

# FORAGING ECOLOGY OF THE NECTARIVOROUS ANT *CAMPONOTUS FORELI* (HYMENOPTERA, FORMICIDAE) IN A SAVANNA-LIKE GRASSLAND

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Retana, J., Bosch, J., Alsina, A. & Cerdà, X., 1987. Foraging ecology of the nectarivorous ant *Camponotus foreli* (Hymenoptera, Formicidae) in a savanna-like grassland. *Misc. Zool.*, 11: 187-193.

*Foraging ecology of the nectarivorous ant Camponotus foreli (Hymenoptera, Formicidae) in a savanna-like grassland.*— Foraging activity and food collection of the ant *Camponotus foreli* were studied in a savanna-like grassland on the Mediterranean coast. This is a thermophilous species with diurnal activity depending on the hours of flower nectar production. Its main food sources are nectar of flowers and, to a lesser extent, aphid honeydew. Solid prey are very rare. *C. foreli* does not defend these food sources, and this unaggressive behaviour allows its coexistence in space and time with the other ants of the community that exploit the same resources.

Key words: Ant, *Camponotus foreli*, Foraging activity, Dietary spectrum, Nectar-eater.

(Rebut: 19-V-1987)

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## INTRODUCTION

*Camponotus foreli* Emery, 1881 is common in Southern France, Spain and the Algerian coast (BERNARD, 1968), inhabiting dry areas with sparse vegetation. In Spain, it is found in the Ebro and Guadalquivir basins, in the Guadarrama mountain range and along the entire Mediterranean coast (SUÑER, 1982), but it has been little studied. This paper deals with its foraging activity and diet.

## MATERIAL AND METHODS

This work was carried out in Canet de Mar (Barcelona) in a savanna-like grassland (*Hyparrhenietum hirta-pubescentis*). Throughout 1985 two nests of *C. foreli* were observed during the entire period of activity, from March to November. In 12 days of measurement several aspects related to food collection were studied.

### a) Foraging activity

To measure the exterior activity of the colonies, the number of workers that entered and left the nest during the first ten minutes of each hour throughout the day were counted. From these data the total value for each hour was extrapolated and the daily total also calculated. The average number of entries and exits was taken as an activity index.

Environmental parameters were recorded in an attempt to find their influence on the activity of the species. These were: ground temperatures at different levels (surface in the sun and in the shade, and 5, 10 and 30 cm deep), air temperature in the shade, relative humidity, and light intensity.

### b) Dietary spectrum

The diet of *C. foreli* was studied using two complementary methods:

– At the nest, the number of workers that returned with prey were counted. The prey was

taken from the ants for identification in the laboratory, under a stereo microscope. The possible supply of liquid food was also analysed by pressing the gaster of the workers so as to observe the regurgitation of liquid from the crop.

– On flowers and among groups of aphids on the surrounding vegetation, the number of *C. foreli* workers that were collecting nectar or honeydew were counted. To do this, some plants which were inspected every two hours during each day of observation were marked. Since the foraging areas of the colonies overlap, it was impossible to distinguish the workers of each colony and therefore the results are totalled for all of them.

The relative abundance (RA) of plants was estimated from three transects which together added up to a total length of 100 m. In these, the presence or absence of each plant species was made every 0.5 m. The phenology of the main entomophilous plants was estimated.

From the data on the marked plants and those of abundance of the different plant species, the importance of each in the diet of *C. foreli* was estimated. To do this, an index of abundance (IA) of *C. foreli* workers in each plant was devised with the expression:

$$IA_i = \frac{NA_i}{NP_i} \cdot RA_i$$

where:  $IA_i$  is the abundance of *C. foreli* workers in the plant species  $i$ ;  $NA_i$  is the number of workers counted in the marked plants of species  $i$ ;  $NP_i$  is the number of inspected individuals of plant species  $i$ ;  $RA_i$  is the factor of relative abundance of plant species  $i$ .

