rotten logs and in leaf litter at the base of trees, but will occasionally get into leaf trash in palms or in low-down epiphytes (Brown, pers. com.). Adults and pupae were observed on one occasion being brought down a dead tree by rapax workers.

Odontomachus hastatus was the largest (body length 13 to 17.5 mm) and one of the most frequently raided species of Odontomachus. The majority of the 22 adults were collected from 9 raid columns. They were identified as prey from 14 separate raids by 6 rapax colonies. Adults were collected from raid columns of colony E-720 on 5 of the 23 raids observed. In 1967, 3 of the 7 rapax colonies raided hastatus. In 1970, prey samples analyzed from colony E-742 showed that hastatus adults were captured on the 4 days the colony was sampled.

This ant species is usually semi-arboreal and is known to nest in trash

in palms, in bromeliads and even at or near ground level (Brown, pers. com.). A small, damaged, carton nest of hastatus was observed on a folded palm leaf about a meter above the ground in understory vegetation. When attempts were made to collect it, the ants quickly dispersed in all directions (Naumann, pers. com.).

Odontomachus mayi is similar in morphology to O. panamensis but is larger. Adults (n=8) were collected on 6 occasions from raid columns from 2 of the 8 colonies of rapax sampled in 1970. It was not collected in 1967 or in 1971. O. mayi was collected from colony E-720 prey samples on only 4 of the 23 times the colony was sampled.

This infrequently raided species is arboreal and lives in epiphytes and ant-gardens, often in parabiosis with a red Dolichoderus (Brown, pers. com.).

Odontomachus minutus was the smallest species (body length 7 to 10 mm) of Odontomachus preyed upon by rapax. It was the second most frequently raided Odontomachus species from the standpoint of the number of adults (n=30) identified. Adults appeared as prey in columns on 13 occasions and once were taken from a booty cache. About 44% or 7 of the 16 colonies of rapax sampled contained minutus, while approximately 30% or 7 of the 23 raids sampled from colony E-720 contained this species. Three adults were collected from 3 different colonies in 1967.

This species is also primarily a ground-nester. Rotten logs and piles of leaf litter at the base of trees are preferred sites (Brown, pers. com.).

Odontomachus ruginodis adults (n=57) appeared more frequently in raid columns (n=21) than any other species of Odontomachus. The adults were collected from raid columns on 9 occasions and from booty caches on 2 occasions. O. ruginodis adults showed up in 7 of the 23 raids sampled from E-720 or

approximately 30% of the time. It was collected from 4 of the 16 colonies of rapax.

Odontomachus striativentris is one of the largest (body length 12.5 to 14 mm) Odontomachus raided by rapax. It was collected from 3 of the 16 rapax colonies sampled. In all, 32 adults were collected exclusively from raid columns. Records from colony E-720 showed adults in prey samples on 6 of 23 occasions sampled, or approximately 26% of the time. From each of the 2 remaining rapax colonies, one striativentris adult was identified. This species did not appear in prey samples from 1967.

This large striate species is also primarily a ground-nester living at the base of large, especially buttressed forest trees, and also in leaf litter and under fallen, decomposing trees. On one occasion an adult was collected on a leaf with a pupa between her mandibles, apparently fleeing from rapax.

The taxonomic status of striativentris is somewhat nebulous; the specimens collected as prey are possibly not striativentris, but that of an undescribed Neotropical species widely distributed in the Amazon Basin (Brown, pers. com.).

Odontomachus species 15, is a large (body length 13.5 to 14.5 mm) undescribed species. Adults (n=3) were collected the least frequently of any species of Odontomachus. One adult was collected from a raid column of colony E-720 while the remaining adults were taken from another rapax colony from a booty cache within a rotten log.

One subterranean nest of this species was located at the base of a tree, one entrance of which was possibly a small hole in the ground around which rapax workers were clustered. E. rapax was observed entering and leaving the entrance, but no prey was seen. It is not known if rapax was successful or

not in raidng that nest or if the entrance was in fact that used by this species. The nest was later excavated, and a few adults and brood were collected.

On reviewing specimens of this species, Brown noted that it was a widespread, undescribed Amazonian species.

Portocarrero (1965: 28) observed the subterranean nest of O. chelifer (Latreille) in Peru while it was being raided by a column of rapax and noted that as the army ants carried away cocoons, the ants did not attempt to defend their nest. O. chelifer was not recorded from any of the booty samples nor is it known if it occurs in eastern Ecuador.

Neoponera. Eleven of 16 colonies of rapax sampled raided this genus. Of the 230 specimens collected, all but 20 individuals came from raid columns. Of these, 28 adults and 114 pupae were divided into 4 species. The identification of larvae and larviform pupae was not attempted. The unidentified Neoponera specimens totaled 88 individuals.

Cocoons were the most abundant form of Neoponera collected. The largest individual sample of this genus collected from one raid contained 17 pupae taken from one booty cache. Of the specimens collected, 61% were not identified.

Approximately 38% of the Neoponera individuals were not identified to species. The majority of these specimens were larviform pupae (n=70) or larvae (n=17) collected from 11 of the 16 colonies sampled. One unidentified male adult was also collected.

Neoponera crenata, smaller than the next species, is represented by only 2 adults and 2 pupae. They were collected in 1970 from 3 separate rapax raid

columns.

N. crenata nests in hollow plant cavities such as stems and canes and has nests in the ground and in trees (Brown, pers. com.).

Neoponera pedunculata was collected on 13 occasions or about as often as the next species. N. pedunculata was raided by more rapax colonies (n=6) than any of the other Neoponera species. From 5 of these colonies, pedunculata was collected from only one raid, while for the remaining colony, E-720, 8 out of 23 columns sampled contained this species. A total of 16 adults and 31 pupae were identified.

The only character known for distinguishing this species from N. villosa is the difference in the form of the petiole.

Neoponera villosa adults appeared as prey in 25% of the rapax colonies sampled. Specimens were collected from 10 raid columns and one booty cache containing 17 pupae located within a decomposing log. Ten adults and 54 pupae were collected from 4 different colonies. N. villosa appeared in 7 of 23 columns sampled from colony E-720 or approximately 30% of the time. Only one pupa was collected in 1967.

