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Exploitation of food resources by the ant *Tapinoma nigerrimum* (Hym., Formicidae)

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ABSTRACT

Several aspects related to *Tapinoma nigerrimum* foraging have been studied. This ant is diurnal at the beginning of the season (from March to May) but it becomes crepuscular and nocturnal from then to November, when it starts hibernation. During the summertime, its activity outside the nest decreases.

This ant may be considered as omnivorous, since it mainly collects aphid honeydew but also some animal items. Interactions for food between *T. nigerrimum* and other ants are discussed. *T. nigerrimum* appears to be an aggressive species that, in our study area, drives away all other ants but *Pheidole pallidula* from food sources. *T. nigerrimum* and other honeydew-consuming ant species partition the exploitation of this food by tending different aphid colonies or tending them at different times of the year.

KEY WORDS: ant, *Tapinoma nigerrimum*, *Pheidole pallidula*, foraging activity, diet, aphid-tending, aggressive behaviour.

RÉSUMÉ

Quelques aspects de la récolte d'aliment chez la fourmi *Tapinoma nigerrimum* ont été étudiés. Son activité journalière est diurne au commencement de la saison (mars à mai). En été, il y a une diminution de l'activité extérieure de l'espèce, et le rythme devient crépusculaire et nocturne, jusqu'à l'arrivée de l'hivernation en novembre.

Tapinoma nigerrimum est une fourmi omnivore. Son régime alimentaire est constitué de cadavres d'insectes et surtout du miellat d'aphidiens. Les interactions entre cette fourmi et les autres en ce qui concerne les ressources alimentaires solides sont discutées : *T. nigerrimum* est très agressive; elle s'attaque

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aux autres fourmis et les empêche d'exploiter les ressources alimentaires, mais elle est maintenue à l'écart de celles-ci par *Pheidole pallidula*.

Il y a une répartition espace-temps entre *T. nigerrimum* et les fourmis qui exploitent des ressources liquides semblables et plus particulièrement en ce qui concerne le miellat des colonies d'aphidiens qu'elles élèvent dans les pins.

MOTS-CLÉS : Fourmi, *Tapinoma nigerrimum*, *Pheidole pallidula*, activité de récolte, régime alimentaire, élevage des pucerons, comportement agressif.

INTRODUCTION

Tapinoma nigerrimum (Nylander, 1856) is an originally Ibero-Mauritanian ant with a Mediterranean distribution which nests preferably in places with scarce arboreal stratum (BERNARD, 1980). Its biological features, together with its capacity to withstand floods (BERNARD, 1983), endow this species with a special ability to colonize coastal areas, where it is particularly abundant (PASSERA, 1977; FERNANDEZ & RODRIGUEZ, 1982; ESPADALER & RODA, 1984).

The species builds shallow extensive nests, often at the base of the plants, and with entrances characteristically surrounded by accumulated sand (BONARIC, 1971) or by typical domes (CASTELLO & ARIAS DE REYNA, 1982). Colonies are composed of several nests inter-connected by two-direction trails of workers that may be several meters long.

This colony structure renders field studies difficult, so knowledge of the species' ecology is still fragmentary (BERNARD, 1950; ESPADALER & RODA, 1984; ACOSTA *et al.*, 1986; FERRADAS *et al.*, 1986). In this paper several aspects related to *T. nigerrimum* foraging activity in the field are studied.

MATERIAL AND METHODS

Field work was carried out in 1985, 1986 and 1987 in Canet de Mar (Barcelona, Spain) at a 50 m. a. s. l. site, 750 m. away from the coastal line. The vegetation of the area (*Hyparrhenietum hirto-pubescentis*) is typical of degradated zones, with a herbaceous layer, a higher grass stratum and sporadic pine trees (*Pinus pinea*).

The study of the foraging activity of an ant like *T. nigerrimum*, that forms extense colonies, raises considerable methodological difficulties, since nests have many entrances connected by worker trails, whose volume varies from moment to moment according to colony requirements and food availability. Therefore, to study the species' activity, three complementary methods have been used on the 12 days (and nights) of observation from March to November 1985.

1. Activity at trails. The number of workers in a trail crossing to and from a line marked with a thread 2 cm above ground surface, was counted for three minutes of each hour for 24 hours on every sampling day. The extrapolation of the results obtained gives the activity per hour and day. So as to relate activity with environmental parameters, air temperature, relative humidity and light intensity were measured every hour.

