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BEHAVIOR OF THE ARMY ANT *Eciton burchelli* WESTWOOD (HYMENOPTERA FORMICIDAE) IN THE BELEM REGION. II. BIVOUACS.

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ABSTRACT

This paper is based on studies of *E. burchelli* and *E. hamatum* behavior in the Amazonian forest, carried out along two years. The core is the analysis of *E. burchelli* and *E. hamatum* nesting and their variation in a tropical rain forest.

Several bivouacs were recorded of eight *E. burchelli* colonies and one of *E. hamatum*. We observed the types of bivouacs locations, bivouac patterns, exposure degree, duration of the nomadic bivouacs and distances between the bivouacs. These characters are related to the colony condition and seasons. A comparison is made between the species studied and also with the data obtained at Barro Colorado Island by other authors.

RESUMO

O trabalho baseia-se em observações feitas sobre o comportamento de *Eciton burchelli* Westwood e *Eciton hamatum* Fabricius na região Amazônica, Belém, PA. durante os anos de 1966-1968. O objetivo do presente estudo refere-se ao processo de nidificação de ambas espécies e de suas variações de acordo com o tipo de mata, épocas do ano e condições internas da colônia.

Durante o período de estudo fizeram-se as seguintes observações: tipo de locais utilizados para nidificação; padrões dos ninhos ou bivaques; grau de exposição; duração dos bivaques nômades e distância entre os bivaques estabelecidos durante a fase nômade. Estes caracteres foram relacionados com as condições das colônias das espécies estudadas. bem como com as estações do ano. Fizeram-se comparações dos resultados obtidos com os já coletados por outros autores na Ilha de Barro Colorado, Zona do Canal.

INTRODUCTION

The Neotropical ants of the tribe Ecitonini share with the Dorylinae of the Paleotropical region a carnivorous diet, a nomadic life cycle and large sized colonies (not below 100,00 individuals to hundreds of thousand or even millions in some species).

Because the diet of army ants consists almost, if not entirely, of the flesh of other animals, these ants present a complex pattern of life in which the capacity of establishing permanent nests has been lost or very extensively modified. The army ant nest or "bivouac" (Schneirla, 1933, 1938) is temporarily formed by the ants own bodies, without the manipulation of foreign materials.

The studies of the bivouacs as an adaptive factor in the terrestrial species of the army ants *E. burchelli* and *E. hamatum*, were developed at Barro Colorado Island by Schneirla (1933, 1971), Schneirla, Brown and Brown (1954) and Jackson (1957). In these papers detailed discussions of the formation and internal composition of bivouacs have been published.

According to Schneirla, Brown and Brown (1954), the bivouac is a key factor for the adaptation of the *Eciton* species to nomadic surface life. These authors also proved that the bivouacs differ strikingly in relation to the activity phase, the nomadic bivouacs being more exposed to the general environmental conditions than the statary ones, which tend to occur within a natural cavity. The internal temperature of the bivouac in both phases is higher and very less variable than the environmental temperature, and the internal microclimatic condition shows more stability in the statary phase bivouac than in the nomadic phase.

Among the environmental factors affecting terrestrial *Eciton* species, the relative humidity is perhaps the most crucial. Schneirla (1971) observed that a relative humidity of 50% or less is lethal for the worker and for the colony also and so the bivouac must provide the colonial microclimate with the necessary adjustments to face the general atmospheric variations.

The present paper is part of a project dealing with *E. burchelli* behavior in the Amazonian forest. These studies were carried out for two years (April 1966 to June 1968) in a forest reserve at the "Instituto de Pesquisa e Experimentação Agropecuárias do Norte" (IPEAN), in Belém, Pará State, Brazil in collaboration with the Smithsonian Institution, Washington. The mentioned reserve was called APEG-Área de Pesquisas Ecológicas do Guamá (Ecological Research Area). For more information about the area (vegetation, annual climate pattern, etc) see Teles da Silva (1975). The core of this paper is the study of *E. burchelli* and *E. hamatum* nesting in a tropical rain forest.

MATERIAL AND METHODS

An identification code number was applied to each colony and consists of the capital letter E followed by Arabic numerals. The colonies were observed daily with the aid of a field assistant.

Several bivouacs of *E. burchelli* colonies (E-O, E-1, E-2, E-2A, E-2B, E-3, E-4, E-14) were observed including one of *E. hamatum* (E-7).* During the observations the following data were recorded: substratum used for the bivouac establishment, colony condition, season, bivouac pattern, relative exposure of bivouacs, bivouac height, duration (hours) of the nomadic bivouac, distances between the bivouacs, etc. The pattern and relative exposure of the bivouac, were described in Schneirla, Brown & Brown (1954) as follows:

a) *Cylindrical* (standard type): when the bivouac cluster tends to be a symmetrical modified cylinder with vertical central axis; the diameter decreasing from top to bottom.
b) *Compound:* cluster formed among many supporting structures to the ground.

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* More details on the studied colonies are in Teles da Silva (in press), Table I.

c) *Curtain:* bivouac formed under the side of a tree log, or interbuttress space of a tree. It has a form of "half-cylinder"
d) *Plug:* the ant cluster closes a cavity of a tree hollow or hollow log.
e) *Pouch:* the bivouac ceiling is usually far from the ground so that the base of the cluster hangs in midair.

Temperature records of all nomadic bivouacs established during one nomadic phase (duration of 12 days) were taken 51 times for the E-O colony. For the nomadic bivouac temperature records were taken daily at different hours, from 08 AM to 18 PM, with 2 hours intervals. The temperature record in each interval is the mean of three sucessive readings. Air temperature was measured just at bivouac level with immersion-type mercury-in-glass thermometers (0-50°C). The internal and external temperatures of a statary bivouac (E-1 colony) were taken at each 2 hours intervals throughout the 24 hours of the day.

RESULTS

A. *Bivouac locations*

During the course of the present study 137 *E. burchelli* bivouacs and 40 of *E. hamatum* were recorded. From Table I, where the results are summarised, it is ascertained that from 114 *E. burchelli* nomadic bivouacs observed the majority was found beneath logs (25%) and in hollow logs (32%). From the 23 statary bivouacs observed 61% were established in hollow trees and 17% in hollow logs. In *E. hamatum* the preferred sites for nomadic bivouacs were beneath logs (35%) and under leaves or tree roots (41%). In this species the establishment of statary bivouacs occurred only beneath logs (50%) or hollow logs (50%).