## RESULTS

### a) Foraging activity

The first *C. foreli* workers were found on flowers of *Euphorbia* sp. at the end of March. However, the nests under observation were not active until somewhat later, towards mid-April. Until the end of May activity was minimal and the presence of ants on flowers sporadic. During this period of the year the

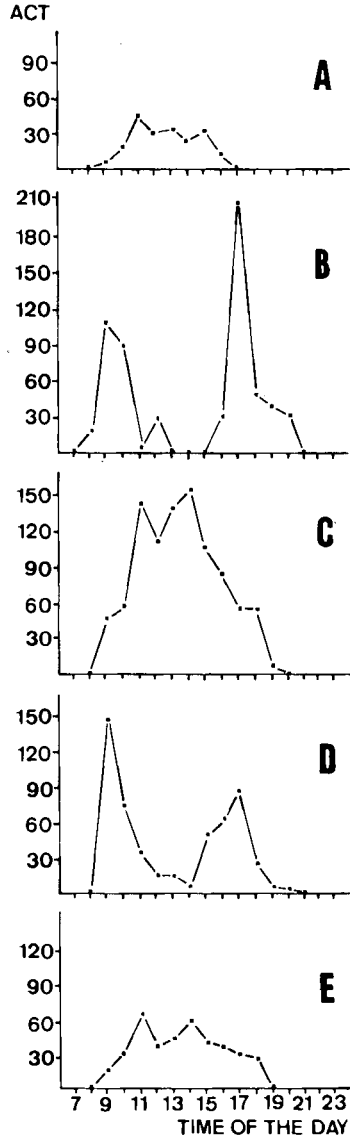


Fig. 1. Daily activity curves of *C. foreli* nests in: A. May 19; B. July 13; C. August 7; D. August 21; E. September 16. (Average mean of entries and exits per hour.)

Curvas diarias de actividad de *C. foreli* en: A. 19 mayo; B. 13 julio; C. 7 agosto; D. 21 agosto; E. 16 septiembre. (Semisuma de entradas y salidas por hora.)

pattern of daily activity was unimodal with a maximum at the hottest period of the day (fig. 1A).

This changed drastically in summer when the pattern became bimodal (fig. 1B). It was possible to confirm in the field that this change was not triggered by an endogenous rhythm, but instead was a response to the high temperatures recorded in this period at noon: on August 7, when the temperature was lower than normal all day, the activity did not drop at midday (fig. 1C), while a few days later, August 21, the temperatures reached high values once more and the bimodal curve was reestablished (fig. 1D). Activity dropped considerably from September onwards (fig. 1E), and ended in November. Similar variations in activity patterns due to harsh environmental factors during the dry period have been observed in many ant species of warm zones (SHEATA & KASCHEF, 1971; LEVIEUX, 1979; Levieux, pers. com.).

In milder seasons, *C. foreli* was active during the hours of sunlight, starting at day-break, when there was a massive exit of workers from the colony, ending at twilight when the ants that were still outside returned to the nest. Therefore, the workers did not spend the night out of the nest, although there were rare exceptions. At the beginning of June, when *Silene inflata* was in flower, some workers spent all the night within these flowers tending aphids of the species *Brachycaudus (Acaudus) populi*. This could be because the characteristic corolla structure in the flowers provided a favourable microclimate.

This strictly diurnal activity shows that solar radiation is one of the environmental factors that most directly affects the daily rhythms of the colonies, either by raising the temperature or by stimulating nectar secretion of the flowers, which is an essential food for the species.

Temperature is another critical factor governing foraging activity. At temperatures under 19-20°C activity outside the colony ceased almost completely. On the other hand, this species is tolerant of heat, in kee-

ping with the areas where it habitually nests, which are dry and hot. In Canet de Mar, maximum activity took place at temperatures between 23-33°C in the shade, equivalent to 25-50°C in the sun. When it was hotter, the workers did not leave the nest, although they did remain in the flowers, where humidity and temperature were more benign. For example, on August 21 at 2:00 pm the ground temperature was 50°C and there was almost no workers on it, while in the flowers, at one meter above the ground, the temperature was only 33°C and the ants were gathering nectar as usual.

#### b) Diet

As in many other species of *Camponotus* (GOTWALD, 1968; SANDERS, 1970, 1972; LEVIEUX, 1975; LEVIEUX & LOUIS, 1975; GANO & ROGERS, 1983; CURTIS, 1985) nectar and homoptera honeydew were the food resources most frequently exploited by *C. foreli*. Of the 1300 ants observed returning to nests A and B, only 47 workers (3.7%) were carrying solid food. Most of this was the remains of various arthropods, although some was excrement of vertebrates.