2. Activity at baits. On every sampling day 30 plastic discs with different food baits (honey, biscuit, sausage, cheese, ham and bacon) were laid all over the study area. Every two hours the number of ants feeding at each bait was noted. This method has some advantages and some disadvantages in

comparison with the former: the data obtained with this method involve different nests, so potential bias due to special conditions of a given nest is avoided, but baits represent an exceptionally rich food source, a fact that may, somehow, modify normal activity of ants (WHITFORD *et al.*, 1980; CERDA *et al.*, 1988). Aggressive interactions with other ants at these baits may also alter the natural activity pattern, since *T. nigerrimum* may be forced to abandon them due to other species.

Data obtained at each bait may either be considered individually or be totaled so as to determine the activity at baits in general from the number of baits occupied or from the total number of workers counted at all baits every 2 hours and every day.

3. Activity at flowers and aphid colonies. Every two hours the number of workers collecting nectar or aphid honeydew was counted on a number of previously marked plants. These included:

– Four branches of pine tree (*Pinus pinea*) where aphids of the species *Cinara maritimae* dwelled.

– Thirteen fennel plants (*Foeniculum vulgare*) where ants collected the nectar of flowers and honeydew of *Aphis fabae*.

– A minor number of other plants (*Galactites tomentosa*, *Daucus carota*, etc.) selected according to their abundance.

To analyze the diet and the foraging strategy of the species, the following methods were used:

1. Solid items brought to the nest by workers were taken for later identification and measurement.

2. To discover potential food preferences, different types of items (dead insects, snails, seeds, etc.) were offered to workers in the field. The elicited response was considered to be positive when the animal tried to take and drag the item, and negative when, after touching it with its antennae it showed indifference or went away.

3. The above mentioned censuses of ants on the vegetation allowed us to know the preferences of *T. nigerrimum* from among different kinds of liquid food: nectar of different flowers and honeydew of different aphid species. The liquid diet of *T. nigerrimum*, and that of other ant species in the area, has been compared by using Schoener's Proportional Similarity Index (PRICE, 1975).

4. To complete these observations and know the efficiency of liquid food collecting (measured as the percentage of workers carrying liquid food with regard to all foragers) we have used the technique of gaster-pressing (CHERIX, 1981): some ants walking along a trail or descending a pine tree trunk were taken and their gaster was gently pressed; those ants carrying liquid in their crops regurgitated a droplet when so treated.

5. Finally, the baits already described allowed us to observe the foraging behaviour of *T. nigerrimum* workers and their defense of large-sized food items when confronted with other ant species.

RESULTS

1. FORAGING ACTIVITY

Activity of *T. nigerrimum* in Canet de Mar varies according to the season of the year (fig. 1): in the first months, activity is exclusively diurnal (fig. 1 A), since night temperatures are too low (less than 10°C); however, from June, activity ceases at midday (when temperatures exceed 30°C in the shade), starts again in the afternoon and continues all through the night (fig. 1 B). Daily activities obtained at trails and at baits are similar, although the latter is more constant at night due to the presence of an important food source. The number of workers of *T. nigerrimum* tending aphid colonies is much more constant: from April (when aphids start appearing on pine trees) workers can be found collecting honeydew 24 hours a day, a pattern also observed in summer months, even when activity at trails ceases at midday (fig. 1). The fact that this ant exploits this type of food with preference to other food available may be related to the particular microclimate

