FORAGING ACTIVITY AND DIET IN SOME NEOTROPICAL PONERINE ANTS. I. *ECTATOMMA RUIDUM* ROGER (HYMENOPTERA, FORMICIDAE)

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ABSTRACT

Analysis of the patterns of food-gathering activity in *Ectatomma ruidum* Roger revealed clear differences between those of the dry season and the rainy season, though the diet remained mainly carnivorous. The rainy season was characterized partly by less total foraging activity (compensated for by a 1.5-fold higher yield), and by a decrease in carbohydrate intake and an increase in protein intake. Also, a wider range of prey was captured during the rainy season, and a substantially greater fraction was energy-rich prey (larval type); at the same time, active predation increased sharply relative to necrophagy, which was three times greater in the dry season. The correlations between these various factors, meterological conditions, and the life cycle of the especies are discussed.

KEY WORDS: Ponerines, *Ectatomma,* rythm of activity, foodgathering behavior.

RESUMEN

El análisis de las características de la actividad de aprovisionamiento de la hormiga *Ectatomma ruidum* Roger indica claras diferencias entre los datos obtenidos en época de secas y en época de lluvias, aun cuando la dieta se mantiene principalmente carnívora. La época de lluvias se caracteriza por una actividad general más baja (compensada por un aumento de un 50% de la tasa de éxitos en la captura), una disminución del aprovisionamiento en carbohidratos y un aumento en el de proteínas. Una variedad más amplia de presas se nota también en época de lluvias, además de incluir una fracción de presas ricas en energía (de tipo larvas) mucho más importante. Al mismo tiempo, se puede notar que la depredación aumenta de manera notable en comparación con la necrofagia que presenta un valor tres veces más alto en época de secas. Se presenta una discusión sobre las correlaciones entre esos factores varios, las condiciones meteorológicas y el ciclo biológico de esta especie neotropical.

PALABRAS CLAVE: Ponerinos, *Ectatomma*, ritmo de actividad, alimentación, comportamiento.

The twelve species of the genus *Ectatomma* Fr. Smith (Kugler and Brown, 1982) are widely represented in Central and South America. Members of this genus live both in forests, open spaces, and even arid regions, but are quite strictly limited to the tropics. Like most Ponerinae, *Ectatomma* spp. are carnivorous and may play a role in the control of arthropod populations.

Long ago, local inhabitants, notably in Guatemala (Cook, 1904, 1905), pointed out to researchers the possible usefulness of some of these species as natural regulators of crop parasites and in 1904, *E. tuberculatum* was investigated with a view to introducing it into cotton plantations in Texas (See the many publications of Wheeler and Cook between 1904 and 1906).

However, there has not yet been any detailed study of the pattern of foraging or of the diet of *Ectatomma* spp. In the work reported here, we set out to fill this gap by obtaining the necessary information concerning *E. ruidum*, determining whether this species has any role in protecting plants.

MATERIALS AND METHODS

E. ruidum Roger is a terricolous species that ocurrs in plantations, savannas and rain forests from sea level to an altitude of 1500-1600 meters (Weber, 1946). Its range extends from the states of Michoacán and Veracruz in Mexico to southwestern Ecuador and the northern border of Brazil in the Amazonas region (Weber, 1946, 1946; Brown, 1958; Kigler and Brown, 1982). In Mexico, in the Soconusco (Chiapas State), this species is very common in coffee and cocoa plantations, and it is the dominant terricolous species in the region studied, at Rosario Izapa, where its density is about 2700 nests per hectare. Such a density is not exceptional for this especies, considering the figures given by Levings and Franks (1982) for Panama, which range from 1800 to 6100 nests per hectare.