This lack of solid prey contrasts with the intense activity of aphid tending, and even more so, of visiting flowers, which leads to a very high proportion of workers returning to the nest with liquid food in their crop (table 1). The difference in numbers of ants entering and exiting with liquid is highly significant (chi-square contingency,  $P < 0.001$ ).

*C. foreli* is, of all the ants of the area, the most exclusively nectarivorous, as indicated by both the great variety of flowers it visits

Table 1. Proportion of workers of *C. foreli* that enter or leave the nest with or without liquid food in their crop.

*Proporción de obreras de C. foreli que entran o salen del nido con o sin alimento líquido en el buche.*

Contents of the crop	Entries	Exits
With liquid	270 (85%)	20 (33%)
Without liquid	48 (15%)	40 (66%)
Totals	318 (100%)	60 (100%)

and its abundance on them. Table 2 summarises the flowering periods of the most important entomophilous plants and shows on which of them workers of *C. foreli* were found. Not all the plants were exploited in the same manner. On some, the ants were engaged obviously in nectar collection, as for example in the Umbelliferae *Daucus carota* and *Foeniculum vulgare*, on whose flowers the *C. foreli* workers spent long periods collecting the nectar as it was produced. However, on other plants like *Galactites tomentosa* or *Centaurea aspera*, the ants had not been observed collecting nectar but simply biting or licking the bracts of the calyx without reaching the corolla. Some plants were visited assiduously over their flowering period (among these *D. carota* and *F. vulgare* stand out), there were others that even though are abundant, they were never or rarely visited (*Ononis natrix*, *Lathyrus lathifolius*, *Sedum sediforme*).

There are several factors that influence whether the plants are visited or not: the accessibility of nectaries and the corolla depth, the nutritional value of the nectar, the adap-

tations of some plants which tend to reduce the negative effects of the ants, a more efficient exploitation by other groups of insects, etc. In our case, the flowers most exploited by *C. foreli* and the other ants of the area have in common very open corollas, an observation which agrees with the results obtained by HERRERA et al. (1984) in a study of the ants of Southern Spain.

Honeydew produced by aphids was another important food resource for *C. foreli*. As in the case of nectar, different aphid species were used to a different degree. The most numerous species was *Aphis fabae*, present throughout the vegetative period of the fennel (*F. vulgare*), which was frequently tended by *C. foreli*. Other aphids, such as *Brachycaudus cardui*, *Cinara maritimae* or *Eulachnus tuberculostemmatus*, which were exploited intensely by other ants of the area, received visits from *C. foreli* only rarely.

Figure 2 shows the abundance of workers throughout the year at the principal sources of liquid food. Numbers of ants on plants that were not very abundant or those that received few visits by *C. foreli* are not shown because

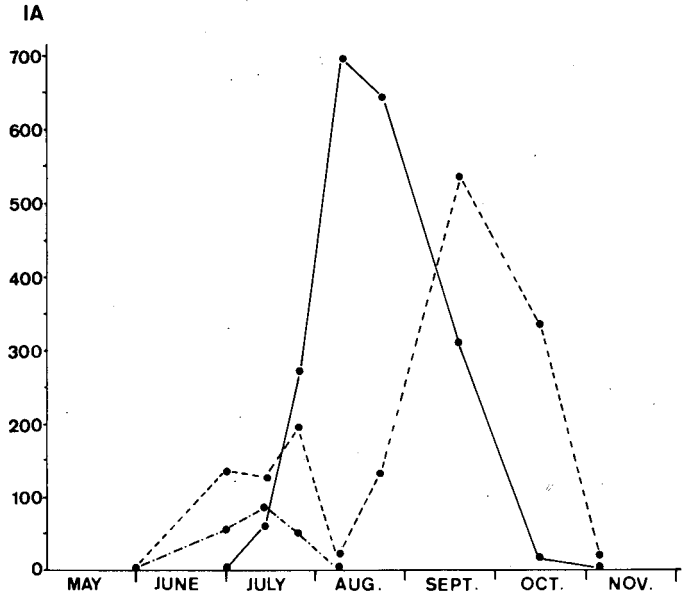
Table 2. Flowering periods over the year of the most important entomophilous plants in the study area. Flower quantity: + not very abundant; ++ abundant; +++ very abundant. Presence of *C. foreli* workers on the flowers: \* collecting nectar; o. Nectar collection not proved.