The above results show the increased plasticity of *E. burchelli* when compared to *E. hamatum* as regards bivouac locations.

B. *Bivouac patterns*

The bivouac patterns described by Schneirla, Brown and Brown (1954) are based upon the manner the cluster of ant bodies hangs from a support to the ground. The standard bivouac pattern for *E. hamatum* and *E. burchelli* colonies is the cylindrical type. But considerable variations occur, mainly related to environmental heterogeneity, colony size and conditions.

For *E. burchelli* colonies the 113 records of nomadic bivouac types demonstrated that the cylindrical pattern is more frequent (47%); the other types were recorded in the following frequency: plug (35%), compound (8%), curtain (2%) and pouch (2%). For the statary bivouac the common pattern was the plug type since in 23 bivouacs 78% were of that type, 13% pouch, 4% cylindrical and 4% curtain.

Variations in bivouac patterns were observed and these were found to be seasonal. Table II shows that in the dry season the bivouac patterns are less variable than in the rainy season. During the dry season, 36 nomadic bivouacs were found to be of four types, the cylinder and plug patterns being more frequent (47% and 42% respectively). In the rainy season the 52 nomadic bivouacs observed were also of the cylinder and plug types but other types, characteristic

TABLE I — Types of bivouac locations used by *E. burchelli* and *E. hamatum* colonies at Belém region. N—P= Nomadic Phase; S—P= Statary Phase.

Type of bivouac site	Eciton burchelli				Eciton hamatum			
	N-P		S-P		N-P		S-P	
	No	%	No	%	No	%	No	%
Beneath log	28	25	2	9	12	35	3	50
Beneath leaves, tree buttresses	21	18	-	6	14	41	-	-
log, tree buttresses, ground vines as suport	21	18	3	13	2	6	-	-
Tree hollow	7	6	14	61	-	-	-	-
Hollow log	37	32	4	17	6	18	3	50
TOTAL	114	-	23	-	34	-	6	-

TABLE II — Patterns of *E. burchelli* bivouacs in relation to colony condition and season. N—P= Nomadic Phase; S—P= Statary Phase.

Bivouac Type	Dry Season				Rainy Season			
	N-P		S-P		N-P		S-P	
	No	%	No	%	No	%	No	%
Cylinder	17	47	-	-	18	35	1	7
Plug	15	42	14	100	22	42	8	57
Curtain	3	8	-	-	3	6	1	7
Compound	-	-	-	-	7	13	-	-
Pouch	1	3	-	-	2	4	4	29
TOTAL	36	-	14	-	52	-	14	-

TABLE III — Patterns of *E. hamatum* bivouacs in relations to colony conditions. N—P= Nomadic Phase; S—P= Statary Phase.

Bivouac Type	No	%	No	%
Cylinder	26	76	3	50
Plug	6	18	3	50
Curtain	2	6	-	-
TOTAL	34	-	6	-

of more exposed sites were also recorded: the curtain (6%), compound (13%) and pouch types (4%). The more drastic difference between the bivouac patterns in the dry and rainy seasons showed up in the statary bivouac. Table II shows that during the dry season the bivouacs are only of the plug pattern; in the rainy season 5 types were recorded the plug (37%) and pouch (29%) being the more frequent ones.

The bivouac patterns described by Schneirla are, of course, intimately related From Table III it is ascertained that in this case there are only three nomadic bivouac types, and all of them form the cylinder pattern. In the statary phase only the plug and cylinder types appear. Unfortunately bivouac records were gathered for this species only during the rainy season.

The bivouac patterns described by Schneirla are, of course, intimately related to the conditions of the bivouac location sites and consequently with the degree of exposure of the bivouacs. Following Schneirla, Brown and Brown (1954) and Schneirla (1971) the exposure of the bivouacs is related to colonial conditions. They also showed the nomadic bivouacs to be more exposed than the statary ones.

During the nomadic phase, a variation in the exposure degree and patterns in relation to the stage of larval development was observed in Belém. Table IV shows that in the first nomadic days the curtain and compound types (more exposed bivouacs) are recorded while in the last nomadic days the plug bivouac (sheltered bivouac) is more frequent. It seems that when the colony has mature larvae, there is a need of increased protection and so the establishment of the bivouacs occurred at more sheltered locations. The same was observed for *E. hamatum*. The cylinder (frequentely exposed) and curtain bivouac are more frequent in the first nomadic days than the plug pattern (See Table V).

C. *Elevated bivouacs*

The most striking difference concerning bivouac locations among Ecitonini species is their position in relation to ground level. The bivouacs of *Labidus praedator, Labidus coecus, Neivamyrmex* sp, *E. rapax, E. vagans,* etc. for example, are almost never exposed above the ground surface. The *E. hamatum* and *E. burchelli* are called "terrestrial species" because the establishment of their nests and daily raids take place practically on the ground level. These species extend their raid columns among the lower and higher vegetation, so the bivouac is not infrequently established in an elevated position.

Table VI shows that *E. burchelli* colonies formed more elevated bivouacs (nomad and statary) than *E. hamatum*. The same table shows that for *E. hamatum* bivouacs above 1 meter were never recorded and that a greater percentage of elevated bivouacs was recorded in the statary phase (17%) than in the nomadic one. Considering all nomadic and statary bivouacs together (12 bivouacs) only one was formed above the ground level. For *E. burchelli* the data of Table VI demonstrate the statary bivouacs to be almost entirely formed above the ground level, since of 23 statary bivouacs, 83% were in elevated locations, and frequently above 1 meter. In the nomadic phase the establishment of the bivouacs occurs frequently on the ground (86% in 114 bivouac records). Elevated bivouacs below and above 1 meter (14%) also occur. The data shows that the colonies of *E.*

Table IV — Bivouac patterns of five *Eciton burchelli* colonies in relation to the nomadic days.

NOMADIC DAYS	FREQUENCY OF BIVOUAC PATTERNS										TOTAL
	Cylinder		Plug		Pouch		Compound		Curtain		
	No	%	No	%	No	%	No	%	No	%	
1º- 3º	12	54	8	36	-	-	1	4	1	4	22
4º- 6º	9	56	4	25	1	6	1	6	1	6	16
7º- 9º	8	33	11	46	-	-	2	8	3	13	24
10º-12º	5	29	7	41	1	6	3	18	1	6	17
13º-15º	1	17	4	67	1	17	-	-	-	-	6
16º-18º	-	-	3	100	-	-	-	-	-	-	3
TOTAL	35	40	37	42	3	3	7	8	6	7	88

Table V — Pattern of bivouacs during two Nomadic phase of *E. hamatum* colony (E-7) in relation the nomadic days.