This species ranges from southern Texas to northern Argentina and it nests in the soil, in logs, stumps, and hollow trees, branches, and epiphytes. The workers, which sting severely when disturbed, forage for insects during the day, often in bright sunlight (Muesebeck, et al. 1951: 785).

Neoponera species 21 is known from 27 pupae collected on 8 occasions from columns of 5 colonies of rapax. On 4 occasions this species was collected from one raid from each of 4 different colonies, while for colony E-720 this prey species was collected from 4 of the 23 raids sampled or approximately 17% of the time. Three pupae were collected in 1967.

Pachycondyla. The largest (body length 19 mm) of 9 species within this genus, P. crassinoda, occurs in Colombia, Venezuela, Trinidad, the Guianas, Ecuador, Bolivia, and Peru (Kempf 1961: 193). It is the only species within the genus known to be raided by rapax.

This species is the largest species commonly preyed upon by rapax. Because of its size and morphology, adults and brood of this species were not difficult to separate from other species of prey in booty samples. In all, 33 adults, 36 pupae, and 8 larvae were identified. Individuals were collected from 11 of the 16 colonies of rapax sampled. P. crassinoda was found in 15 columns, 4 of which were emigration columns, and one booty cache. No other species of ant was raided by as many different colonies of rapax as crassinoda. Prey samples from colony E-720 showed that crassinoda was collected only 3 times. Raid columns of colony E-772 contained this species on the 4 occasions this colony was sampled.

P. crassinoda nests in the ground under logs (Brown, pers. com.).

Ectatomma. One species of Ectatomma is known from Limoncocha, and it was found among the prey of rapax. These Ectatomma adults are 11.7 to 11.9 mm long, within the size range of common ponerines captured by rapax.

Ectatomma tuberculatum adults (n=4) were taken from 3 separate raid columns of colony E-720 in 1970, and once from colony E-532 in 1967. These adults were possibly captured by rapax workers while foraging. E. tuberculatum is one of the most commonly seen ants at Limoncocha since its foragers frequent the upper surfaces of low plants. It nests underground at the base of small trees and saplings.

Paraponera. The largest worker ant at Limoncocha, Paraponera clavata,

(body length 18 to 26 mm) was taken from columns of E. rapax on 3 separate occasions in 1970. The first one, mostly intact except that both front tibae and the hind right tarsal segments were missing, was collected from a raid column. The second one, decapitated and dismembered almost beyond recognition, the remains of which were a partially cleaned out thorax and intact abdomen, was collected from an emigration column. The last individual was identified from a petiole and gaster picked out of a raid column. It is not certain whether the nest of this species was raided, or if the workers were captured alive or injured away from their nest.

The only other army ants that are known to kill this species are E. dulcius and E. burchelli, although it is very unusual for E. burchelli to successfully kill P. clavata. P. clavata appears to be avoided by E. hamatum (Rettenmeyer 1963).

P. clavata nests at the base of trees and was found on many occasions nesting at the base of spiny palm trees.

Formicidae : Formicinae

Gigantiops. The highly distinctive Neotropical formicine, Gigantiops destructor, was sampled from 9 different colonies of rapax and 20 separate raids. Raid columns yielded the greatest number of individuals, (n=137), while 5 booty caches had 66 specimens. Pupae were by far the most abundant stage collected (n=193) with an additional 11 adults and 11 larvae rounding out the total. For colony E-720, 48% or 11 of the 23 raids sampled contained Gigantiops.

This ant species lives in subterranean colonies that can number over 1,000 individuals (Kempf and Lenko 1968). When their nest was raided, the

adults fled carrying eggs and larvae between their mandibles much in the same manner as Dolichoderus adults. Very few pupae were observed being carried in this manner. The adults fled the nest and ascended the vegetation and leaped from leaf to leaf until they were out of the range of the army ants. There they stood or walked about until the danger had passed. When collected with an aspirator they gave off a strong formic acid odor.

E. hamatum on a number of occasions also raided Gigantiops and there appears to be heavy predation pressure upon Gigantiops by the 2 species of army ants in eastern Ecuador.

Kempf and Lenko (1968: 228) stated that G. destructor usually enters into a parabiotic relationship with the formidable ponerine, Paraponera clavata. They stated, "Although this association doesn't seem to be obligatory, where both species live side by side, there seems to exist, nevertheless, a natural tendency toward it." They also mention that G. destructor never was seen to show any aggressiveness towards P. clavata, preferring to hide or run away if approached, and both species tolerated each other. This parabiotic association was not observed in eastern Ecuador where both species are abundant. Perhaps this parabiosis is characteristic in the tree-covered savanna region in central Mato Grosso, Brasil, but is not present in the rain forest regions which are more typical habitats for both species of ant.

G. destructor is distributed throughout most of the Amazon basin and extends south as far as north or central Mato Grosso, Brasil. The discovery of Gigantiops in eastern Ecuador is the first record in Ecuador and the most western locality for this monotypic genus.

Camponotus. The most diverse genus attacked was Camponotus. Included are at least 18 species collected from 6 rapax colonies. From colony E-720

alone, 16 species were collected. No one species was collected from more than 2 rapax colonies nor was any one species collected on more than 4 separate occasions. All individuals were obtained from raid columns unless otherwise stated. A total of 266 specimens was collected.

Camponotus species 1: all 8 adult workers were collected from rapax colony E-720 on 3 separate occasions in 1970.

Camponotus species 2: six adult workers of this unusual rust colored species were collected from 2 rapax colonies on 4 occasions. All were collected from colony E-720 except for one worker collected in 1967.

Camponotus species 3: this species, perhaps a subcaste or polymorphic form of species 2, was sampled from 2 rapax colonies. One of the 2 specimens collected, belongs to the same sample as 2 adults referred to as species 2. The remaining worker was collected in 1967.

Camponotus species 4: one specimen, tentatively identified as Camponotus (Tanaemyrmex) agra (Fr. Smith), was collected in 1967.

Camponotus species 5: five adult workers of this species, similar to the above specimen but smaller, were collected on 2 occasions from colony E-720.

Camponotus species 6: twelve adults of Camponotus (Myrmothrix) nr. abdominalis, were collected from 2 rapax colonies on 3 occasions in 1970. All of the individuals have large heads, and orange and brown bands on the gaster.

Camponotus species 7: thirty adults were collected from 2 rapax colonies on 3 separate occasions. One of the adults was taken in 1967. This species, somewhat similar in appearance to the preceeding species except in color, shows a greater degree of polymorphism, possibly due to the greater sample size.