Measurement of activity cycles

To draw up curves of the daily activity of *E. ruidum* and the pattern of food gathering, we recorded all the trips of the foragers, distinguishing between entrances and exits and recording the number of entrances of ants carrying collected material. In view of the frequent comings and goings of a number of workers (domestics, guards, foragers), within about 20 cm of the main entrance, only those trips that went more than 30 cm from this entrance were considered. Counts were made in the dry season (two nests with 80 to 120 individuals each, observed between January and February 1982) and in the rainy season (two nests with 80 to 120 individuals each, observed in August 1984). The counting was performed in one 5-min observation every 15 minutes, which gave 4 counts per hour, from which the mean hourly activity was estimated. Recording took place between 05.00 and 20:00 hours, except for a few extra observations made between 20:00 and 23:00 hours. In order to avoid disrupting the nocturnal activity of the workers, the night-time observations were made in red light. At the same time, we studied the possible effect of environmental factors on the timing of daily activity, by recording the humidity and air temperature (at 50 cm from the ground, under plant cover) as well as soil temperature (at depth of about 2 cm) near the entrance to the nests.

Determination of the diet

During measurement of the activity cycles the nature of the material carried by workers was also noted. The material was estimated as either plant material, fruit, liquid, or prey of animal origin. In addition, at nests other than those being used for activity measurements, the material collected by workers was sampled over periods of 2 to 3 hours, distributed mainly during the peaks of food-gathering. In the case of material of animal origin, when possible, account was taken of whether it was alive, was freshly killed, or had been dead for some time. These criteria, sometimes quite difficult to apply, tended to minimize the fraction of the prey considered to have been actively hunted, and the results thus obtained are merely indicative. However, such observations seem to be a useful index of the relative importance of predation and necrophagy in providing the society with protein. The samples were subsequently analyzed in the laboratory.

RESULTS

The population of an adult society varies between 50 and 200 individuals, among whom there may be several females; but almost all newly founded colonies have only one fertilized female, and polygyny is probably only secondary, although in one case a newly founded was observed that contained two associated females. The entrance to a nest, often hidden under litter, is an opening about 3 mm in diameter, followed by a sloping tunnel that leads to chambers situated at various levels that may go down as far as 2 m. Some of these chambers contain the brood; some are apparently empty; others, according to Weber (1946) are used for the storage of prey, though this use was not observed in the nests reported here. On the other hand, a nest sometimes has several (two or three) entrances, lying within a radius of about 0.8 m around a main entrance, through which the workers of the society made most of their entrances and exits. These supplementary entrances led to annex chambers used for food storage and occasionally for the brood, but didnot seem to have a network of underground galleries; the traffic recorded between the various entrances was on the surface, and apparently was conducted by workers that especialized in this function. Individual marking of workers from two nests showed that in both cases this traffic was always by the same individuals. The structure of the nests seems to vary greatly, depending on the environment and probably on the season, and other types have been described (Weber, 1946,).

Daily activity cycles

The daily variation in activity is shown in Figures 1 and 2. In order to adjust for differences in population size between colonies, activity is expressed, for each hour, as a percentage of total mean daily activity

(a) Dry season

The activity was mainly diurnal (Figure 1): it began between 07:00 and 08:00, with the earliest movements (no more than 0.30 m from the nest entrance) at 05:30 (i.e. at first light) remaining at a low level until 07:00. Activity stopped abruptly a little after sunset, at about 19:00.