Nomadic Days	FREQUENCY OF BIVOUAC PATTERNS						TOTAL
	Cylinder		Plug		Curtain		
	No	%	No	%	No	%	
1º- 2º	3	75	1	25	-	-	4
3º- 4º	3	75	-	-	1	25	4
5º- 6º	4	100	-	-	-	-	4
7º- 8º	4	100	-	-	-	-	4
9º-10º	3	75	-	-	1	25	4
11º-12º	1	25	3	75	-	-	4
13º-14º	3	75	1	25	-	-	4
15º-16º	3	75	1	25	-	-	4
17º-18º	2	100	-	-	-	-	2
TOTAL	26	76	6	18	2	6	34

Table VI — Frequency of elevated bivouacs in relation to *E. hamatum* and *E. burchelli* colony conditions.

PHASE	FREQUENCY OF ELEVATED BIVOUACS							
	E. hamatum				*E. burchelli*			
	On ground	Below 1meter	Above 1meter	% elevated	On ground	Below 1meter	Above 1meter	%elevated
Statary	5	1	-	17	4	4	15	83
Nomad	6	-	-	0	98	7	9	14
TOTAL	11	1	-	8	102	11	24	24

burchelli have a greater tendency to establishing their bivouacs at elevated sites. This tendency of *E. burchelli* colonies is ummatched among the doryline ants. No significant differences in the frequency of elevated bivouac formation for *E. burchelli* was noted in relation to the dry and rainy seasons. During the rainy season and when the colony is in a "varzea" forest, the bivouacs are established in elevated conditions during the tide period of the Guamá River (South limit of the APEG Area). This is more evident for the statary bivouac, because the colony settles in a spot for about 20 days. The colony in statary conditions during the tide period of the Guamá River presents several secondary changes of the bivouac, with a gradual evacuation of the ants from the parts of the bivouac gradually reached by the water level. Thus the bivouac becomes elevated and it can change in form and position, e.g., the cylindrical becomes a pouch. The same was observed under the action of rain.

D. *Relative exposure of the bivouac*

The different exposure of the bivouac in relation to colony condition and season was observed by Schneirla (1933) and Schneirla, Brown and Brown (1954). These papers disclosed that statary bivouacs of *E. hamatum* and *E. burchelli* are formed in more sheltered sites, that is, beyond the protection of the mass of clustered ants enclosing the queen and brood, the statary bivouacs have frequently a physical surrounding wall.

After analyses of 114 nomadic bivouacs, of *Eciton burchelli* colonies in Belém, 49% were found to be exposed and 51% sheltered. In the statary condition, of 23 bivouacs 22% were exposed and 78% sheltered. For *E. hamatum* of 34 bivouacs observed 75% were exposed and 15% sheltered; of 6 bivouacs in the statary condition 33% were exposed and 67% sheltered. From the above data it seems that the *E. hamatum* bivouacs are formed in more exposed sites than the *E. burchelli* ones. If we consider however, the degree of bivouac exposure of *E. burchelli* in relation to the seasons, the results are quite different. During the dry season, *E. burchelli* colonies established 49 nomadic bivouacs and 35% were exposed and 65% sheltered; in the rainy season from 66 nomadic bivouac records 61% were exposed and 39% sheltered.

This is more evident after observing Figure 1. During the rainy season (January to May), the frequency of exposed bivouacs is higher and gradually becomes low after June (starting of the dry season) when the sheltered bivouacs become more frequent. But the exposure condition is not merely a by-product of seasonal change. Figure 2 presents data analysing the exposure degree of 42 bivouacs in relation to the sequence of their establishment during the nomadic phases both in dry and rainy season. It can be seen that the first bivouacs are exposed; from the 6th bivouac on, the exposure degree decreased. It was observed however, that during a nomadic phase of *E. burchelli,* the colony migrations could not occur daily. Therefore, the bivouac durations must be longer than 24 hours and the number of bivouacs established is less than the nomadic days. Considering the exposure degree of the bivouac in relation to the nomadic day, it can be seen in Figure 3 that from the 3rd to 10th nomadic day the bivouacs established are exposed; afterward the frequency of sheltered bivouacs increased. These observations are seasonally independent and probably more dependent upon brood age and queen condition.

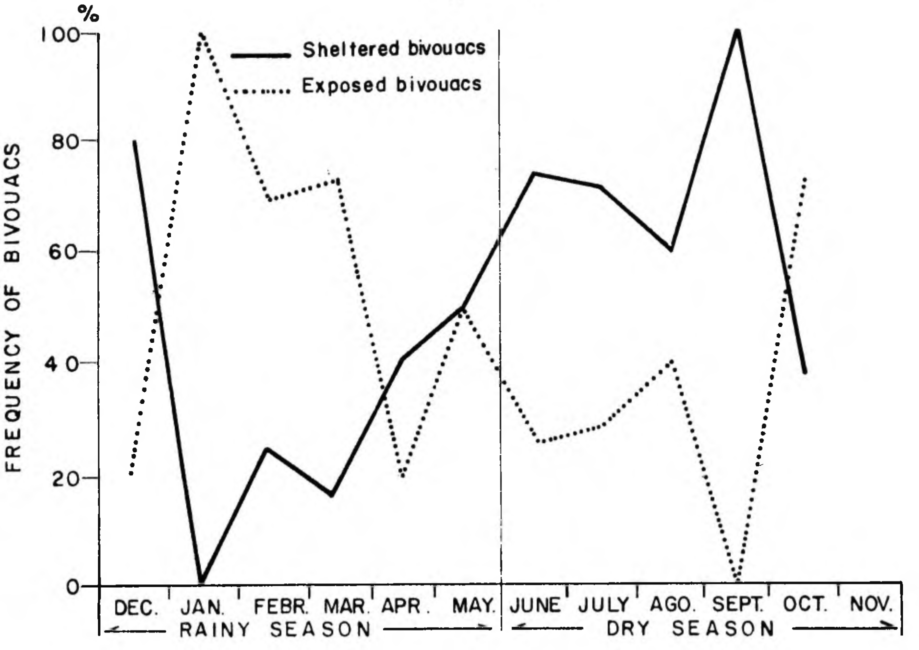

Figure 1 — **Frequency (%) of sheltered and exposed nomadic bivouacs of *Eciton burchelli* colonies recorded during rainy and dry season of Belém region.**