Camponotus species 8: one specimen of this large alate species was collected from colony E-720 during the nomadic phase. This ant is similar in appearance to the 2 preceeding species but possesses a different color pattern.

Camponotus species 9: two alate individuals of this black shining species were collected from 2 columns of rapax E-720.

Camponotus species 10: this is the largest Camponotus (body length 20 mm) collected from colony E-720. One alate individual was collected.

Camponotus species 11: this specimen is similar in size and appearance to the preceeding large Camponotus workers, except for its large rectangular, grasshopper-like head. This individual was collected from colony E-720 at the beginning of the statary phase.

Camponotus species 12: two alate adults were collected from E-720 in 1970 while the remaining worker was collected in 1967.

Camponotus species 23: two adults were collected from a booty cache of colony E-720.

Camponotus species 24: three alate adults (head and alitrunk) were collected from 2 rapax colonies in 1970. Two of those adults were from colony E-720.

Camponotus species 25: four workers were taken on 3 occasions from 2 rapax colonies. Three adults were taken from colony E-720.

Camponotus species 26: five workers, similar to the above species but smaller and with a scale-like petiole, were collected from a booty cache under the stem of a palm frond on the ground. These ants belonged to a colony whose nest was knocked down while cutting through the underbrush. The nest was composed of 4 large leaves held together by an inner light brown non-elastic rubbery textured membrane. Between the leaves was a labyrinth of

passageways. No brood was seen. This nest was taken for reference collection along with 13 adult inhabitants.

Camponotus species 27: two individuals of this species were collected on 2 occasions; once in 1967 and once from colony E-720 in 1970. This ant builds its carton nests on the under sides of palm fronds and is highly polymorphic in color and shape.

Camponotus species 28: this adult was collected in 1970 from colony E-720 near the end of the statary period.

In addition to the 89 specimens identified to species, there were 177 unidentified items collected from 9 colonies of rapax. They included 1 adult and 10 adult gasters, 153 pupae, and 13 larvae. From 8 of the army ant colonies, Camponotus was collected on only 1 occasion each and for colony E-720 the genus was collected from 12 of the 23 samplings.

Formicidae : Dolichoderinae

Dolichoderus. Two species of Dolichoderus were raided by 7 different colonies of rapax. Adults and pupae were easily identified, but larvae of the two species were impossible to differentiate. Both species have subterranean nests.

Dolichoderus (D.) attelaboides is the best known of the 7 species within the genus. In all, 28 adults, 21 pupae and 4 larvae were taken from 5 colonies of rapax on 11 separate occasions. Of the 16 rapax colonies sampled, 31% contained this prey species. This subterranean ant was present in 5 of 23 samples from colony E-720. Specimens were collected from 9 raid columns, 1 emigration column, and 1 booty cache.

Dolichoderus (D.) rugosus, although raided by the same number of colonies

of rapax as attelaboides, was raided more frequently than the above species. D. rugosus was raided on 18 separate occasions, 13 of which were staged by rapax colony E-720, for a 57% recovery from that colony. Odontomachus haematodus was identified from 12 separate raids from the same colony. Adults (n=56) were the most abundant stage, while 9 pupae and 1 larva were also identified from 13 raid columns, 3 emigration columns, and 2 booty caches.

Adults of D. rugosus were collected on several occasions on leaves with brood between their mandibles.

Vespidae : Polistinae

The subfamily Polistinae contains 25 genera, 21 of which (about 126 species) have their ranges centered in tropical Central and South America (Evans and Eberhard 1970). Three species of Stelopolybia, including one undescribed species, were taken from columns of rapax.

Stelopolybia cuzcoensis was collected on one occasion from a raid column of rapax colony E-720. On 2 July 1970 the first piece of wasp prey was picked from the raid column between 4:30 and 5:30 PM. Observations ended at 1:00 AM the following morning although wasp brood was still being brought in. A total of 439 individuals were taken from the column, 18 of which were adults or nearly mature pupae, 225 pupae, and 196 larvae. Larvae were distinguished from the pupae in that the former still had fecal material in the hindgut. Few adults were seen in the column.

This species is known to nest in hollow cavities in standing trees, and it is possible that large colonies may have over 1,000 adults in residence at one time.

Stelopolybia puraensis was collected from 2 colonies of rapax. One

adult, without wings or front legs, was collected about 2:30 PM from a raid column leading to the nomadic bivouac of colony E-742.

This species was next observed being raided by rapax colony E-720. The nest, impossible to see from the outside, was hanging in a cavity within the basal cone-shaped labyrinth formed by many long supporting roots of a stilt palm. This palm is referred to as 'pambia' by the local Quechua Indians. About 12:00 PM, rapax was first observed entering and leaving this root complex, but the ants were not carrying prey. The wasp nest was not discovered until about 8:30 PM by back tracking along the raid column which was transporting larvae and pupae to the bivouac 10 m away. The nest, 5 to 8 cm above the ground, had a group of workers clustered below it bridging it with the ground.

The nest, at the time it was collected, contained 5 eggs, 68 larvae, and 58 pupae. The cluster of ants below the nest contained 45 pupae. It was later estimated that a maximum of 177 pupae, 100 larvae and 50 eggs had been removed by rapax workers. A swarm of 36 wasps was collected about 3 m from the nest hanging on a leaf at the tip of a branch about 1.6 m above the ground.

A total of 575 rapax workers were in the nest or on it at the time it was collected. Of these, 548 were old workers and 27 were callows. Approximately 3% were workers under 5 mm in length. Only about 5% of the ants actually participating in the raid within the nest or clustered below it were callows. The rapax colony was in its 6th nomadic day.

It is probable that rapax had raided the nest earlier that day, but waited before transporting the prey to the bivouac. The small size of the wasp swarm suggests that a portion of the adults may have flown away earlier. It is also interesting to note that few eggs were present in the cells of the

wasp nest, and if rapax had in fact occupied the nest several hours before removing the brood, they would have had time to eat the eggs. The question remains as to why rapax had apparently waited so long before transferring their prey to the bivouac.

S. paraensis on a separate occasion, was observed carrying away bits of snake meat from a recently dissected skull. They probably took it to their nest where they fed it to the brood. This is possibly why the above nest, when dissected, emitted such a pungent, fetid odor.