*Periodos de floración de las principales plantas entomófilas del área de estudio. Número de flores: + Poco abundante; ++ Abundante; +++ Muy abundante. Presencia de las obreras de C. foreli en las flores: \* recogiendo néctar; o. Recolección de néctar no comprobada.*

Plant species	30-III	20-IV	19-V	1-VI	15-VI	1-VII	13-VII	24-VII	7-VIII	21-VIII	16-IX	14-X	4-XI
<i>Alyssum maritimum</i>	+	+	+++*	+									
<i>Euphorbia sp.</i>	+*	+*	+*	+*									
<i>Medicago spp.</i>		+	+++										
<i>Antirrhinum majus</i>		+	+	+o									
<i>Galactites tomentosa</i>		+	++	+++	+								
<i>Lathyrus lathifolius</i>		+	+	+++*	+								
<i>Ononis natrix</i>		+	+++	+++	+								
<i>Vicia benghalensis</i>		+*	+++*	+++*	+								
<i>Silene inflata</i>			+o	+o									
<i>Borago officinalis</i>			+*	+*									
<i>Centaurea aspera</i>				+o									
<i>Scabiosa atropurpurea</i>				+	+++*	+++	+++	+					
<i>Echium vulgare</i>					+								
<i>Daucus carota</i>					+*	+++*	+++*	+*	+*				
<i>Sedum sediforme</i>						+	+++	+					
<i>Foeniculum vulgare</i>							+	+++*	+++*	+++*	+++*		
<i>Inula viscosa</i>												+++*	+*

Fig. 2. Abundance of workers of *C. foreli* on the principal sources of liquid food. IA. Index of abundance; ---- *Daucus carota* nectar; — *Foeniculum vulgare* nectar; ---- *Aphis fabae* honeydew.

Presencia de las obreras de *C. foreli* en las principales fuentes de alimento líquido. IA. Índice de abundancia; ---- Néctar de *Daucus carota*; — Néctar de *Foeniculum vulgare*; ---- Melaza de *Aphis fabae*.



of low IA values. Initially, workers went to the plants that were in flower. When *D. carota* flowered, the ants regularly collected nectar from this Umbellifera, and also tended aphids on fennel, which started its vegetative period around this time. This latter activity occupied more workers than did the exploitation of *D. carota* because this plant was not very abundant. The collection of nectar from *D. carota* ended at the start of August, at the end of its flowering period. Meanwhile, when *F. vulgare* reached its flowering peak, workers abandoned aphid tending and concentrated on inflorescences of this species. As the flowers deteriorated in condition, the workers returned to the aphids.

## DISCUSSION

These results indicate a predominance of nectar collection over that of honeydew, and even more so over the use of solid prey. The fact that *C. foreli* is principally a nectar-eater, limits its activity outside the colony to periods of nectar production. On a daily basis, activi-

ty is limited to the hours of sunlight, when nectar is secreted. On an annual basis, the periods of activity coincide with flowering periods of the principal plants used by the species.

As in many other species that feed principally on nectar and honeydew, colonies of *C. foreli* may store reserves for periods of scarcity in the form of large quantities of lipids that are accumulated in the fat bodies of some larger-sized workers. This phenomenon, called adipogastry (WILSON, 1971), has been observed in some *Camponotus* of the desert (EMERY, 1898; WHEELER, 1928) as well as in some Iberian species such as *Camponotus micans* (X. Espadaler, pers. com.). This fat serves as a food reserve, not only for the workers, but also, through the metabolism of salivary secretion, for the larvae (WHEELER, 1928). Storage of energetic reserves is typical in habitats in which food supply is unpredictable (CARROLL & JANZEN, 1973). In this case, nectar is a predictable resource in space but not in time, since it runs out over the day and appears and disappears with the start and end of flowering period of each plant species.