As Table I shows, the correspondence between the daily mean numbers of entrances and exits was far from perfect: 1.4% excess entrances for nest A and 1.4% excess exits for nest B. These differences suggest either that some foragers spent the night out of the nest, under shelter or in an annex chamber, or that there is a little nocturnal activity (between 20:00 and 05:00). In fact in some very open biotopes (as at our study site), activity may sometimes continue beyond 20:00, a phenomenon that is apparently related to the brightness of the moonlight. Such variations in daily activity patterns with changes in light intensity are known in other species of ants, notably in ponerines such as *Paraponera clavata* (Hermann, 1975; Hermann and Young, 1980) or *Neoponera villosa* (Lachaud, unpublished). There are also crepuscular/nocturnal species that may nevertheless be found by day under dense plant cover, or in more open environments when the weather is very cloudy. There were three peak activity periods: 08:00-09:00, 10:30-13:00, and 16:30-19:00. These peaks were separated by two troughs of activity; one of these, from 09:00 to 10:00, was facultative; the other, from 13:30 to 16:00, corresponded to the time of day when the relative humidity was lowest and the temperature of the soil near the entrance to the nest was highest. There was very good correlation between the number of entrances and exits for each hour, with the calculated Spearman's rank coefficient being $p= 0.881$ fort nest A and $p= 0.823$ for nest B, significant at the level $p<0.01$. The hourly distribution of entrances and exits was, on the whole, very balanced, from which it can be deduced that in *E. ruidum* the duration of a foraging trip is less than one hour. Observations of the nests in which foragers were individually markerd showed that with a few exceptions this was indeed the case. Very often one forager was seen to make several trips within an hour; about a third of the activity recorded was due to journeys that covered such short distances (1.5 to 2 m) from the nest.

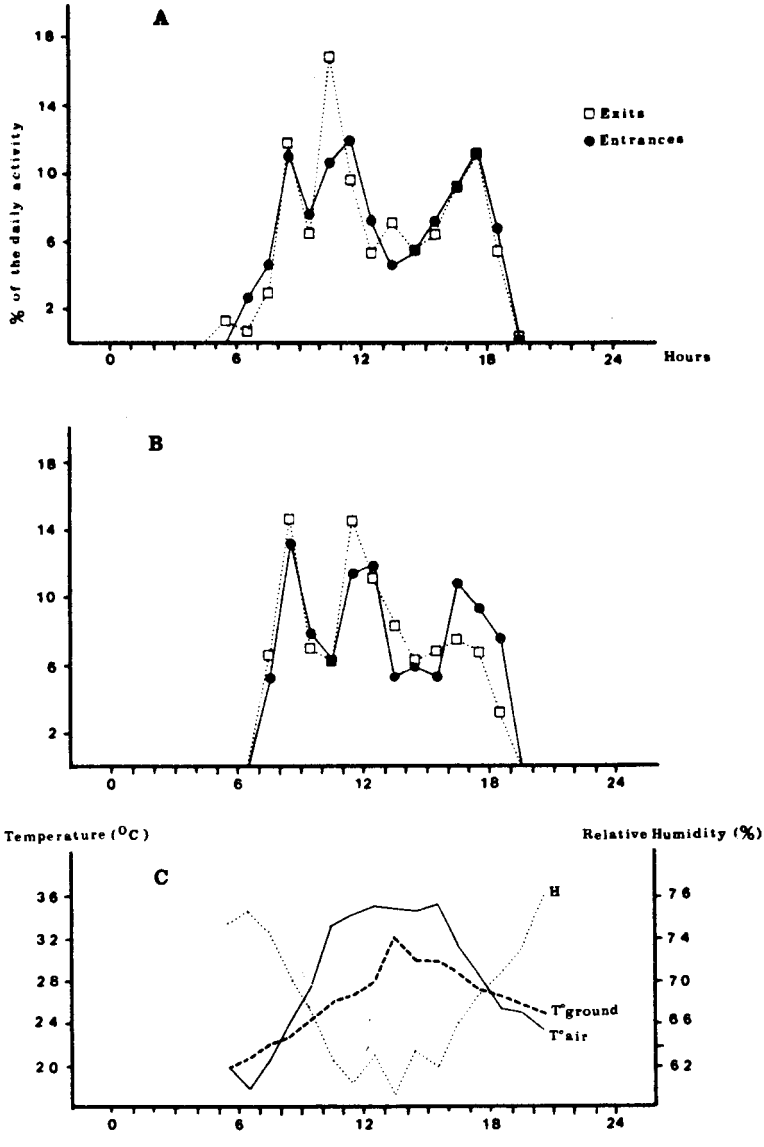

Fig. 1 : Mean daily activity pattern of *E. ruidum* in the dry season (in two nests, nest A (A) and nest B (B), followed for 4 days) and mean fluctuation of air temperature, ground temperature, and relative humidity (C).