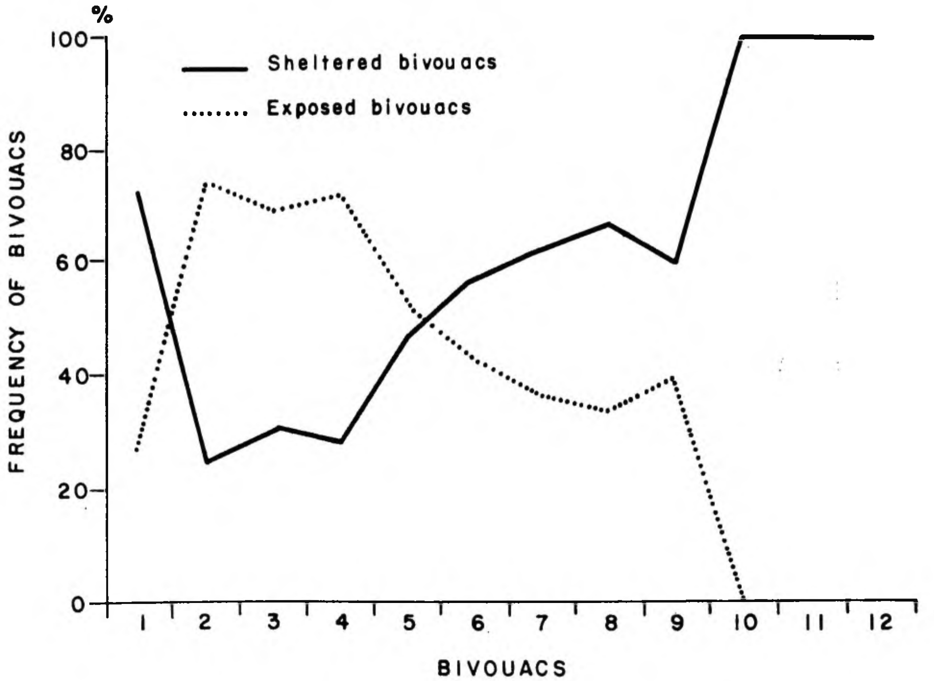

Figure 2 — **Frequency (%) of sheltered and exposed Nomadic bivouacs of *E. burchelli* colonies in relation to the establishment sequence.**

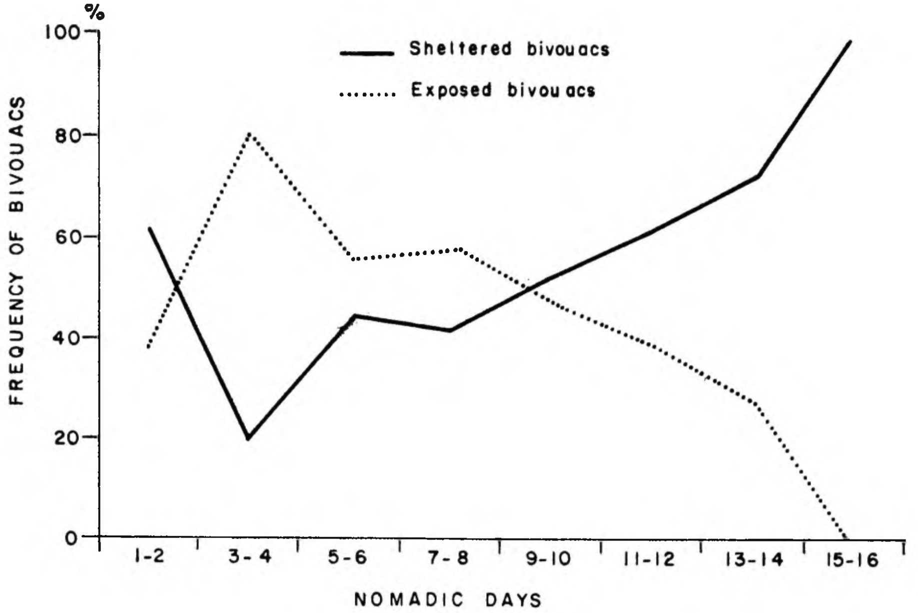

Figure 3 — Frequency (%) of sheltered and exposed *Eciton burchelli* bivouacs in relation to the nomadic days.

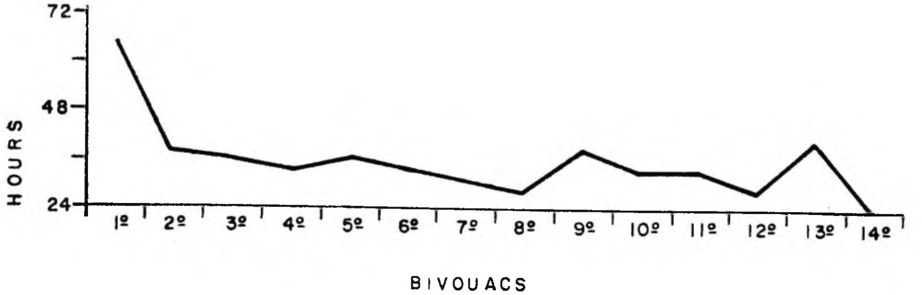

Figure 4 — Durations (hours) of the bivouacs established during the nomadic phases of five *E. burchelli* colonies in relation to the establishment sequence.

E. *Duration of the bivouacs*

The duration of the nomadic bivouacs relates to the beginning and number of colony migrations during a nomadic phase, and also to the migratory activity. For *E. hamatum* colonies it was observed that the migratory activity is higher than the recorded for *E. burchelli*. In 86 nomadic days (5 nomadic phases) of an *E. hamatum* colony 86 bivouacs were recorded; then the duration of each bivouac of this colony was 24 hours. The same did not occur in *E. burchelli* colonies, since the colonies stay more time at the given place.