These fluctuations in the main supply of food and the small size of the colonies make the defense of a territory too expensive. *C. foreli* can be considered an "insinuator" species in the sense of WILSON (1971), because it does not defend its food sources and instead coexists in space and time with the other ants. This has been verified by observations on the behaviour of the ants not only on the flowers and groups of aphids, but also on baits of honey that we placed in the field to carry out parallel studies. The lack of intraspecific and interspecific conflicts (even with other species as aggressive as *Camponotus cruentatus* or *Camponotus sylvaticus*) allows the foraging areas of the different colonies to overlap almost completely. This enables the exploitation of a greater number of food sources and at the same time keeps the colony population within certain limits, without the high cost implied if there were conflicts with nearby nests.

All these aspects of the foraging ecology of *C. foreli* revolve around the basic components of its diet, principally nectar and, to a lesser extent, honeydew. Nectar is rich in sugars, and it has been also confirmed that aminoacids are regular constituents as well (BAKER & BAKER, 1973). Likewise, honeydew has been recognised as a complete combination of nutrients as it contains sugars, aminoacids, proteins, minerals and vitamins (WAY, 1963). Therefore, both can provide a complete diet for the colonies of *C. foreli*. It would be interesting to determine the precise contribution of each food type to the energetic and proteinic requirements of the different life stages and castes of the colony, and whether the few solid prey taken to the nest are really necessary or not.

#### ACKNOWLEDGEMENTS

We are grateful to Prof. Jean Levieux (Orléans) and to Dr. Xavier Espadaler (Bellaterra) for his comments of the manuscript, to Dr. Antonio Meliá for the identification of the aphid species, and to Andreu Bonet for the description of the vegetation of the study area.

#### RESUMEN

*Ecología de la recolección de la hormiga nectarívora Camponotus foreli (Hym., Formicidae) en un prado sabanoide.*

En este trabajo se analizan diferentes aspectos de la autoecología de la hormiga *Camponotus foreli* en un prado sabanoide en Canet de Mar (Barcelona). Esta especie, común en la cuenca mediterránea, nidifica en lugares secos, orientados al sol y con escasa vegetación.

La actividad diaria de la especie es exclusivamente diurna, extendiéndose desde la salida del sol hasta el anochecer. La curva de actividad es unimodal en primavera y otoño, pero se hace bimodal en verano (fig. 1) al cesar la actividad al mediodía a causa de las elevadas temperaturas. Su máxima actividad se desarrolla con temperaturas comprendidas entre 25-50°C (temperatura del suelo al sol), siendo una de las especies más termófilas de la zona.

En la dieta de *C. foreli* la importancia del alimento sólido es relativamente escasa, pues únicamente el 3,7% de las obreras regresan al nido con presa. El análisis de estas presas muestra un espectro variado con una mayoría de restos de artrópodos (tabla 1). Esto contrasta con la gran actividad de estas hormigas en los grupos de áfidos (recolectando melaza) y, sobre todo, en las flores de la zona, donde recogen líquidos azucarados que transportan al nido. Esta especie es la más nectarívora de las que componen esta comunidad, tanto por la gran variedad de flores que visita como por su abundancia en las mismas. En la tabla 2 se indican los períodos de floración de las principales plantas entomófilas del prado sabanoide estudiado y en cuáles de ellas se han observado obreras de *C. foreli*: las Umbelíferas *Daucus carota* y *Foeniculum vulgare* son las plantas en cuyas flores son más abundantes las obreras de la especie, durante junio y julio en la primera, y en julio, agosto y septiembre en la segunda (fig. 2).

La ecología de la recolección de alimento de *C. foreli* gira en torno al néctar, componente esencial de su dieta. Su actividad externa depende directamente de los períodos de producción de néctar, recurso que se agota a lo largo del día, y aparece y desaparece con el inicio y fin de la floración de cada especie vegetal: durante el día la actividad se restringe a las horas de luz (cuando las principales flores visitadas por esta hormiga producen néctar); durante el año, la actividad estacional sigue paralela a la floración de las plantas más importantes.

*C. foreli* no defiende sus fuentes de alimento, y esta conducta no agresiva permite su coexistencia espacial y temporal con otras hormigas de la comunidad que explotan recursos similares.

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