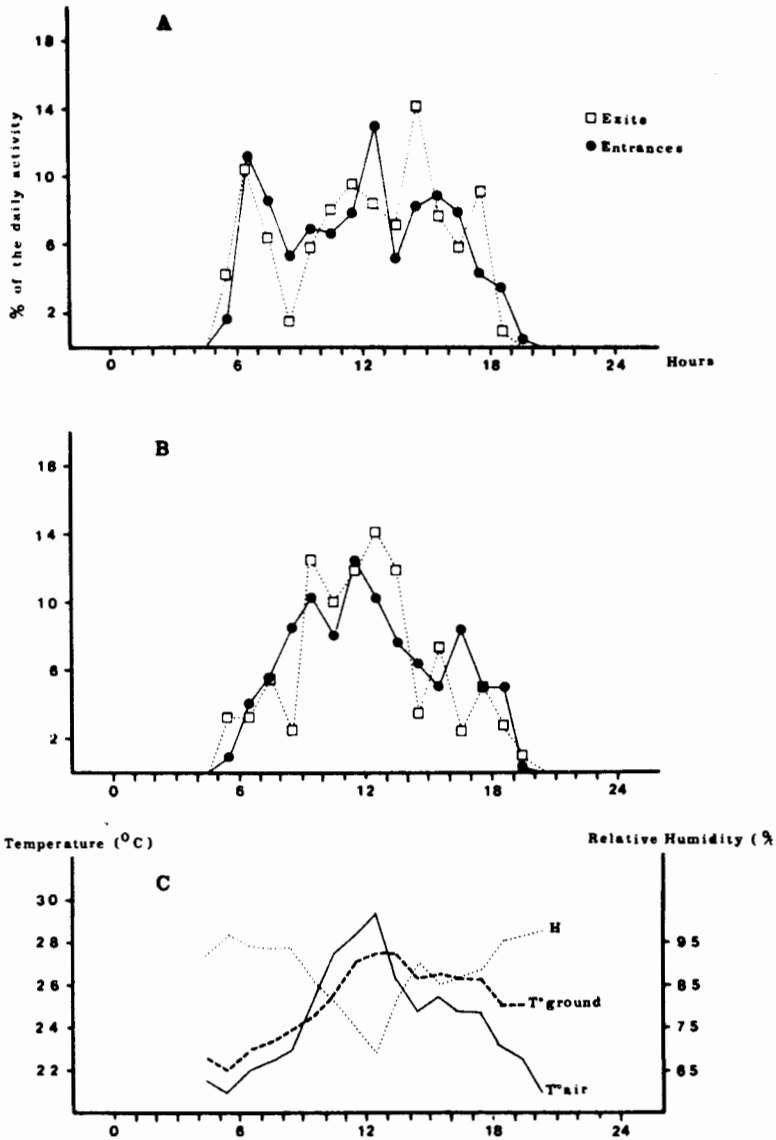

Fig. 2 : Mean daily activity pattern of *E. ruidum* in the rainy season (in two nests, nest C (A) and nest D (B), followed for 3 days), and mean fluctuation for nest D of air temperature, ground temperature, and relative humidity (C).

(b) Rainy season

Activity began between 05:00 and 06:00, with the first movements starting from 04:00 to 04:30. The peaks of activity varied, depending on the nest (Fig. 2), and was distributed between 06:00 and 18:00. After that, the activity decreased, and stopped at about 20:00. The correspondence between the peaks of entrances and exits, although still significant ($p= 0.645$ for nest C and $p= 0.563$ for nest D), was less good than in the dry season ($p<0.02$ and $p<0.05$, respectively, versus $p<0.01$ for nests A and B in the dry season). This seems to reflect longer trips by each forager. On the other hand, the daily mean numbers of entrances and exits (Table I, nests C and D) were exactly the same, from which it can be deduced that there really was no nocturnal activity at all in this season. The correlation between the temperature (recorded only for nest D) and the level of activity of the societies was much clearer in the wet season than in the dry season (significance level $p<0.01$), but applied more to air temperature ($p= 0.853$) than to soil temperature ($p= 0.670$); furthermore the correlation was no longer negative, but positive.

