FORAGING ECOLOGY OF THE APHID-TENDING ANT *CAMPONOTUS CRUENTATUS* (HYMENOPTERA, FORMICIDAE) IN A SAVANNA-LIKE GRASSLAND

A. ALSINA, X. CERDÁ, J. RETANA & J. BOSCH

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Foraging ecology of the aphid-tending ant Camponotus cruentatus *(Hymenoptera, Formicidae) in a savanna-like grassland.*– Several aspects of the foraging ecology of the ant *Camponotus cruentatus* were studied in a savanna-like grassland on the Mediterranean coast. This species is a diurnal insect in spring and autumn, but it extends its activity to the whole day in summer, a feature not observed in any other ant species on the area. It has a wide margin of tolerance to environmental conditions and only very extreme temperature values stop its activity. Its dietary spectrum is quite narrow. Few animal remains, among which excrements of vertebrates are the most frequent, are carried to the nest. Its main food source is honeydew of aphids tended on the surrounding vegetation. *C. cruentatus* is an aggressive species and defends its food sources against other ants.

Key-words: Ant, *Camponotus cruentatus,* Foraging activity, Dietary spectrum, Aphid-tender.

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Anna Alsina & Jordi Bosch, Dept. de Biologia Animal, Fac. de Biologia, Univ. de Barcelona, Avgda. Diagonal 645, 08028 Barcelona, Espanya.– Xim Cerdá & Javier Retana, Lab. de Zoologia, Fac. de Ciències, Univ. Autònoma de Barcelona, 08193 Bellaterra, Espanya. (Reprint requests should be sent to Xim Cerdá.)

INTRODUCTION

Camponotus cruentatus Latreille, 1802 is a common species in all the Mediterranean region, from Portugal to Italy and throughout North Africa. It is widespread in the Iberian Peninsula, both on the coast and in the interior, although it is never found above 1000 meters a.s.l. (SUÑER, 1982). Typically a woodland insect, it can become predominant on calcareous slopes with pine or live-oak forests (BERNARD, 1983). It is more rarely found in forests with less extreme slopes and in scrub areas (SUÑER, 1982).

Little is known about its ecology. It has been found gathering nectar from several plants (HERRERA et al., 1984), carrying insects to the nest, and associated with aphids (SUÑER, 1982; ACOSTA et al., 1986) and Lycaenid caterpillars (MARTIN CANO, 1981). ACOSTA et al. (1986) studied age and biometric variability of the workers and established the relationship of these factors with the role of the workers in the colony. DELALANDE (1986) recorded the activity rhythms of this species in a Mediterranean community. In this work we discuss several aspects related to food collection and activity patterns of *C. cruentatus* in a littoral community (Catalan coast).

MATERIAL AND METHODS

The observations were carried out in Canet de Mar (Barcelona, NE Spain) in a savanna-like grassland (*Hyparrhenietum hirto-pubescentis*), one of the most disturbed communities of the original live-oak grove coastal ecosystem. The vegetation is characterised by a herbaceous layer made up of *Brachypodium retusum, Sedum sediforme, Medicago spp.,*

etc., a higher grass stratum of *Hyparrhenia hirta, Foeniculum vulgare* and *Psoralea vituminosa,* principally, accompanied by sporadic pine trees (*Pinus pinea*).

The ecology of this species was studied throughout 1985 by observing a colony that was relatively isolated from others of the same species. The results were compared with those from other nearby nests.

a) Diet

To study the diet of *C. cruentatus,* three sampling approaches were employed with the object of covering all the food sources exploited by the species.

- The first consisted of gathering prey brought by workers to the nest in ten minute periods each hour on every sampling day. By extrapolation, the number of prey brought to the nest each hour as well as the total number for each day of observation was calculated. The prey was identified in the laboratory, under stereo microscope.
- To analyse the use of liquid food sources, counts were done every two hours of the number of ants that gathered nectar and tended homoptera on previously marked plants. In addition, ants were counted every two hours on branches on nearby pine trees. From these data estimation of the total number of *C. cruentatus* workers on each source type in the foraging area of the colony was carried out. The sum of all ants counted on one day on each source was used as an estimator of exploitation of this type of food. The index of exploitation (IE) is obtained by dividing these numbers by the maximum value.
- To correlate the presence of the ants in these food sources with the liquid food taken to the nest, the method of gently pressing the gaster of the workers that returned to the nest with no apparent prey within their mandibles was used; if they were carrying liquid food in their crop, it was regurgitated in form of a small droplet. This method has been used previously by CHERIX (1981) and RETANA et al. (1986).