Stelopolybia species 22 was collected from one raid column of colony E-720. One adult, 21 larvae, and 5 pupae were collected from 3 samples taken at different times of the day beginning at 11:20 AM.

Sphecidae : Trypoxyloninae

Trypoxylon. One female of Trypoxylon superbum was collected from a raid column of E-720 about 4:45 PM on 23 July 1970.

Bivouacs

Schneirla (1971) stated that there are contrasts in the degree of bivouac specialization among epigaeic doryline genera. Eciton generally forms complex hanging bivouacs capable of much internal structural and behavioral differentiation. E. burchelli and E. hamatum are considered epigaeic species because most of their bivouacs are found above ground and the majority of their colony activities take place on or above the forest floor. Schneirla stated that rapax was perhaps the most hypogaeic species within the genus and thought this might be related to the fact that it is the one Eciton in which major workers lack great tong-shaped mandibles. Although Schneirla

never observed rapax, he concluded that they would be less able to defend themselves against vertebrate predators than the other better equipped Eciton species, and had consequently become hypogaeic (Schneirla 1971: 61). No bivouac locations for E. rapax are mentioned in the literature.

Statary Bivouacs

Three statary colonies of rapax were found in 1970 at Limoncocha, and all were bivouacked in quite different locations. One was subterranean within an Atta colony, another above ground within the trunk of a fallen tree, and the remaining one within the basal portion of a cut stump.

C. W. Rettenmeyer in 1967 and M. G. Naumann on a number of occasions since have observed rapax living with Atta at a number of sites at Limoncocha. The author's observations indicated that E. rapax and Atta were compatible even though other species of Eciton have been observed raiding and carrying away Atta pupae and larvae (Rettenmeyer 1963, Torgerson and Akre 1970: 399, Schneirla 1971: 159).

E. rapax colony E-720 lived in the nest of Atta cephalotes opaca for at least 27 days. In 1967 Rettenmeyer found rapax colony E-540 bivouacked in the same Atta nest. An attempt at that time to locate the bivouac was unsuccessful after excavating part of the Atta nest to a depth of 40 to 45 cm. The Atta nest was located approximately 660 m in the forest along the trail which runs northwest from the Limoncocha commissary.

The Atta mound was oval and covered an area 9.0 to 10.5 m in diameter with a large buttressed tree on the western edge (Figs. 6-7). There were 10 recognizable entrances to the nest, but only 5 were used at any one time by rapax. The highest point on the mound was located on the north side of

the tree, 61 cm above the surrounding terrain. The irregular mound sloped away from the tree and was kept free of most low vegetation and leaf litter by the leaf-cutter ants. It was composed of little clumps of reddish-brown lateritic soil that had been carried out as the Atta constructed underground chambers. The mound had become well compacted over the years and one could walk on top without sinking in, except for a few places where there was fresh soil or a thin roof on an underground chamber.

The Atta mound was shared by a number of other insects. There was a single colony of Paraponera clavata adjacent to the buttressed tree, but the colony was rather small and never interfered with observations. Around the base of the buttressed tree were 6 colonies of stingless bees, Trigona (Partamona) testacea testacea, with soil turrets all facing away from the tree. Neither the Trigona nor the Paraponera were ever seen to be molested by Atta or E. rapax workers, although the Trigona occasionally were captured by other species of ants, e.g. Pachycondyla. Above the Atta nest in one of the trees was a colony of dolichoderine ants that occasionally descended and disrupted observations. They were attracted to the presence of sweat, and were almost constantly licking it off field sacks, clothing, tools, etc.

The location and depth of the rapax bivouac within the Atta mound is not known, although probably it was deep within the ground. Eidmann (1936) observed Neivamyrmex orthonotus 4 m below the surface in the fungus chambers of an Atta nest. E. rapax usually used the entrance facing the direction they raided on any particular day. The army ants were observed on June 18 entering one northern entrance that Atta workers were using simultaneously to carry out soil. That entrance was never used again by colony E-720, although it appeared to be one of the biggest entrances. E. rapax was never

seen using entrances that had heavy leaf-cutter activity and were seldom seen travelling for any great distance along Atta trails.

On a number of occasions E. rapax was observed crossing Atta cephalotes columns without incident. Once, when leaf-cutter activity was fairly heavy, 4 medium-sized rapax workers were spaced at intervals of an ant and a half apart the width of the 10 to 12 cm wide leaf-cutter column. Other rapax crossed over, apparently using the stationary ants as guides although they would always drift in the direction of heaviest flow of Atta traffic. Usually, rapax transversed the column by weaving around the Atta workers and soldiers. Atta never slowed up for rapax workers, who always yielded the right-of-way. On either side of the leaf-cutter column there was a pile-up of rapax waiting to cross, but once having crossed they would resume their normal gait.

Colony E-737 was discovered on 14 July in a statary bivouac in a fallen tree in a cultivated yuca, papaya and banana grove (Fig. 8). A Quichua Indian reported the ants had been there about a week, but detailed observations were not made on this colony before 14 July 1970. The forest around the grove had been cut, and at that date there were dense patches of second growth at least a year old alternating with cultivated areas. The main trunk of the fallen tree was 60 to 68 cm in diameter, 20 m long, and split by at least 4 major cracks and many minor ones. Being severely splintered and fractured, it provided numerous protected chambers for the ants. The log had been there at least several months judging from the decay and passalid beetle pupae and adults in it.

On 14 July, 30 rapax workers were seen standing inside the log on the split edge at the west end of the bivouac area. The slightest disturbance

caused them to come running out. There were more than 50 cocoons and ant heads (probably all booty) in a refuse deposit 60 cm in length along this split. Only 4 to 5 dead rapax workers were found in this refuse deposit along with various living arthropod scavengers. Additional empty cocoons and a little refuse were seen scattered about 1 m under the bivouac area where workers were seen. Aspiration at the refuse deposit caused workers to rush out. Between 3:30 and 4:10 PM a weak raid column extended as far as 10 m from the bivouac, but it ended soon afterwards.