Food-gathering activities

The sequence of steps in food capture was observed in the laboratory and in the field. Prey was detected at a distance of 1 to 2 cm, and the forager then stopped, and also stopped moving its antennae. Then followed a phase of reconnaissance of the object, involving palpation with antennae and tarsi (prothoracic legs); then the forager seized the prey with its mandibles, stung it, and rapidly took it back to the nest. Very often the ant interrupted the return journey to sting or try to sting the prey, regardless of whether it had been alive or dead when captured, and even if it was a piece of tuna or hardboiled egg offered as bait. Stinging the prey occurred in about 80% of the 25 cases observed; in the rest the prey was abandoned.

(a) Dry season

A comparison of food-gathering patterns (entrances with collected material) with the daily activity patterns (exits) of the foragers (Figure 3, nests A and B) shows an excellent correspondence between the peaks of activity recorded in both cases ($p= 0.893$ for nest A, $o = 0.782$ for nest B; correlation significant at the level $p<0.01$). In other words, more material was collected as the number of foragers in the foraging area increased; this apparently trivial observation is nevertheless interesting, since this rule does not apply to all species, as we have observed with another member of the same genus, *E. tuberculatum* (Lachaud et al., in prep.). In addition, this correlation confirms that length of a foraging trip (out and back) was less than hour.

Table I

Comparison of pattern of entrances and exits and of success rate of food-gathering by *E. ruidum* in the dry period (nests A and B) and in the wet period (nests C and D).

Nest	Total Entrances per day	Total exits per day	Entrances with prey (% of total exits)	Entrances with carbohidrates (% of total exits)	Overal food-gathering (% of total exits)
		DRY		SEASON	
A	443	431	10.8%	0.5%	11.3%
B	367	377	9.5%	2.2%	11.7%
		WET		SEASON	
C	303	306	16.5%	0%	16.5%
D	270	267	22.2%	0%	22.2%

The number of entrances with collected material represented, on average, only 12% of the total trips, which is a very low success rate compared with other ground-hunting ponerines such as *Neoponera apicalis*, which has a success rate of 80-90% (Fresneau, 1985; Lachaud, unpublished data). This is, however, less than the real value, since of the workers returning with liquid it includes only those bearing a drop of liquid between the mandibles, while those who returned with their crops full could not be counted. *E. ruidum*, indeed, supplement their protein diet with carbohydrates; of the total material collected by the foragers, 28.8% was carbohydrates.

The distribution of collected material (from 170 samples) is shown in Table II. The major part (54.7%) was made up of food of animal origin, representing more than 25 families of insects, from 10 orders, in addition to the arachnids. Despite this apparent eclecticism, there was some specialization of the predation towards other Formicidae (mainly of the genus *Pheidole* in the dry season), which alone constituted nearly 35% of the total food of animal origin brought back to the nest.

Diptera and Homoptera were also objects of such specialization, although to a lesser extent.

The majority of prey were collected as adults (88%), but only 25% were hunted and captured alive by the foragers, the others being taken already dead. Lastly, 16.5% of the material brought to the nest was of plant origin (pieces of dried leaves, wood, grass, etc.), and was probably used for construction work and furnishing the inside of the nest.

(b) Rainy season

Peaks of returns with food (Figure 3, nests C and D) were very slightly shifted relative to the peaks of exits ($p= 0.622$ for nest C, $p= 0.645$ for nest D, correlation significant at the level $p<0.02$, i.e. slightly lower than in the dry season ($p<0.01$)). This seems to confirm the hypothesis that the foraging trips become longer in the rainy season.