The hours of nectar production were determined in the flowers of fennel (*Foeniculum vulgare*), the only plant on whose flowers considerable numbers of *C. cruentatus* workers were observed. Two groups of randomly chosen inflorescences were selected. In the first, the flowers were protected from the activity of ants or other nectarivorous insects by covering them with fine gauze during the day. At dusk the flowers were observed with a hand magnifier (10x) to detect the possible presence of nectar. In the second group the flowers were protected during the night and observed in the early morning. If nectar was present in the first group of flowers, a daily production of nectar would be implied. If, to the contrary, there was nectar in the second group, the production would have taken place at night.

b) Foraging activity

To study the activity of *C. cruentatus,* the number of ants that entered and left the nest during ten minute intervalls every hour for a whole day was counted. A total of 12 measurements were taken from March to November, which covers the entire active period of the species. The average mean of entries and exits was taken as an index of activity.

Together with the hourly measurement of activity, the following environmental factors were recorded: ground temperatures at diferent levels (0.5 cm, surface in the sun and in the shade, 5, 10 and 30 cm deep), air temperature in the shade, relative humidity and light intensity.

c) Foraging area of the colony

The vegetation surrounding the colony was inspected and the workers found there were located. Many of these workers were followed on their way back to the nest, especially those that were further away, so as to ascertain that they belonged to the colony. In this way, the total extend of the foraging area was assessed. The limits were set at the furthest points in which workers of the colony were observed.

RESULTS

a) Diet

The diet of *C. cruentatus* in Canet de Mar is composed of sugary liquids and, to a lesser extent, solid prey. However, the proportion of workers that arrive at the nest with obvious prey within their mandibles is very low, comprising only 5.9% of the total. This figure is in agreement with the data in the literature for other species of *Camponotus* (SANDERS, 1972; CURTIS, 1985; Levieux, pers. com.). It is important to note that all of these items were taken to the nest in the daytime, even though activity also occurs at night.

Table 1 presents the results of the analysis of 116 items taken from the workers. Clearly, the most frequently collected animal remains are the excrement of vertebrates (reptiles, birds, small mammals). Usually, they were small-sized whole excrements (mean 5mm length, n=70) and were carried individually by the workers. Only occasionally did the workers carry small pieces that had been broken off from larger excrements.

Some arthropods were also taken by the workers. Generally they were very dehydrated and small (mean 5mm length, n=30) in proportion to the size of the workers (6-14mm length). This distinguishes this species from others of the same community (e.g. *Aphaenogaster senilis* and *Cataglyphis cursor*), that base their diet on animal remains and which collect much larger items in relation to their own size (unpublished data).

Very few seeds and plant remains were taken to the nest during the study period, as was to be expected, as it is known that they are unimportant in the diet of the genus. Only on given occasions (CURTIS, 1985) has the collection of a large amount of plant elements been recorded, and then in relation to nest construction.

As far as the apparent inefficiency of the workers that do not appear to transport any prey is concerned, there are some possible explanations. Some may be carrying liquid food, while others, as SANDERS (1972) says, may form part of a group of available individuals in the exterior of the nest. So as to distinguish the two, the aforementioned method of pressing the gaster and observing the presence or not of regurgitated droplet was applied. The results in table 2 confirm that a high pro-

Table 1. Number and percentage of loads taken to the nest by workers of *Camponotus cruentatus* (n=116).

Número y porcentaje de los diferentes tipos de presas aportadas al nido por las obreras de Camponotus cruentatus *(n=116).*

Loads	N	%
Excrements	79	68.1
Small mammals	45	38.8
Birds	26	22.4
Reptiles	5	4.3
Not identified	3	2.6
Arthropods	31	26.7
Formicidae	8	6.9
Heteroptera	4	3.4
Homoptera	3	2.6
Diptera	4	3.4
Lepidoptera	3	2.6
Other Insects	3	2.6
Araneida	5	4.3
Isopoda	1	0.9
Gasteropoda	2	1.8
Plant remains	4	3.4

Table 2. Proportion of workers entering (with and without prey) or leaving (without prey) the nest with or without liquid food in their crop.