There was no raid on 16 July at 8 AM when we arrived. From 8:00 to 9:30 AM, during intermittent light rain, Naumann, Rettenmeyer, 2 Quichuas, and I cut up the tree with the aid of a chain saw (Fig. 9). Before the cutting commenced, rapax workers could be seen hanging and clustered in several cracks. The first cut was made 3.5 m from the base of the trunk, and the dense fractured wooden planks were easily lifted off one by one. In spite of this tremendous disturbance of their nest, the ants did not swarm out or show any massive aggressive behavior towards us as E. burchelli would have. Successive cuts were made clear through the log at meters 7.9, 10.5, and 14.6. The temperature varied between 25°C on the outer edge to 27°C in the middle of the log between the planks, while the ambient temperature was 23°C.

Cocoons of rapax brood were usually found in the center of the log lying on flat surfaces between the split boards. The first big cache of cocoons was between 2.5 and 5 m from the base of the trunk. Between m 2 and m 3 the wood was quite wet with considerable amounts of soil and organic debris upon which the cocoons were lying. Between m 3 and m 5 the substrate was drier. Between m 5 and m 8 the cocoons decreased in numbers probably due to the decrease in space between the boards. At m 8 the ants had to exit because of

the absence of internal passageways but reentered the trunk at m 10.5, where the fracture continued to m 14.6. Workers and cocoons were also discovered between m 10.3 and m 11.2 on the underside of the log between the bark and the trunk. The cocoons were a mixture of all sizes and not segregated according to size.

The physogastric queen was discovered about 9:10 AM at m 12.5 walking south with a relatively small group of workers accompanying her. She was immediately put into a separate plastic bag with about 50 workers. The wood where she was discovered was dry and 25°C. The presence of eggs in the log near her suggested that she had probably been in that section for some time before being collected. The smallest workers were first found with egg brood at m 7 where the wood was also relatively dry, and many were collected with eggs still clutched between their mandibles.

In the laboratory nest the queen actively ran around but was not as active as the contracted queen from colony E-731 collected July 10 and still alive in a laboratory nest. She continued laying eggs throughout the day, even while being photographed, 10:20 to 11:45 AM and while etherized, 3:00 to 3:50 PM. From 3:00 to 3:10 PM she laid 7, 4, 13, 6, and 7 eggs in one-minute periods. The next morning at 7:15 AM she was found on her side with her legs twitching. She was immediately preserved along with the eggs she oviposited in the lab nest.

The only myrmecophiles found in the area of the queen and eggs were Trichatelura and numerous small limulodid beetles. Trichatelura and Vatesus adults were taken in areas with cocoons, but no limulodids were seen.

Colony E-772, discovered on August 18, had a statary bivouac within a cut stump of a large tree with a central hole about 10 to 13 cm in diameter.

The colony was hanging to one side in a compact cluster about 2 m from the entrance. Beneath the inclined stump was an immense number of empty cocoons indicating the colony was in its final statary days. The colony emigrated from 3:45 until about 6:25 PM when all the ants had left the bivouac. The total emigration time was 160 minutes, a short duration since most emigrations of E. hamatum last at least 4 hours. The queen was not seen.

Nomadic Bivouacs

Five colonies of Eciton rapax were observed during their nomadic phase. Ten bivouacs were above ground and 3 were subterranean. On the first nomadic day, 29 July 1970, colony E-720 moved 166 m from the statary bivouac site to within the hollow trunk of a fallen and partially decomposed 'pambil' palm tree. The main body of the bivouac was seen plugging the entire cavity about 2 m from the entrance. A smaller cluster of ants was hanging in front of it. The bottom of the log was partially filled with water-soaked decomposing organic matter. There was also a cache of prey about 1 m from the entrance and empty pupal cases littered the bivouac floor. Once the log was accidentally jarred and the ants, mostly callows in a small cluster, began heading towards the open end of the log in a massive wave, as though starting an emigration. After about 5 minutes they settled down and reformed along one side of the roof of the log. The log, heavily saturated with a noticeable rapax colony odor, was abandoned after two days on the 3rd nomadic day.

The bivouac made on the 3rd nomadic day was located under the base end of a large, old and weathered buttressed log lying on its side. Beneath the log the ground was very moist with a great accumulation of spongy organic debris, mostly rotten wood. This site was at the distal end of the raid of

the previous day.

On the 4th nomadic day the colony moved about 145 m to a bivouac well hidden beneath two large palm trees that had recently fallen. The colony remained there for two days (N-5 and 6). On the 5th nomadic day rapax did not begin its daily raid until 9 AM. It was first feared the colony had emigrated the night before, sometime after 7:30 PM when observations on raiding had terminated for the day. Fortunately they were still there, huddled under the palm fronds, and ants came running out when the fronds were disturbed. The ground under the fronds was very wet, but there was no strong colony odor common of enclosed sites.

On the 6th nomadic day the colony moved 180 m to a bivouac divided into 2 parts: one within the standing portion of a 'pambil' palm with the entrance about .75 m from the ground, and the other under or within the partially hollow trunk of the same palm lying on its side.

On the 7th nomadic day colony E-720 moved about 60 m to a huge, 'guayacan' log. The ants emigrated on the 8th nomadic day, leaving from one of the small holes they had entered the previous evening, located about halfway up the side of the 54 cm diameter trunk. The colony was not followed after that date, 5 August 1970.

Three nomadic bivouacs of colony E-772 were observed in 1970. One was within an 8 m long rotting hollow 'pambil'log, 20 cm in diameter. The following day, 19 August, they bivouacked about 100 m north in what appeared to be an abandoned mammal den, partially filled with leaves and tightly closed by roots that had grown over the entrance. Three days later, the colony emigrated about 75 m north into a large active mound of Atta cephalotes opaca. They remained there for at least 3 days before emigrating. This

colony was never observed carrying brood, and the queen was never seen. Workers were always backtracking to previous bivouac sites, sometimes as many as 3 days after they had left the area. Because of this behavior it is believed that the colony had lost its queen, possibly before the statary phase. The colony had many callows.

Colony E-731 emigrated from a subterranean mammal nest, covered with a mound of sticks 50 to 60 cm high, about 200 m through dense vegetation to the base of a stilt palm around which had collected a dense mass of twigs, palm fronds, and other organic debris. A very dense tangle of vines also entwined the tree.

Colony E-738 bivouacked within the basal cavity formed by the roots of a Ficus tree. The vertically hanging bivouac, located about .5m from the entrance, was easily disturbed by hitting any one of the many roots. The colony emigrated that evening about 100 m south, the last ant leaving the bivouac at 9:42 PM. The new bivouac was located along the air strip in an enormous log riddled with numerous tunnels and cavities.