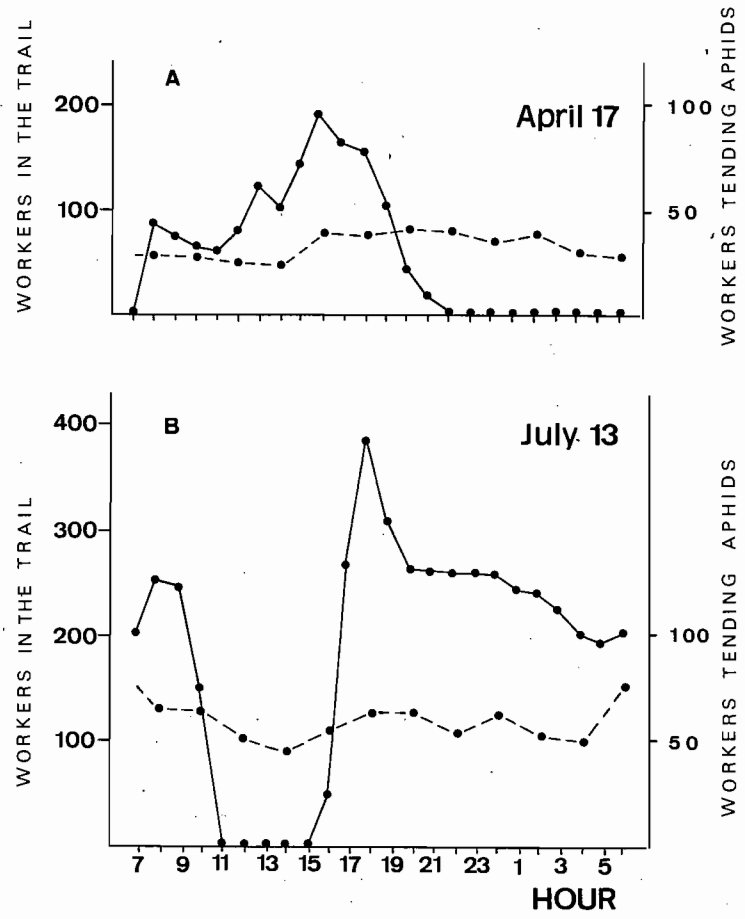

FIG. 1. – Daily activity curves of *Tapinoma nigerrimum* in Canet de Mar. (A) April 17; (B) July 13. Y-axis: left-scale: number of workers crossing a line across the trail during three minutes (———); right-scale: number of workers tending aphids on four branches of pine tree (– – –). X-axis: time of the day (local standard time).

in lower pine tree branches which receive less solar radiation and do not suffer such pronounced fluctuations of temperature, as on the ground surface or as other not-so-shady plants (CERNUSCA, 1977, in LARCHER, 1980). In this way workers are able to stay at aphid colonies and exploit honeydew continuously.

Seasonal activity of *T. nigerrimum* starts at the end of February (fig. 2) and is particularly high from May to June, when temperatures are relatively cool. Before April, foraging activity is still not important, trails are not permanent and most workers forage individually. Later, external activity increases sharply and *T. nigerrimum* becomes a dominant species at baits and on pine trees for the whole night and part of the day. In July its activity decreases rapidly, just as *Pheidole*

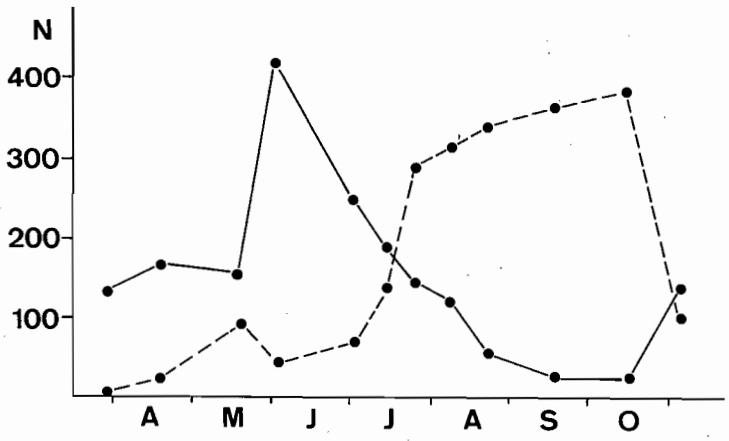

FIG. 2. – Seasonal activity of *Tapinoma nigerrimum* and *Pheidole pallidula* at the baits, estimated as the number of baits occupied by each species on every sampling day. Solid line: *T. nigerrimum*. Broken line: *P. pallidula*.

pallidula, another ant species on the area which interacts with *T. nigerrimum* at baits, becomes more and more abundant (see below).

2. DIET AND FORAGING STRATEGY

T. nigerrimum is an omnivorous ant which preferably collects sugary liquids, but also some animal carcasses. Table I shows the types of items that workers

TABLE I. — *Number and percentage (in brackets) of different types of items collected by* Tapinoma nigerrimum *workers in Canet de Mar* ($N=106$).