Proporción de obreras que llegan (con y sin presa) o abandonan (sin presa) el nido con o sin alimento líquido en el buche.

Content of the crop	Entries without prey	Entries with prey	Exits
With liquid	356 (82%)	7 (37%)	10 (14%)
Without liquid	80 (18%)	12 (63%)	60 (86%)
Totals	436 (100%)	19 (100%)	70 (100%)

portion of ants that enter the nest without solid prey are carrying liquid in the crop (almost 82%). The figures for the workers that enter the nest with a solid prey and for those that leave it, are lower (37 and 14% respectively). GOTWALD (1968) analysed the crop content by dissecting the workers of *Camponotus noveboracensis* that were returning to the nest and he also confirmed the large proportion of ants with crops practically full of liquid. In all, 80% of the foragers returned to the nest carrying liquid, in comparison with only 5.9% carrying solid prey.

This liquid food supply is related to the presence of *C. cruentatus* workers in the vegetation near the colony, either licking nectar on flowers or tending aphids. Three stages can be distinguished in the use of these sources over the year:

1) Until mid-June, workers do not go to the flowers nor the aphids then present, which are nevertheless visited by other ants such as *Camponotus foreli* or *Tapinoma nigerrimum*. Only sporadic visits to *Alyssum maritimum* flowers were recorded during this period.

2) From June to late-July, large numbers of *C. cruentatus* were recorded on a pine tree near the colony collecting honeydew produced by the aphid *Cinara maritimae*.

3) From August to November, the workers actively visit the plants of the Umbellifera *Foeniculum vulgare* (fennel) where they gather nectar from the flowers and tend aphids of the species *Aphis fabae*.

These results are expressed in figure 1 in total values for each day of measurement and for the entire area exploited by the colony. We observe that the exploitation of the aphids on the pine tree is much more important than that of the other liquid food sources. The collection of nectar from fennel requires fewer workers than that of honeydew of the aphids present in this plant, and it ends sooner, at the end of flowering period.

b) Foraging activity

In Canet de Mar, some species of ants follow, within narrox margins, constant activity patterns over the season. Thus, *Cataglyphis cursor* is a strictly diurnal species, while *Camponotus sylvaticus* is a twilight and nocturnal species (unpublished data). In contrast, the activity rhythms of *C. cruentatus* vary considerably. The daily curves for the different periods of the year are shown in figure 2. During the first months, the activity is diurnal

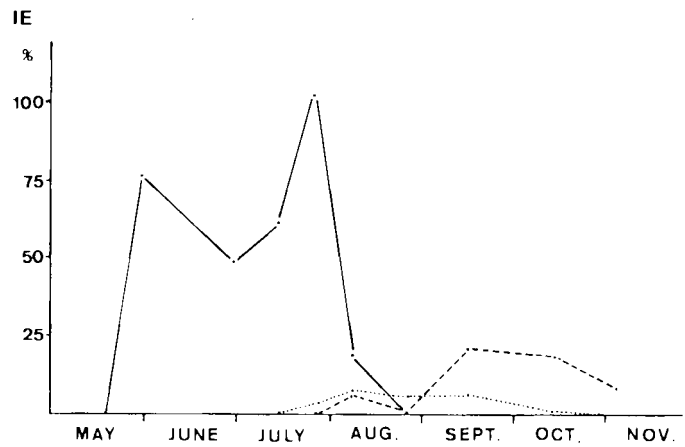


Figure 1. Exploitation over the year of liquid food sources by *C. cruentatus:* —— aphids on pine tree; – – – aphids on fennel; ···· nectar from fennel. X-axis: months of the year; Y-axis: exploitation index (IE) (%).