Colony E-742 bivouacked at the base of a small spiny palm tree. The bivouac covered an area of approximately 1 x 1.2 m and was composed of many pockets and chambers partially within the ground, below a pile of loosely packed twigs, leaves, and stems. The colony had very young larvae and when the bivouac was excavated, ants and brood were found scattered evenly throughout the area. The queen could not be located.

SUMMARY AND CONCLUSIONS

Eciton rapax is a large army ant confined to the Amazon basin in South America. It is one of the most conspicuous of the Neotropical army

ants; the head and thorax being gunbarrel blue-black and the gaster a striking yellow-orange color. The species is epigaeic in raiding and nesting but its bivouacs are in somewhat more sheltered locations than many of those of E. hamatum.

E. rapax has only one major raid column system from the bivouac during any one day. Statary raid columns ranged in length from 60 to 270 m. During the statary phase, there often was not a continuous raid column connecting the bivouac and the raid front. The longest interruption in raid column traffic was 135 minutes. The raid front ranged in width of from a few ants up to 10 m including as many as 3 different fronts diverging from one base colomn. Most raiding occurs on the forest floor, but E. rapax sometimes climbs at least 15 m up trees.

When disturbed by people, rapax was nonaggressive and, as a rule, retreated and hid under debris on the forest floor rather than biting or stinging. This timid ant had a fairly weak, innocuous sting, at least to humans, when compared to the sting of E. hamatum or E. burchelli. The largest workers, referred to as majors, lack the formidable recurved mandibles characteristic of the majors of all other 8 Eciton species known from workers.

One colony of rapax (E-720) was followed probably through the entire statary phase of 27 days, and through part (8 days) of its nomadic cycle. This is the longest statary period recorded for any Eciton species. The length of the statary period for E. burchelli varies from 19 to 22 days and that of E. hamatum from 17 to 22 days for colonies with worker broods.

Statary bivouacs were either subterranean, located within an Atta colony, or above ground within a log or stump.

On one occasion during the nomadic phase, they bivouacked in an Atta

colony and twice bivouacked in subterranean mammal nests. Ten epigaeic bivouacs were also observed in locations varying from within hollow trunks of fallen palm trees, to beneath stumps or logs, within the cavernous root complex of a strangler fig tree (Ficus), or at the base of a spiny palm tree in the porous, detritus.

A relatively limited number of genera of Hymenoptera are preyed upon by rapax. Ants (Formicidae) were the primary food, but occasionally wasp nests were raided (Stelopolybia, Vespidae : Polistinae). The genus most often taken from raid columns was Odontomachus, including 8 species. The following genera, listed in decreasing order of abundance as sampled from raid columns, make up the majority of the diet of rapax: Odontomachus (n=81), Camponotus (n=35), Neoponera (n=35, Dolichoderus (n=29), Gigantiops (n=20), Pachycondyla (n=16), and Stelopolybia (n=3). Cocoons with pupae were the most common form of prey found, followed by larvae, adults, and eggs.

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I wish to thank Drs. Naumann for identifying polistine prey, Rettenmeyer for identifying various formicine prey and William L. Brown, Jr., (Cornell University) for identifying most species of the ponerine prey. I also acknowledge Dr. Neal A. Weber for identifying attine ants and Dr. Alvaro

Wille for identifying the Trigona species.

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APPENDIX

THIS BOOK CONTAINS NUMEROUS PAGES THAT WERE BOUND WITHOUT PAGE NUMBERS.

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Fig. 1.--*Eciton rapax*. Top: largest worker or major and smallest worker. Bottom: side view of a major. Note the short mandibles which are atypical for majors of *Eciton* species.

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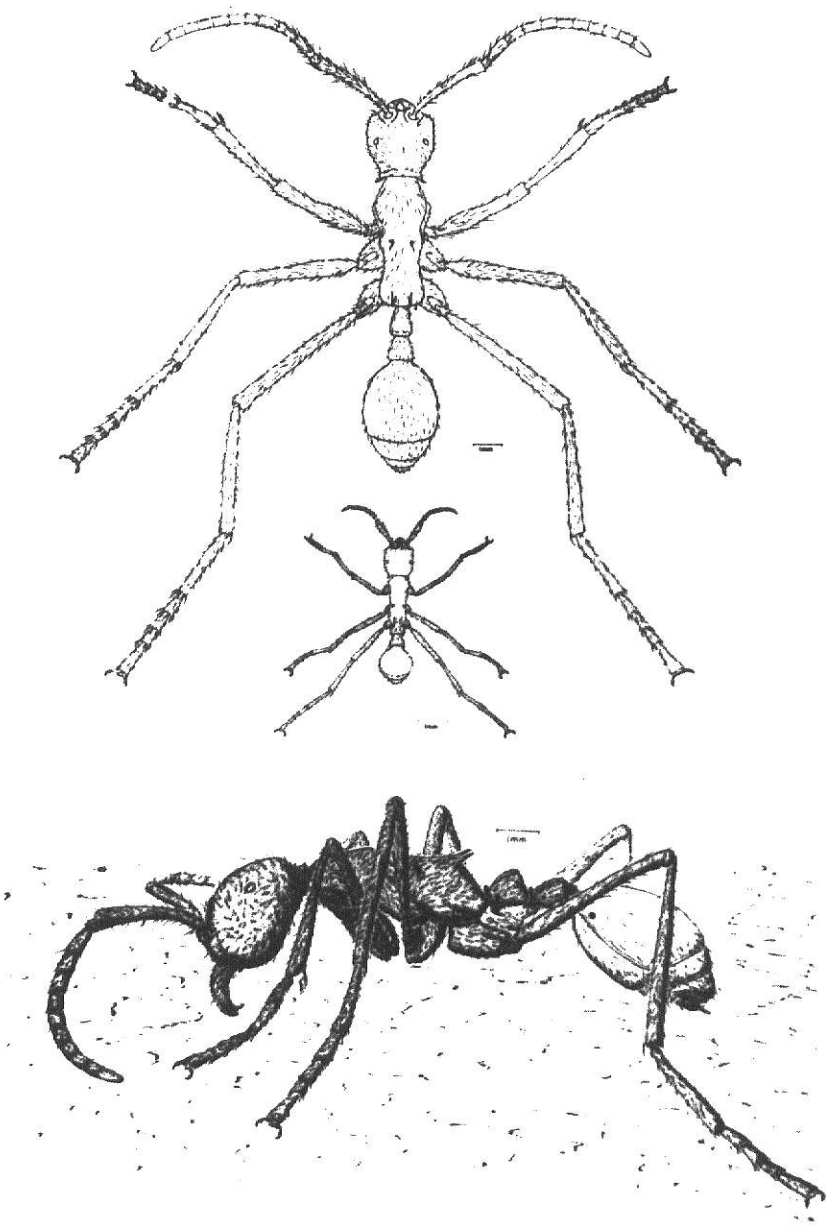

Fig. 2.--Distribution of Eciton rapax. Only localities with known coordinates are plotted and numbered as listed in Table 1. Additional localities are given in that Table. The chain of peaks represents the approximate eastern extent of the Andes Mountains.