The data of *E. burchelli* colonies at Belém region showed that the first nomadic bivouacs have an enlarged duration (30 to 54 hours). Figure 4 shows that from the 2^{nd} to 14^{th} bivouacs, the durations decreased, being always lower than in the first bivouac. This is more evidente since in 365 nomadic days (27 nomadic phases of five colonies), 18% of the colonies spent in the first bivouacs; 12% in the second and, then the percentage gradually decreased.

Concerning bivouac durations in relation to the seasons it was found that in the rainy season the mean duration of the bivouac was 32 hours and in the dry season 29 hours, or that during the rainy season the bivouac durations are a little longer and there is less colony migration.

The bivouac duration seems to be influenced also by the colonial division process, as ascertained by the observations on colonies E-2A and E-2B which resulted from a process of colonial division. The colony E-2A formed during 44 nomadic days (2 nomadic phases) 17 bivouacs, the bivouac mean duration being 54 hours. This duration is longer in the second nomadic phase after the division process, therefore in 31 days the colony presented 6 nomadic bivouacs and each one lasted 5 days. Concerning colony E-2B, in 111 nomadic days 66 bivouacs were recorded, and the mean duration of each one was 31 hours, that is, similar to the colonies.

F *Inter bivouacs distance*

The distance between a previous bivouac and the new one formed after finishing a raid, is equal or less than the distance length for the raid column developed by the colony during the nomadic day (Schneirla, 1944b; 1945).

In Belém the mean distance among 116 bivouacs established by three colonies was equal to 52 meters, with a variation of 10 to 180 meters. However, observing Figure 5 some considerations can be drawn concerning colony condition and distance between the bivouacs according to the establishment sequence. The figure shows that the mean distance between the statary to the first nomadic bivouac is always less than the mean distances between the other bivouacs established afterward. The mean distances between the last bivouacs are larger than in the first ones. The same figure presents the mean distances between the bivouacs formed by an *E. hamatum* colony. For this species the mean distance was higher than the recorded for *E. burchelli*, so for 86 records the mean distance was 157 meters (variation of 10 to 400 meters). In relation to the establishment sequence, as in *E. burchelli* colonies, the mean distances between the bivouacs are higher in the last bivouacs and the first nomadic bivouacs are formed near to the statary bivouac.

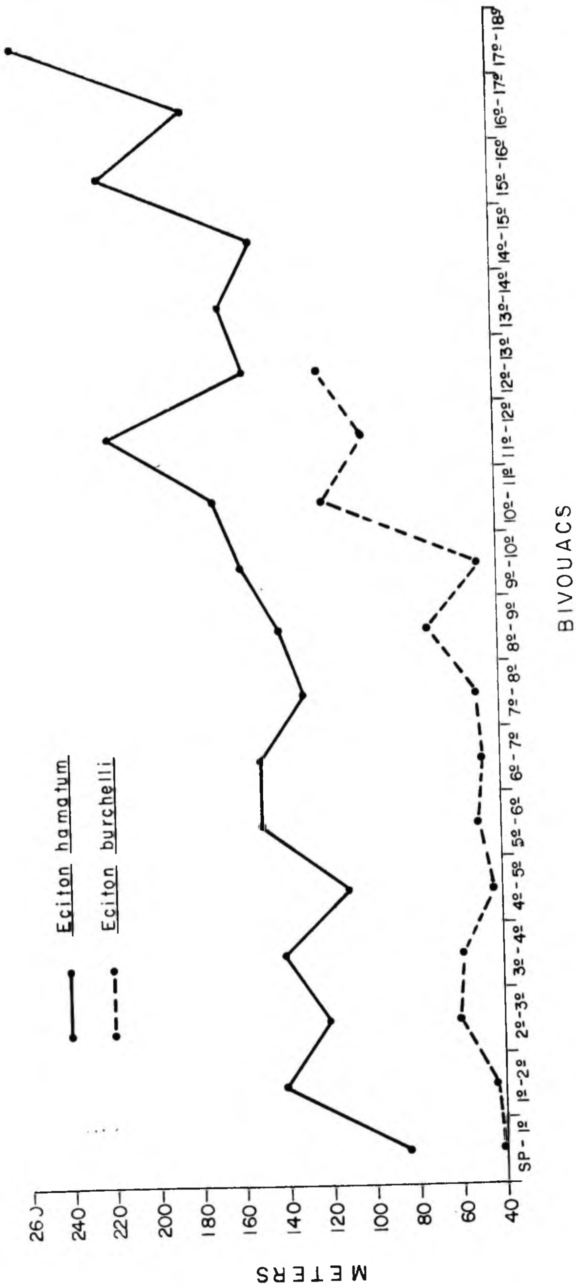

Figure 5 — Mean distances between the nomadic bivouacs of *E. hamatum* and *E. burchelli* colonies in relation to its establishment sequences.