Explotación a lo largo del año de las principales fuentes de alimento líquido por parte de C. cruentatus*:* —— *áfidos del pino:* – – – *áfidos del hinojo;* ···· *néctar del hinojo. Abcisas: meses del año; ordenadas: índice de explotación (IE) (%).*

and more or less constant over the day. Gradually, the curves enter the night period and, in June, July and August, the activity is continuous around the clock. This is the period of maximum activity being the variations are also largest because the environmental factors reach extreme values (on one of these days, July 24, the exterior temperatures were so high –see later– that activity stopped at midday). After the end of August, activity becomes exclusively diurnal once again and gradually decreases. In November workers can only be seen removing dirt from the interior of the nest and preparing for hibernation. Afterwards, during the winter, activity ceases completely.

This continous activity has also been observed by DELALANDE (1986) in another Mediterranean community. It can be explained by the fact that the colony bases its feeding on the honeydew which is produced continously throughout the day by the aphid *Cinara maritimae*. This has been observed in other species that utilise the honeydew of aphids as their main food source (HENNAUT-RICHE et al., 1980; CHERIX, 1981). However, other ants of the study area that also tends aphids (such as *Tapinoma nigerrimum* and *Camponotus sylvaticus*) do not carry out their activity over the whole day.

Although the number of ants leaving and entering the colony is a good indicator of the activity of the species, it is not necessarily an estimate of the number of workers found outside the nest in a given moment. The workers of *C. cruentatus* are always present on the pines and plants with aphids during the day although the exterior activity of the colony may stop occasionally. For example, the number of workers dedicated to tending aphids on fennel plant on September 17th was almost constant, with slight variations throughout the day even though the number of ants entering the colony ceased at twilight and did not recommence until the following morning (fig. 1J). Other authors studying other species have noted this continued presence of the ants with their tended homoptera (CHERIX, 1981; GREENAWAY, 1981). GOTWALD (1968) observed that the workers of *Camponotus noveboracensis* remain with them when it rains and then both move to the underpart of leaves.

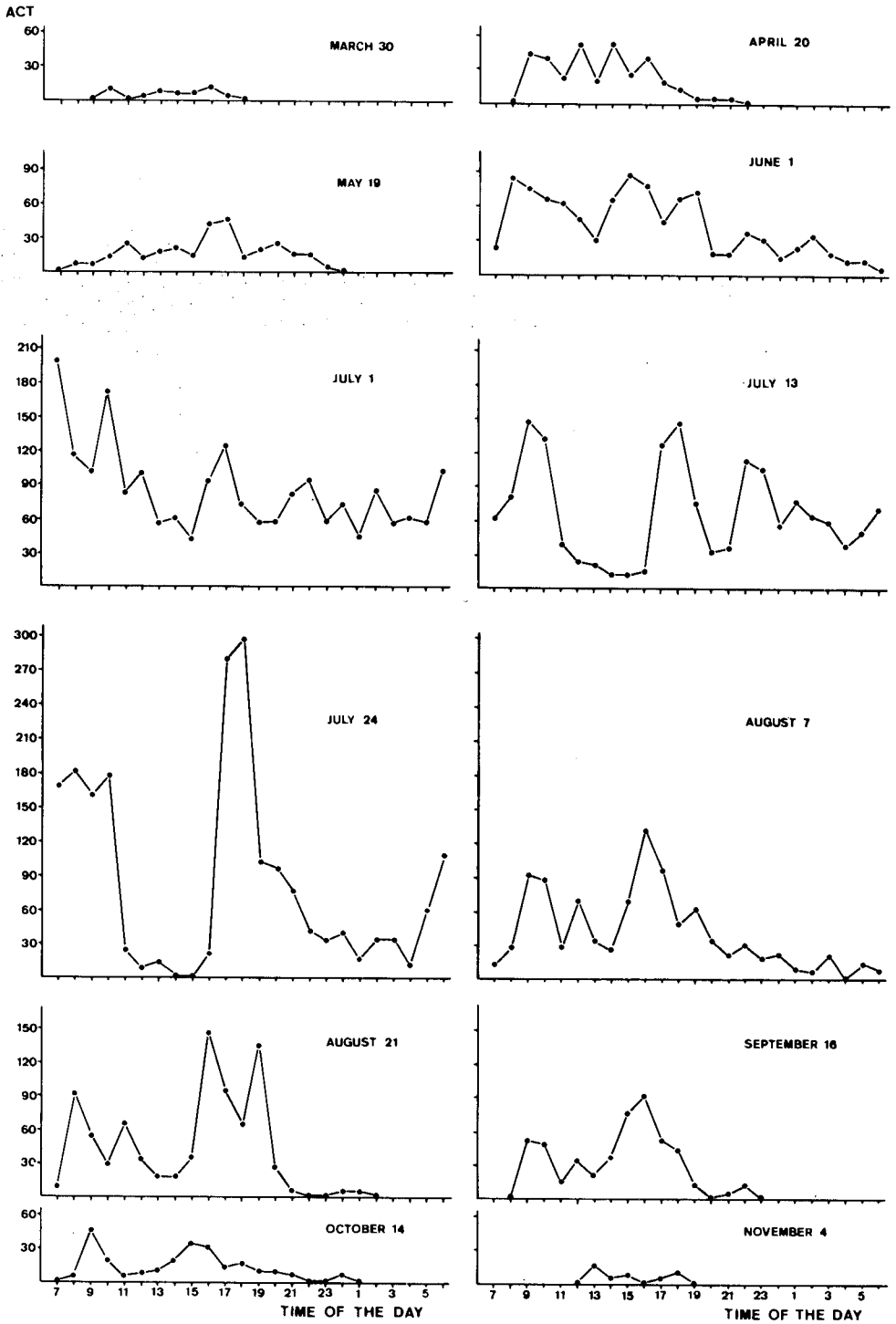
On the other hand, the collection of nectar of *Foeniculum vulgare* is strictly diurnal, even though the exterior activity of the colony continues throughout the day. This can be explained by the fact, which we verified, that this plant only secretes nectar during the day.