The success rate, although very low -on average only 19.2%- was higher than in the dry season. Though the quantity of plant and organic material brought back to the nest scarcely varied (15.9% of the collected material in the rainy season, compared with 16.5% in the dry season), there was a much smaller fraction of carbohydrate intake in the form of fruit pulp. Liquids completely disappeared from the diet, which was mainly made up of animal proteins.

These animal proteins represented 79.7% of the total of material collected (in 232 samples) and were made up, as in the dry season, of arachnids and about ten orders of insects, among which Hymenoptera, especially the family Formicidae, were strongly represented. However, the diet had diversity, since it also included other arthropods (isopods, diplopods, chilopods, etc.) and molluscs, which formed a substantial fraction (16.8%) of the total prey collected. About 65% of the prey captured were adults, and, in contrast with that observed in the dry season, 68% of the prey (instead of 25%) were hunted and caught alive.

DISCUSSION

A comparison of activity patterns shows that in any season *E. ruidum* displayed mainly diurnal activity, spread over a longer period in the rainy season (when it lasted about 2 hours longer); this longer period was compensated for in the dry season by nocturnal activity, albeit at a very low level. It is difficult to establish a realiable relationship between variations in daily activity and factors such as air temperature, ground temperature, and relative humidity. All the same it can be noted that in the Neotropical zone,the ground temperature (with a daily variation of 12° C in the dry