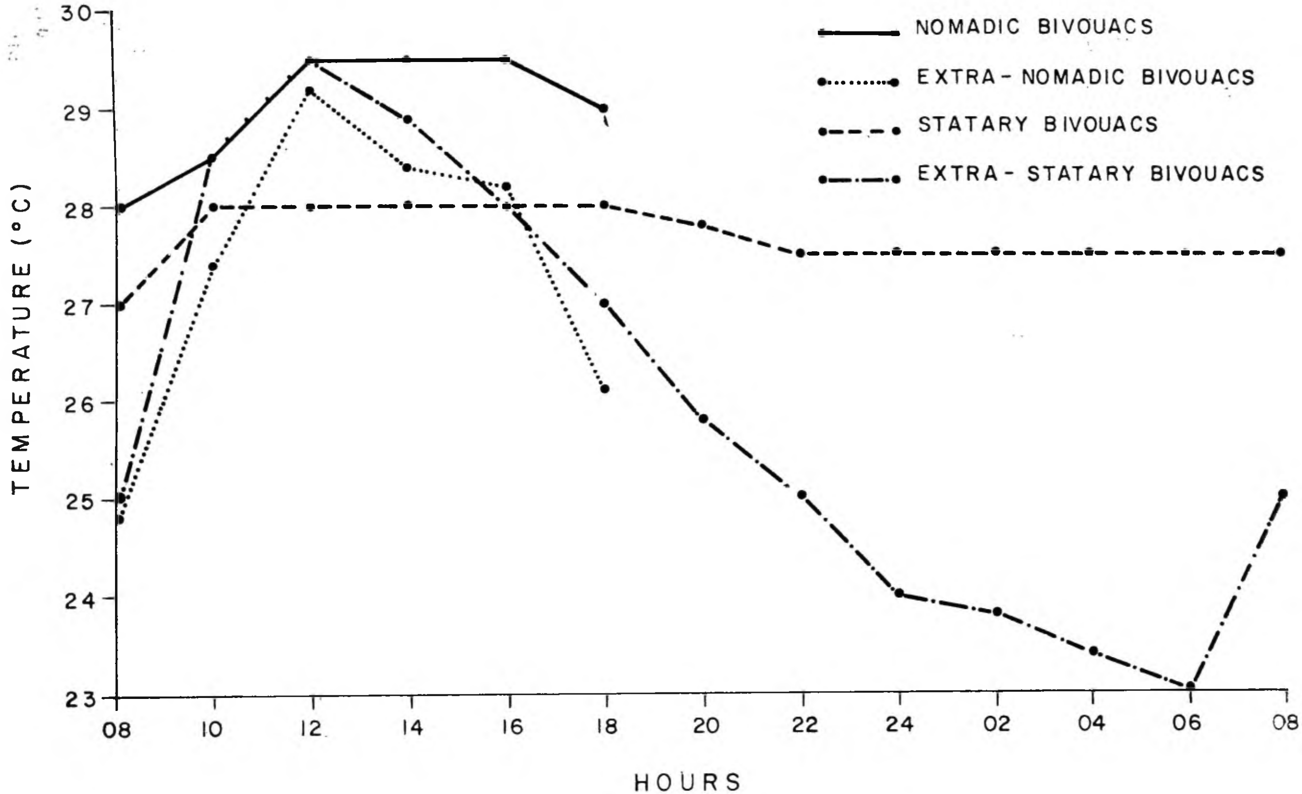

Figure 6 — Intra and extra temperature readings taken at 2 hours intervals throughout a statary day and all days of a Nomadic phase in two *E. burchelli* colonies (E. O. and E-1). The internal temperature was taken on the bivouac center and each record is a mean of successive readings.

G. *The bivouac temperature*

The temperature of nomadic bivouacs was recorded during 12 days in a nomadic phase (colony E-0, duration of 18 days). The temperature was measured from the 5th nomadic day on. The atmospheric temperature was 27°C ± 4.5°C (51 readings) while the central part of the bivouac presented 28.6 ± 2.6°C.

Considering the nomadic bivouac mean temperature in relation to the time of the day, Figure 6 shows that the temperature of the central part of the bivouac is more constant than the environmental one, so that in the interval of 08-12 hours a.m. the fluctuation was 5°C while in the bivouac temperature the variation was only 1.5°C.

The extra and intra temperature data of a statary bivouac is presented in the same figure. The bivouac temperature changed from 27°C (6 hours a.m.) to 28°C (12 hours a.m.) while the extra bivouac temperature presented a variation from 23°C (6 hours) to 29.5°C (12 hours a.m.). The intra bivouac temperature during the statary period remained constant irrespectively of the fluctuation of ambient temperature; the most critical periods for colony seems to be between 8 to 12 a.m. hour and 8 p.m. to 6 a.m. In the first interval the ambient temperature increased 4°C and dropped 3°C in the second. In these periods the intra bivouac temperature varied only 1°C which demonstrates the capacity of the colony in controlling efficiently its microclimate.

Concerning the nomadic bivouac, the temperature of the statary is less variable and remained constant during the critical periods.

DISCUSSION

The army ants of Neotropical and Paleotropical region have retained primitive carnivorous dietary characteristics based on predatory foraging activities and have developed reproductive capacities supporting large colonies and a nomadic way of life cycle. The nomadic way of life cycle is considered by several authors (Wilson 1958a, 1971; Wheeler 1910, 1936) as the main character for the biological success of the Dorylinae and Ecitoninae in relation to other ants of the "poneroid complex" (Brown, 1954), such as in relation to the species of the genera *Leptogenys, Phyracaceas* and *Simopelta*. These ants, known as legionary ants, have a nomadic group predatism behavior and somewhat large colonies. According to Wheeler (1928) and Wilson (1958a; 1971) the nomadic colony is essential for a social insect to maintain a carnivorous diet since this would be practically impossible if the colonies had a permanent nesting site. The above authors and also Schneirla, Brown and Brown (1954) agree that the changes in the nesting site were enforced by depletion of food in the occupied area. So the temporary nest or bivouac is a key factor in the adaptive pattern of the army ants to the carnivorous habits and nomadic way of life and conversely the study of the bivouacs are of major importance in understanding the behavior of the army ants and also their evolution.

A detailed discussion of the formation and internal composition of bivouacs has been published by Schneirla (1933, 1949b, 1971), Schneirla, Brown and Brown (1954) and Rettenmeyer (1963). Following Schneirla (1971) the bivouac of all army ants has four main roles. It serves as a base and center of operation for the colony. This is obvious when the colony is in a nomadic phase when each new nest gives the colony the advantage of invading other areas and capturing booty. In this aspect it is important to consider the number of bivouacs established and the diversity of booty captured by the species. In the course of the present study *E. hamatum* established as many bivouacs as the number of nomadic days, and so the colony migrates daily. The data collected agree with that of previous authors evidencing that *E. hamatum* colonies attacked more wasp nests of the genera *Polybia* and *Polistes* and some ants, while *E. burchelli* captured the most variable booty types, attacking several Arthropoda species and some Vertebrates. This, of course, is related with the different raid pattern of the two species, that is, column raid for *E. hamatum* and swarm raid for *E. burchelli* (Rettenmeyer, 1963). In the case of *E. hamatum* it seems that there is a necessity to change the nest site every nomadic day because the colony, in this way, will have more oportunities in the new site to capture the specific booties. This is reinforced also by the raid column lengths and by the distance between the bivouacs that are longer than in *E. burchelli.* Then, for *E. hamatum* the daily changes of the center of operation (bivouac) give the colony more advantages than for *E. burchelli.* The distances of the raid columns, between the bivouacs and the number of migrations are, of course, related to the internal conditions of the colony (relation of the workers with the broods and queen, etc.).

A second role of the bivouac pointed by Schneirla (1971) is that the bivouac is a shelter for the colony. The clustered ants around the brood and queen increase the protection against predators (coatimundis, ant-eaters) and also provides a physical shelter against climatic variations giving the colony an homogeneous internal microclimate.