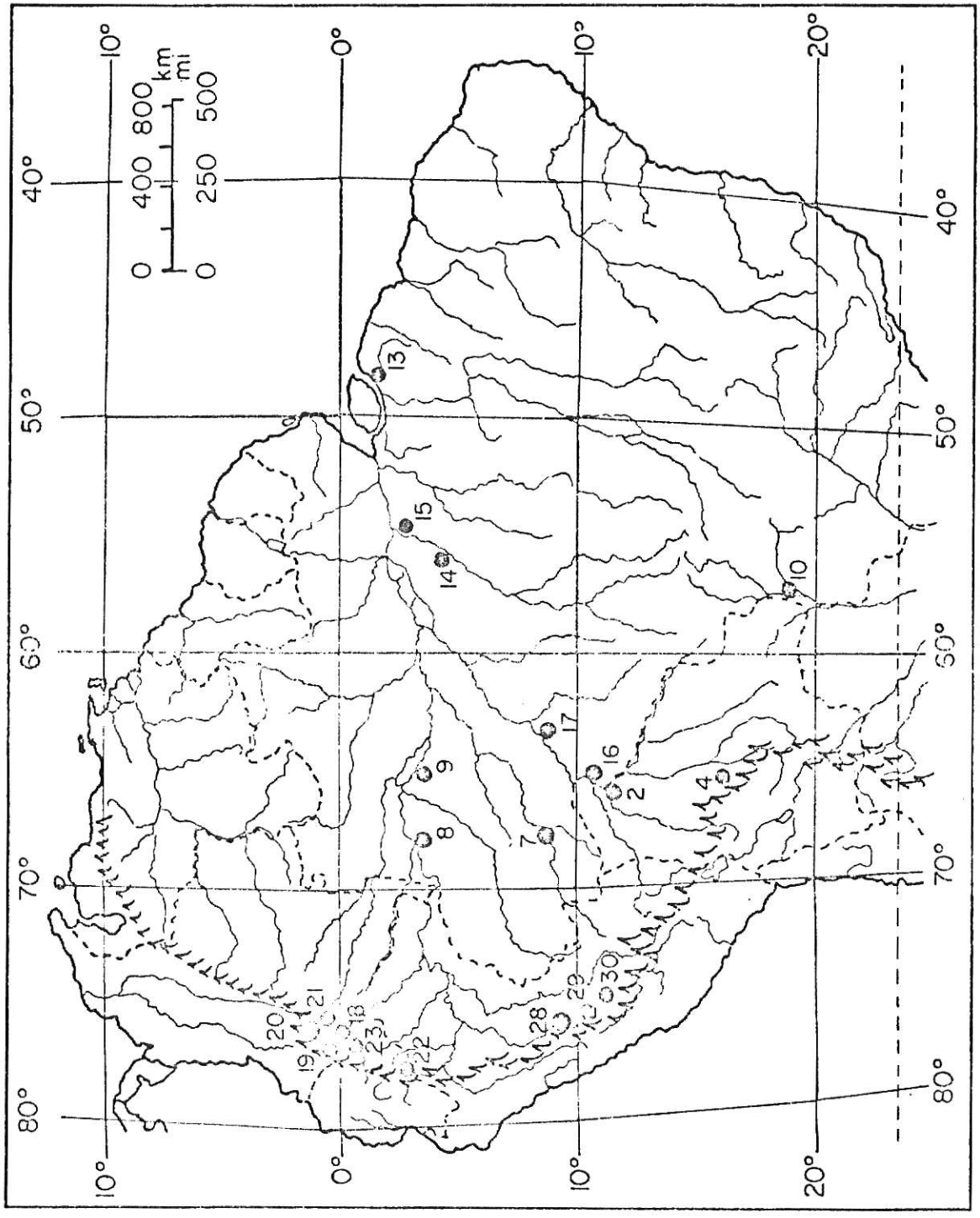
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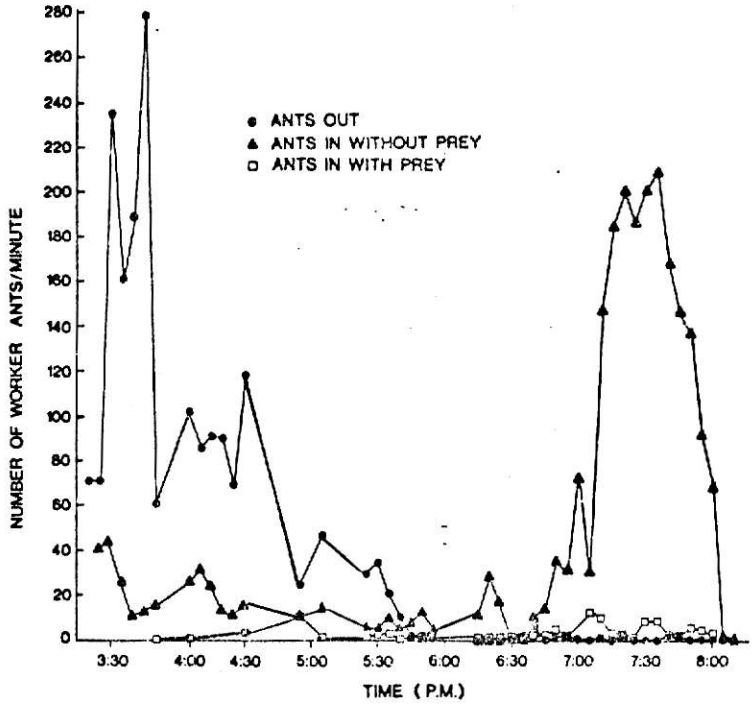
Fig. 3.--Graph depicting the movement of E. rapax (E-720) workers along a single raid column on 24 July 1970 during the statary phase. The only raid of the day began at 3:00 PM.