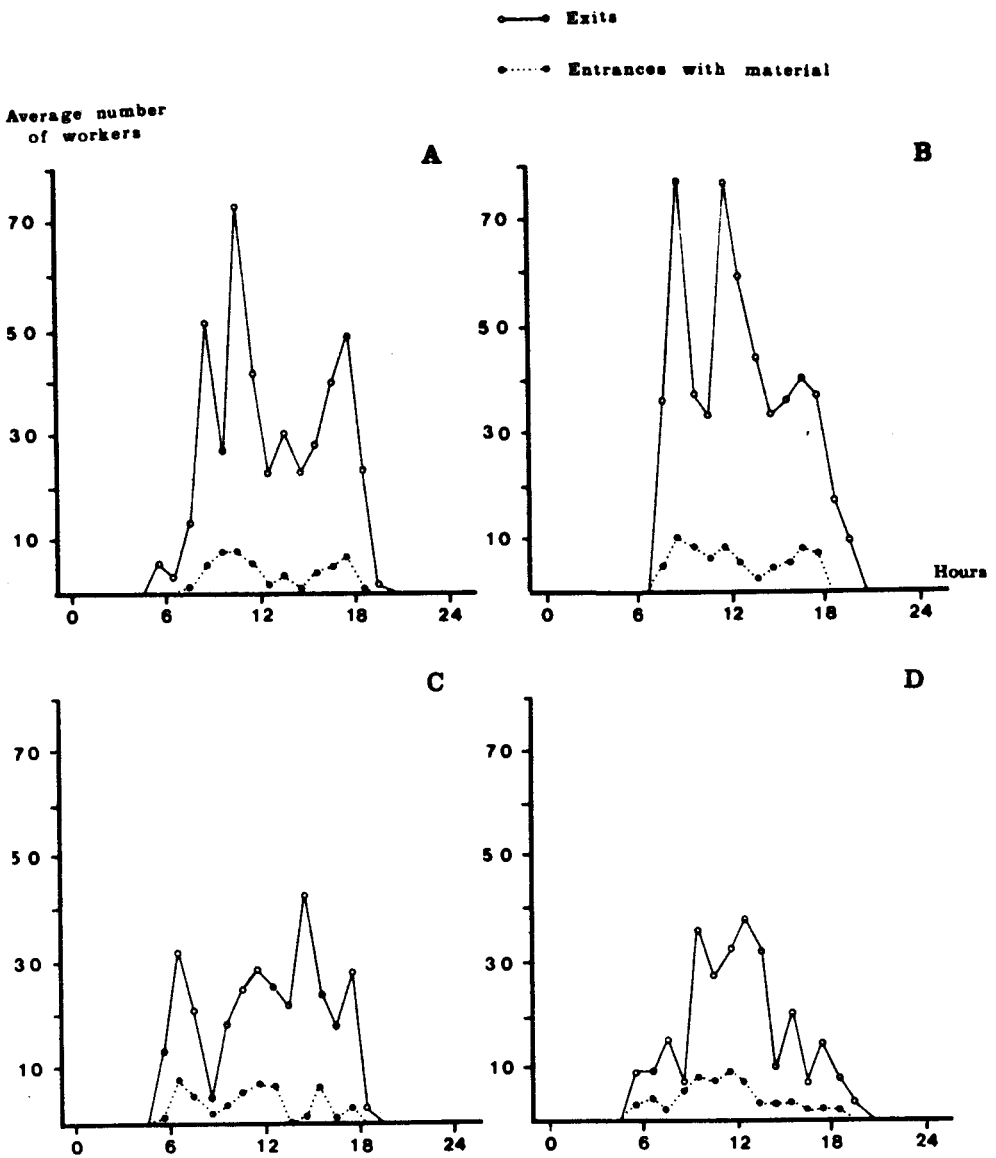

Fig. 3 : Comparison of the mean food-gathering pattern and the mean daily pattern of activity of *E. ruidum* (exits from the nest in nests A, B, C, and D.)

season) seems to be involved in modulating the activity of *E. ruidum*; this contrasts with what Lvieux and Louis (1975) reported for tropical regions, where the variation in ground temperature was too slight (6° C during the day) to play a role in regulating the activity of *Camponotus vividus*. There are, however, other factors whose effects on the activity pattern of *E. ruidum* are clearer. The main one seems to be variation in light intensity. The ants started to become active at sunrise and stopped at sunset, and it is noteworthy that the longer period of activity in summer (the rainy season) coincided with an increase in the day length.

Rain is also a major factor, but its effect varies according to the season. When it rained lightly during the dry season, entrances and exits continued, but they became fewer as the downpour became greater. Exits ceased when the rain was heavy and violent but, in contrast to what is observed in *E. tuberculatum* (Lachaud et al., in prep.), foragers that were outside at the time did not rush back to the nest in great numbers. This difference is linked, apparently, to the characteristics of their habitat: *E. tuberculatum* is arboricolous and the plant cover offers sufficient protection to allow the foragers to return when the firts drops fall. In the case of *E. ruidum*, which is terricolous, the open habitat offers little or no protection on the route back to the nest and the workers merely remain where they are, seeking shelter under leaves or dead branches. In all cases, exits began again normally as soon as the rain stopped.

In the rainy season, on the other hand, although the rain slightly disturbed the activity cycle depending on the violence of the rainfall, it seldom totally inhibited foraging activity. During light rain (fine even rain or scattered large drops, for example) the activity, and particularly the exits, far from stopping, seemed to increase; during heavier rain, foraging activity decreased greatly but nervertheless continued except when the rain occurred at the end of the day. However, during this season when it rains every day, the daily activity (entrances and exits) was relatively constant for each nest, with the workers tending to make maximum use of the hours when it was not raining. This phenomenon would partially accounts for the shifts (by about one hour) between the peaks of activity recorded for any given nest from one day to an other as a function of when the rain started, and also for the lesser regularity of the pattern of activity recorded in the rainy season.

Regarding diet, the seasonal variations were much less drastic than can be observed in some other species, such as *Brachyponera senaarensis* (Lévieux, 1979a and b), which are mainly granivorous in the dry season but become almost exclusively carnivorous in the rainy season. In the case of *E. ruidum*, environmental factors (temperature, humidity, and density of fodd supply) change much less than in the case of *B. senaarensis* and the changes recorded are of the same type as for many other species (Bernstein, 1974,

Table II

Material brought back to the nest by foraging *E. ruidum* in dry and wet periods.