The observations of Schneirla, Brown and Brown (1954) and Jackson (1957) and also the present data suggest that the bivouac sites are not chosen at random. The present data show there is a tendency for the colonies of *E. burchelli* and *E. hamatum* to establish the bivouacs on certain locations. In these sites the ants probably capture the most of booties and therefore, they are guided to stay in places by their preys. This is reinforced by the greater variation found in the location types of nomadic bivouacs than in statary phase. In *E. burchelli* the 23 observed statary bivouacs were established on four locations in which tree hollows and hollow logs were the most frequent and the establishment of the nomadic bivouacs occur in 5 different types of sites. The same was observed for *E. hamatum* colonies. By comparing the records of the location types of *E. burchelli* bivouacs with those of *E. hamatum* it is evident that in the first there is more variation and this agrees with the diversity of site inspected by *E. burchelli* colonies during the raid activities. The data for the same species obtained at Barro Colorado by Schneirla et al. (1954) demonstrated the same. These authors recorded the temperature and relative humidity of bivouac sites and verified that the sites more used by the colonies have a more stable microclimate than the control (more exposed site). They also verified that the sites of statary bivouacs have a more stable relative humidity than those of nomadic bivouacs.

According to these locations there are several ways in which the cluster of ant bodies hangs from supporting structure to the ground. Then the bivouac patterns described by Schneirla et al. (1954) are related with the types of establishment locations and their microclimate and they reflect an adjustment of the bivouac as a shelter.

In the *E. burchelli* colonies in the Belém area a variation in bivouac patterns was recorded according to the season and colony condition. It was observed that during the dry season the most frequent nomadic bivouac type is the cylinder (47%) and plug (42%) patterns, which are the types of more sheltered bivouacs. Schneirla, Brown and Brown (1954) observed this for the same species also recording that in 151 bivouacs, 46% were cylinder and 11% plug; in the rainy season they observed that the most frequent types are the cylinder (50%) and pouch (19%), frequently more exposed bivouacs. The statary bivouacs presented the same changes. During the dry season in Belém the *E. burchelli* colonies established only plug bivouacs while in the rainy season we recorded five types of bivouacs located in more exposed sites (curtain, pouch and compound types).

By comparing the nomadic and statary bivouacs the patterns presented are seen as an adaptation to the colony condition also. The statary bivouacs are established in more sheltered places (Table I and II). In Table I, of 23 statary bivouacs 61% are established in tree hollows, and in table II, even in the rainy season, the more frequent pattern is the plug bivouac, that is, a more protected bivouac. So, according to the statary or nomadic condition, the bivouacs are established in more protected or open places. In accordance to brood developmental stage and queen condition, the colony responses are different. Our data evidenced that when the colony has pupae, eggs, small larvae and physogastric queen (statary period), there is a need for increased protection as reflected by the types of sites and patterns of the bivouacs.

In the nomadic period the bivouacs are more exposed but there is variation according to the nomadic days or larval age. Table IV evidences that more exposed bivouac patterns (compound, curtain, pouch) occurred from the first to the 10th 12th nomadic days. After the 10th nomadic day the plug pattern in predominant and then, when the larvae attained the maturity stage, there is a need of more protection and there are responses of the adult workers for this. The same is observed (Table V) for the *E. hamatum* colony. This was already suggested by Schneirla in his papers but he presented no quantitative data to support his idea.

Other records demonstrating the role of the bivouacs as shelter places concern the exposure degree of the bivouacs in relation to seasons and colony condition. Figure 1 demonstrates that there are responses of the colony, during the nomadic period, to drier or humid weather, by establishing bivouacs more or less exposed. Schneirla, Brown and Brown (1954) observed the same, recording during the dry season in 152 nomadic bivouacs of *E. burchelli* 70% of exposed bivouacs and 82% in the rainy season. For *E. hamatum* nomadic bivouacs the authors verified the same decreasing of exposed bivouac during the rainy season.

The degree of exposure is related not only to the seasons but also to the colony condition. The statary bivouacs are less exposed than the nomadic ones. However, observing the degree of exposure of the bivouac along the nomadic phase, as shown in Figures 2 and 3, the exposure is modified according to the beginning and ending of the phase. As the nomadic colony presents only larval brood in development we conclude that this different degree of exposure may be related with larval age. This was found also in relation with the bivouac pattern data. The fact demonstrates that there are intense contact of adult workers with the larvae and the workers modify their behavior according to the brood changes, to provide a good condition to larval development. In all studied colonies it was observed that when the colony established the first nomadic bivouac, it contained brood in pupal development (small pupae) and it is observed in Figure 2 and 3 the greater percentage of sheltered bivouacs; then, we can conclude that with brood in pupal development the bivouacs are less exposed irrespective of the nomadic activity.

Other data demonstrating the shelter function of the bivouacs are the establishment of them in elevated sites. Schneirla (1971) found that elevated bivouacs are more frequent during the dry season. He observed also that *E. burchelli* established more elevated bivouacs than *E. hamatum* and he relates this with *E. burchelli* more frequently in higher vegetation during the nomadic period than *E. hamatum.* Table VI shows that indeed *E. burchelli* colonies established more elevated bivouacs (24%) than *E. hamatum* (8%); it is however, in the statary condition that we found a lager percentage of elevated bivouacs (83%) for *E. burchelli* and 17% for *E. hamatum.* We do not agree with Schneirla that *E. burchelli* raids more frequently than *E. hamatum* on higher vegetation since we observed that *E. hamatum* frequently raids in higher places and through tree tops several times the colonies crossed streams about 5 meters wide, very common in varzea forest. However, we never found bivouacs of this species established above 1 meter as in *E. burchelli.* Schneirla observed also underground bivouacs that are more frequent under dry weather. It seems that the bivouac establishment level may depend upon the colony and weather condition. In Belém we found no underground bivouac what may be due to the climate patterns of Amazonian forest that shows a less drastic dry season than that of Barro Colorado Island.

The bivouac is also an incubator for the brood. Schneirla et al. (1954) and Jackson (1957) demonstrated that according to the position of the brood in the bivouac the temperature and humidity are more or less variable. They also verified that there is temperature and humidity control in the internal environment of the bivouac. They recorded that while the external temperature changed about 7°C along the day, the bivouac temperature change only 3°C. Comparable intrabivouac control was observed for humidity. The same was observed by us (Figure 7).