The influence of the different environmental factors on the foraging activity of *C. cruentatus* was assessed using multiple regression analysis, but no significant correlations between them was found. Notwithstanding, extreme temperatures can lead to a total halt of activity. Below 15°C, the workers move very slowly and exterior activity ceases completely. At a ground temperature in the shade above 33-34°C (corresponding to 53-55°C in the sun), activity also ceases. On July 24 activity did not resume until the temperature dropped below this limit and then it did so abruptly with up to 58 exits in ten minutes, which were presumably workers that had stayed within nest because of the high exterior temperatures.

c) Foraging area of the colony

The nest density of *C. cruentatus* is around one or two per 100 m^2 (SUÑER, 1982). However, the colony studied in Canet de Mar was relatively isolated from others of the same species. This made the study of the foraging area of the colony much easier.

Figure 3 shows the foraging area of the colony, which covered 230 m^2, including a pine tree and 14 fennel plants. As seen previously, not all the resources found by the *C. cruentatus* workers in the foraging area are used during the same period. During the first months, the exploited area is practically limited to pine tree A, located 3.5m from the nest and which makes up 6-8% of the territory. When the fennel plants flower, the workers start gathering the nectar and the aphid honeydew found there, and cover almost 100% of the foraging area of the nest.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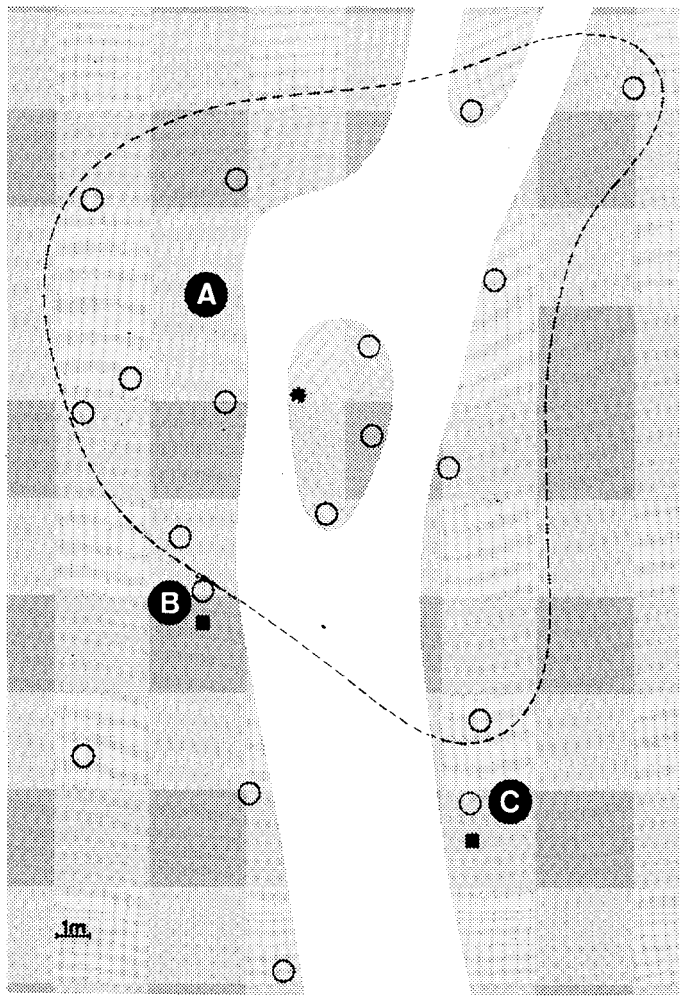