Fig. 4.--Graph of the movement of E. rapax (E-720) workers along a single raid column on 27 July 1970 during the second to last day of the statary phase. The ants were observed leaving the bivouac at 8:00 AM.

Fig. 5.--Graph depicting the movement of E. rapax (E-720) workers along a single raid column on 28 July 1970, the last day of the statary phase.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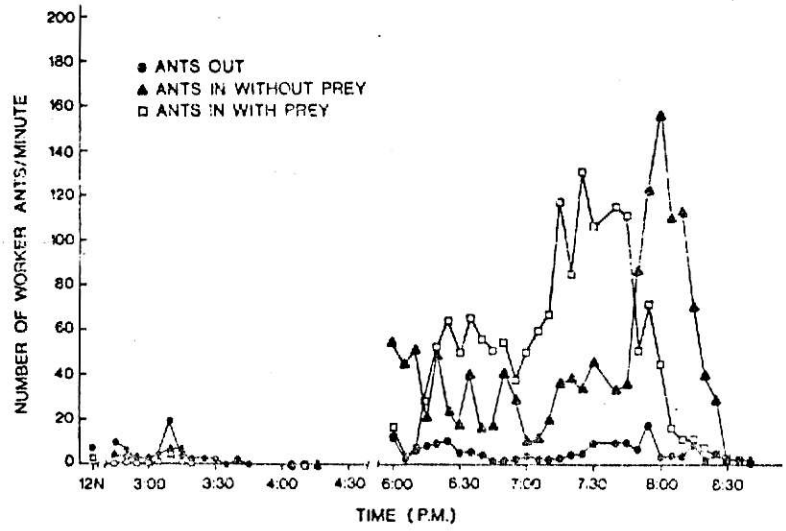
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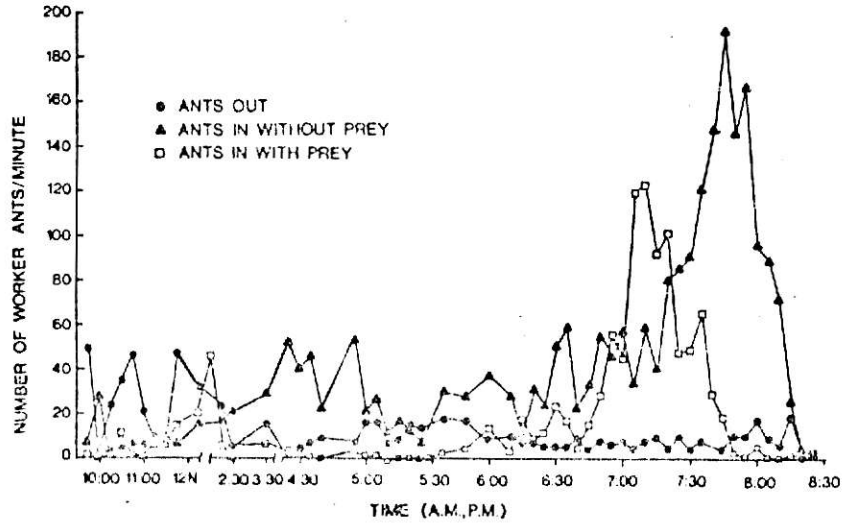
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Fig. 6.--Atta cephalotes opaca nest. Statary bivouac site for Eciton rapax colony E-720 from 2 to 29 July 1970. View looking northeast.

Fig. 7.--Same nest of Atta cephalotes opaca shown in Fig. 6. View looking north.

THIS BOOK CONTAINS NUMEROUS PICTURES THAT ARE ATTACHED TO DOCUMENTS CROOKED.

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Fig. 8.--Statary bivouac site of Eciton rapax E-737. The bivouac was located within the log in a cultivated yuca, papaya and banana grove. The photo was taken 14 July 1970.

Fig. 9.--Statary bivouac site of Eciton rapax E-737 after the log was cut apart on 16 July 1970.

8

9

THE BIOLOGY AND BEHAVIOR OF AN ARMY ANT, ECITON RAPAX

by

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The biology and behavior of Eciton rapax was studied in the lowland tropical rain forest surrounding Limoncocha, Ecuador, at the extreme western extent of the Amazon basin in South America. The mean annual rainfall over a 10-year period, 1961-1970, was 2945 mm. E. rapax has been collected at 30 localities within the Amazon basin and relatively low mountains seem to be effective barriers to its dispersal.

The length of the statary period with worker brood is approximately 27 days, the longest statary period recorded for any Eciton species. The length of the nomadic phase is not known.

E. rapax is a column raider whose raid front ranges in width of from a few centimeters to 4 m and whose single basal raid column forages as far as 270 m from the bivouac in the statary phase. Columns 1 to 3 ants in width are most frequently encountered in the morning until about 11:00 AM and again in the evening from 6:00 to 8:30 PM. Most raiding occurs on the forest floor but occasionally they will ascend 15 m palm trees.

E. rapax feeds upon a relatively limited number of genera of Hymenoptera. Ants (Formicidae) were the primary food. The following genera, listed in decreasing order of abundance, were sampled from raid columns; they make up the majority of the diet: Odontomachus (n=81), Camponotus (n=35), Neoponera (n=35), Dolichoderus (n=29), Pachycondyla (n=16). Occasionally wasp nests (n=3) of Stelopolybia (Polistinae) were raided. Cocoons were the most common form of prey taken, followed by larvae, adults and eggs.

Statary bivouacs were either subterranean, within an Atta colony, or above ground within a log or stump. Nomadic bivouacs were also subterranean, within an Atta colony or mammal nest, or epigaeic within the root complex of a strangler fig tree (Ficus), at the base of a spiny palm tree, within the hollow trunk of a fallen palm tree, or beneath stumps or logs.

The largest workers of rapax are referred to as majors but they lack the formidable recurved mandibles characteristic of the majors of all other 8 Eciton species known from workers. Their behavior is similar to that of the majors of other Eciton species.