This temperature and humidity control, according to Schneirla (1971), is based on properties of the ants. Schneirla gives an example of environmental control: as the forest air cools late at night, ants hooked in the bivouac wall draw closer together while others move between spaces in the wall. Through these actions the ants thicken and tighten their wall so that internal heat is preserved and cool air is shut out. Another control refers to the circulation of air through the bivouac. This is more easy to observe during the raiding when the bivouac wall become more porous permiting the circulation of air, increasing internal evaporation and elimination of the gaseous wastes.

The data about bivouac durations and distances between the nomadic bivouac may be related with the colony condition, raid and emigration activities. The bivouac durations of *E. burchelli* nomadic colonies, as shown in Figure 4, changed according to the nomadic activity development. According to Schneirla (1971), with the development of the larval brood, there is an increase of their stimuli upon the adult workers and the colony excitation is high. Near the end of the nomadic phase the excitation is higher, the ants attack more prey, the raiding is more vigorous. The excitation level and vigorous raiding, according to Schneirla, are prerequisites to migration. Then, the duration of each established bivouac reflects the level of the excitatory effects (chemical and chemiotactual) that exist in the interactions between the adult workers and larval brood. According to the higher or lower stimulation, the adult worker behavior modifies and the bivouac duration may be a response to the internal condition of the colony. We have observed (Figure 4) that the first bivouacs of *E. burchelli* have a longer duration than the following ones. In this species, as already said, the colony has brood in pupal development that emerges in the following nomadic days (until the 6º nomadic day, Teles da Silva, 1972). The colony may stay 3 or more days in the same site and the greater part of the pupae emerge in this period. We observed also in samples of the first migration column of a colony, a great number of eggs that probably will eclode in the subsequent nomadic days. This reflects that in the first nomadic day the colony excitation did not attain a sufficient level to promote emigratory activity because the colony has pupae to emerge and eggs to eclode. The reduction in the duration of the following nomadic bivouacs demonstrated an increase of the stimuli on the adult workers caused by more larval broods and more callow workers emerging. For *E. hamatum* we did not observe this because the colonies did not present in the first nomadic days pupal broods as we observed in *E. burchelli.* The *E. hamatum* bivouacs of the studied colony have since the first to the last bivouac, the same duration of 24 hours, and then, we observed migration in all nomadic days. This difference between the two species may be on account of the colony size, *E. hamatum* colonies being smaller than those of *E. burchelli.* According to Schneirla (1971) in *E. hamatum* colonies chemical and chemicotactual stimulation are transmited among the adult workers more quickly than in *E. burchelli.* He suggested that the interactions between adult and brood in *E. burchelli* colonies are more complex than in *E. hamatum.*

The records of the distances between the nomadic bivouacs constitute another data reflecting the excitatory colony level during the nomadic phase. Figure 5 presents the mean distances between 116 bivouacs (19 nomadic phase) of 3 *E. burchelli* colonies E-1 (12 nomadic phase), E-2 (4 nomadic phase) and E-14 (3 nomadic phase), and 86 bivouacs of an *E. hamatum* (E-7, 5 nomadic phase). The mean distance between statary bivouacs to the first nomadic bivouac in both species is always less than other distances. During 3 nomadic phases of an *E. hamatum* colony (colony 46H-B) Schneirla (1949) observed the same. For *E. burchelli* he suggested the same but did not present quantitative data on migration distances. Figure 5 shows that the mean distances between the *E. burchelli* bivouacs tend to increase after the first bivouacs. In the same Figure we also observed that for *E. hamatum* the distances among the bivouacs are higher than in *E. burchelli.*

During the rainy season *E. burchelli* colonies present the mean distances between the bivouacs with lower volues (between 30 to 40 meters) than those recorded during the dry season (variation of 45 to 85 meters). Schneirla et al.

(1954) and Rettenmeyer (1963) observed the same and suggested that the migration distances may be influenced by the duration of the chemical trails established previously by the same or different colonies. These trails last longer in the dry than in the rainy season and the colonies establish more easily the raids and migration columns. By picket marking a *E. burchelli* raid column during a statary phase we disclosed the workers used many times at least part of the trail route marking. The same colony returns in the following statary phase to the same tree hollow and reused the same route marking during the raid activities. Or then, the colony used the same trail route established 35 days before.

By the records on bivouac durations and distances between them, we can conclude there is not only the influence of external factors but also the reflexes of the internal condition of the army ant colony. Or then, the permanence of the colony (bivouac duration) in a site and the distances between the bivouacs reflect the responses of the workers during the establishment of the bivouacs to stimulation from the brood and queen. This may be considered as data supporting the adaptation of the bivouacs to the condition of the colony and the behavior of the army ants.

The data presented in this paper reinforces the idea that the bivouac or temporary nest is an adaptive factor developed by army ants during their evolution. This behavior is responsible for the maintenance of the primitive carnivorous dietary characteristics based on predatory foraging activities.

CONCLUSIONS

1) The bivouacs of *E. burchelli* and *E. hamatum* differ strikingly in relation to activity phase. The nomadic bivouacs are more exposed to the general atmosphere while the statary bivouacs tend to be more enclosed within a natural cavity.

2) There is a selection of sites in the establishment of the *E. burchelli* and *E. hamatum* bivouacs to provide a more stable microclimate. According to the establishment site there are variations in the bivouac patterns. These patterns changed according to the season and brood condition.

3) There is a variation in the exposure degree of *E. burchelli* bivouacs according to the season, they are more exposed in the rainy season than in dry season. For the nomadic bivouacs the exposure degree changed also according to the larval development, the first bivouacs being more exposed.

4) *E. burchelli* colonies established more elevated bivouacs than *E. hamatum*.

5) The duration of the nomadic bivouacs of *E. burchelli* changed along the nomadic phase and may be related with the interaction degree between adult worker and brood. The bivouac durations of *E. hamatum* colony is less than in *E. burchelli*. This may be related to the more or less quick stimuli transmission due to the difference in colony size.

6) The distances between the bivouacs of *E. burchelli* and *E. hamatum* colonies seem to be related to the interaction degree between adult workers and broods. When the larvae are more developed there are more interactions between them and the workers, and the distances between the bivouacs are larger than in the beginning of the nomadic phase.

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