Figure 3. Foraging area of the observed *C. cruentatus* colony: --- limits of the area; * *C. cruentatus* nest; ■ *C. sylvaticus* nest; ● pine tree; ○ fennel plant; ▒ vegetation; □ path.

Area de recolección de la colonia de C. cruentatus *estudiada: --- límites del área; * nido de* C. cruentatus; ■ *nido de* C. sylvaticus; ● *pino;* ○ *planta de hinojo;* ▒ *vegetación;* □ *camino.*

C. cruentatus is a very aggressive species that defends the surroundings of the nest against any intruder. The lack of other *C. cruentatus* colonies surrounding the nest under observation, made it impossible to assess the relative importance of intraspecific competition, but interspecific competition, however, was observed. In the same area there were quite a few nests of another ants of the same genus, *C. sylvaticus*, which is also very aggressive and defends its food sources. This species feeds almost exclusively on the honeydew secreted by the homoptera; however, their activity is carried out at night and

Figure 2. Daily foraging activity of *C. cruentatus*. X-axis: time of the day (local standard time); Y-axis: activity (ACT) (average mean of entries and exits per hour).

Curvas diarias de actividad de C. cruentatus. *Abcisas: hora del día (hora local); ordenadas: actividad (ACT) (semisuma de entradas y salidas por hora).*

seasonally commences rather late in the year (unpublished data). This reduces somewhat the competition of the two species for the same sources. Notwithstanding, during July and August, the interaction between the two was intense and resulted in fights that took place whenever heterospecific workers met. Then it was common to find many mutilated workers of *C. cruentatus* and others with heads of *C. sylvaticus* attached to their limbs and antennae. We found that gradually, the activity of *C. sylvaticus* increased and that of *C. cruentatus* decreased until in mid-August, pine tree A was almost completely occupied by the former species, although we cannot affirm whether there was a direct or causal relationship between the two situations. In any case there was a clear segregation of the resources exploited by the different colonies of *C. cruentatus* and *C. sylvaticus,* because the other pine trees that are close to the colony of *C. cruentatus* (B and C in fig. 3) were occupied all year by workers of two colonies of *C. sylvaticus,* and ants of the other species were never observed there.

DISCUSSION

Two important aspects stand out in the foraging ecology of *C. cruentatus* in our study area: the considerable variability in time of exterior activity and the relatively narrow range of food resources used.

The daily rhythm of activity was exclusively diurnal in spring, occupied 24 hours in summer, in autumn was diurnal once again and ceased completely in winter. This coincides roughly with the typical seasonal variation in temperate climates. This species has a wide margin of tolerance to the environmental conditions and therefore only very extreme values lead to a decrease in foraging by the colonies.

The diet, on the other hand, is quite restricted. The main food source was honeydew secreted by aphids found in a pine tree near the nest. The other liquid food sources, as well as those of solid food, were used to a much lesser extent by *C. cruentatus*. This is a general trend of the *Camponotus* genus: many authors have studied the feeding habits of different species and all agree that the secretions of homoptera are the main staple of their diet, to such an extent that all of them have been associated with aphids, coccids, etc., which live either on the superficial parts (GOTWALD, 1968; LEVIEUX, 1975; LEVIEUX & LOUIS, 1975; CURTIS, 1985) or on the roots (SANDERS, 1970, 1972; GANO & ROGERS, 1983) of plants.