TYPE OF PREY	DRY SEASON (No.)	(%)	RAINY SEASON (No.)	(%)
Hymenoptera (Formicidae)	32	18.8	40	17.2
Hymenoptera (Others)	1	0.6	16	6.9
Diptera	10	5.9	26	11.2
Lepidoptera	3	1.8	18	7.8
Homoptera	13	7.6	16	6.9
Coleoptera	6	3.5	10	4.3
Orthoptera	2	1.2	3	1.3
Hemiptera	4	2.4	3	1.3
Dictyoptera	3	1.8	1	0.4
Zoraptera	1	0.6	-	-
Neuroptera	1	0.6	-	-
Psocoptera	-	-	3	1.3
Isoptera	-	-	2	0.9
Araneidae	4	2.4	5	2.2
Other	-	-	31	13.4
Undetermined	13	7.6	11	4.7
Fruit	22	12.9	10	4.3
Liquid	27	15.9	-	-
Plant and organic material	28	16.5	37	15.9
Total	170 samples		232 samples	

1975; Whitford and Ettershank, 1975; Lévieux and Diomande, 1978; Lévieux, 1979 a and b). In the rainy season they are reflected in:

- a decrease in the number of active foragers (compare curves of exits for nests A, B, C, and D in Figure 3), compensated for by the increase in the duration of foraging trips and in success rate (rising from 12% to 19.2%);
- a decrease in carbohydrate intake, both in liquid form (which disappears) and in solid form (making up 4.3% of entrances with material versus 15.4% in the dry season);
- an increase in protein intake with, at the time, a greater range of prey, a substantial increase in the fraction that is "energy rich" (larvae), and a very clear increase in active predation relative to necrophagia.

Two main factors may explain these differences: the high density of prey during the rainy season; and the fact that for *Ectatomma* this season corresponds with the period of brood development, so that more protein is needed than in the dry season. Our laboratory studies confirmed that societies with large brood have a diet much richer in protein (flies, mealworms, crickets) than societies made up mainly of adults, which preferentially consume carbohydrates (in the form of honeydew). During the dry season in the field, carbohydrates, that represented 28.8% of the material collected, were brought back to the nest either as droplets carried between the mandibles or as little pieces of fruit pulp (oranges, grapefruit, *Inga* fruit). This fruit pulp was taken into the nest, sucked by the workers of the larvae, and several hours later, when all the juice had been sucked out, thrown out by the workers that clean and maintain the nest. In the study zone, during these observations (January-February 1982) a lot of fruit had fallen to the ground, and this was exploited as the colony's main carbohydrate supply. At other times of year, when the foragers did not come across fruit on the ground, they could climb up the tree trunks and stock up from flows of sap or from the foliage of coffee and orange trees. It is very likely that in this latter case the liquid collected was the honeydew produced by Homoptera on the leaves; in fact foragers were seen soliciting from small black aphids (species undetermined) and from *Toxoptera aurantii* and collecting the anal secretions of these Homoptera. In addition, *E. ruidum* in Ecuador and Trinidad are known to exploit, at least occasionally, the honeydew produced by Homoptera such as membracids and coccids (Weber, 1946).

Whatever the season, *E. ruidum* is mainly carnivorous. Because of this, and considering the high density of nests of this species in the zone of the study, the role of *E. ruidum* as an element of biological control in coffee/cocoa plantations seems to be undeniable. Its capacity to vary its activity pattern and diet according to seasonal variations in the density of prey, together whit its capacity to adjust its foodgathering strategy to the amount and proximity

of food supplies (Lachaud et al., 1984; Lachaud, 1985), have surely contributed to the ecological success of *E. ruidum* in the neotropical region.

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