The collection of excrements is particularly interesting, as no other ant species of the area uses this type of source. This fact, together with the small size of the arthropods gathered by the workers leads to the assumption that this species uses the animal remains that others leave behind. Other species, like *Cataglyphis cursor* and *Aphaenogaster senilis,* collect the remains of much larger and less dehydrated arthropods found in the field earlier. Within the same genus, *Camponotus detritus* also uses excrements as a food source (22% of its solid diet) together with sand particles impregnated with mammalian urine (CURTIS, 1985). According to CURTIS (1985), the fact that intracellular bacteria have been found within the digestive tract of several species of *Camponotus* suggests that the excrement is used as a source of nitrogen.

The relative scarcity of *C. cruentatus* seems to indicate that it is not, in our study area, in its ecologically optimal habitat. This may be a consequence of the strong competitive pressure imposed by the other species. A comparison between these results and those obtained in a more forested area, a more common habitat in its distribution (ACOSTA, 1980; BERNARD, 1983), would enable one to relate the observed differences with the abiotic and biotic factors and thus understand their secondary situation in this community.

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RESUMEN

Ecología de la recolección de la hormiga cuidadora de áfidos Camponotus cruentatus *(Hymenoptera, Formicidae) en un prado sabanoide.*

En este trabajo, realizado en un prado sabanoide de la costa catalana (Canet de Mar, Barcelona), se analizan diversos aspectos de la autoecología de la hormiga *Camponotus cruentatus.*

La dieta de esta hormiga está compuesta por líquidos azucarados y, en menor cantidad, presas sólidas (sólo el 5,9% de las obreras regresan al nido con una presa entre sus mandíbulas). En la tabla 1 se describe el espectro de estas presas: el 68% son excrementos (de vertebrados, reptiles, aves y micromamíferos), el 26,7% son artrópodos, y también hay algunos restos vegetales y gasterópodos. Sin embargo la importancia del alimento líquido en el régimen trófico de *C. cruentatus* es mucho mayor: el 82% de las obreras que regresan sin presa al nido llevan en el buche alimento líquido (tabla 2). Las principales fuentes de alimento líquido son la melaza de los áfidos de las especies *Cinara maritimae* (que se halla en los pinos) y *Aphis fabae* (que se encuentra sobre el hinojo), así como el néctar de las flores de hinojo. En la figura 1 se observa la explotación estacional de estas fuentes de alimento: desde finales de Mayo hasta finales de Agosto las obreras explotan la melaza de *C. maritimae,* siendo ésta la principal fuente de alimento de la colonia; a finales de Julio ya es posible encontrar obreras en el hinojo, tanto recogiendo néctar en las flores, como melaza en los grupos de áfidos de la especie *A. fabae.*

El patrón de actividad de *C. cruentatus* varía considerablemente según la época del año (fig. 2): desde principio de Marzo su actividad es exclusivamente diurna y más o menos constante a lo largo del día. Poco a poco la curva se introduce en el período nocturno, hasta que en los meses de Junio, Julio y Agosto la actividad de la especie se hace continua durante las 24 horas del día. Desde finales de Septiembre la actividad vuelve a ser únicamente diurna y progresivamente la recolección disminuye hasta el inicio de la hibernación, a finales de Noviembre.

El área de recolección de la colonia estudiada alcanza un total de 230 m^2, en los que hay un pino y 14 plantas de hinojo (fig. 3). *C. cruentatus* es una especie muy agresiva que defiende los alrededores del nido y monopoliza las fuentes de alimento que ocupa. Por ello se producen combates interespecíficos con *Camponotus sylvaticus* (especie también agresiva y relativamente abundante en la zona de estudio), aunque hay una tendencia a la segregación espacial y temporal entre las obreras de ambas especies.

En la ecología de la recolección de *C. cruentatus* en el prado sabanoide estudiado destacan dos aspectos importantes: la gran variabilidad temporal de su actividad exterior y la relativa limitación de los recursos alimenticios que explota. Esta especie parece encontrarse en esta comunidad lejos de su óptimo ecológico, dado que es mucho más abundante en los entornos forestales, y su relativa escasez en el área de estudio puede venir determinada por la fuerte presión selectiva a la que se ve sometida por otras especies que explotan recursos similares.

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