Type of items	Frequency	Percentage
Ants	32	(30.2)
Snails	18	(17.0)
Other Insects	13	(12.3)
Spiders	9	(8.5)
Woodlices	1	(0.9)
Vertebrates feaces	1	(0.9)
Unidentified animal remains	32	(30.2)

bring to the nest: most of these are dead arthropods (more than 30% are ants), but snails are also important. Seeds, petals and other plant remains are not at all collected. This trend is confirmed in table II, where the items offered to the workers to evaluate their food preferences are indicated. Individuals tested accepted most arthropods and snails, but systematically rejected plant remains, except for *Centaurea aspera* seeds, which have an elaiosome specially attractive to ants.

The size of solid items carried by *T. nigerrimum* is considerably small (mean = 2.57 mm and 85% of items under 4 mm). This is in correspondence with the foraging strategy of the species. Although most foragers are found on the trails connecting two nests or on the trails connecting one nest with a stable food source

TABLE II. — *Items offered to* Tapinoma nigerrimum *workers. Numbers indicate the frequency of acceptance or rejection of each type of item.*

Type of items	Accepted	Rejected
Animal remains		
Insects	60	0
Spiders	8	2
Snails	13	0
Plant remains		
Centaurea aspera seeds	14	6
Other seeds	1	9
Petals	0	10
Twigs	0	20

(such as aphid colonies on pine trees), a proportion of workers search for food individually and carry to the nest the small items they find. When a worker discovers an item too big, it starts an elaborated mass recruitment system (whose phases have been studied by ACOSTA *et al.*, 1986) which ends up with the establishment of a temporal trail between the nest and the food source. When this happens, food collection may be carried out in two different ways:

– Usually each worker tears a small piece of the item and carries it individually.

– A less common behavior has been observed at sausage and bacon baits, where workers drop small twigs and pebbles that, once impregnated with food, are carried to the nest. This strategy is known as tool using, and is normally used by ants which, unlike *T. nigerrimum*, do not make trophallaxis (AGBOGBA, 1985).

Solid food is quantitatively of relative importance in the diet of *T. nigerrimum*. The foraging efficiency for this type of food (percentage of workers that carry a solid item to the nest with respect to the total number of workers entering the nest) was measured at the beginning of the season, when most trails had not yet been formed and it was still possible to distinguish between workers leaving a nest and those coming back from a foraging trip. The result of 14% efficiency is quite lower than those obtained with other more insectivorous ants of the area such as *Cataglyphis cursor* and *Aphaenogaster senilis*.

Liquid food is much more important to *T. nigerrimum*, as evidenced by the permanent trails connecting nests and liquid food sources and by the continuous presence of workers on plants. By using the technique of gaster-pressing, we have tried to estimate the proportion of workers carrying liquid to the colony: 61% of workers on trails ($n=100$), and 100% of workers leaving pine trees ($n=50$) had liquid in their crops.

The origin of this liquid is diverse: Table III shows the percentages of workers found on the liquid food sources exploited by *T. nigerrimum* in Canet de Mar. As may be observed, honeydew is the only food source quantitatively important, nectar being only occasionally taken. Among aphid species, *Cinara maritimae* (on pine trees) is, by far, the most exploited, *Aphis fabae* (on fennel), and *Brachycaudus* (*Acaudus*) *cardui* (on *Galactites tomentosa*), being of minor importance.

Other ants of the area also feed on honeydew and nectar, mainly three species of the ant genus *Camponotus: C. sylvaticus*, *C. foreli* and *C. cruentatus*. So as to

TABLE III. — *Main liquid food sources of* Tapinoma nigerrimum *in Canet de Mar. Numbers indicate the percentage of workers found on each type of food with respect to all workers counted exploiting liquid food sources* ($n = 11{,}830$). *The asterisk indicates sporadic presence.*

Liquid Food Source	Percentage
Aphid honeydew:	
Cinara maritime (on pine trees)	96.6
Aphis fabae (on fennel)	2.6
Brachycaudus cardui (on *Galactites*)	0.6
Nectar of flowers:	
Daucus carota	0.2
Galactites tomentosa	*
Borago officinalis	*
Lathyrus spp.	*

compare liquid diet of *T. nigerrimum* and these species, similarities between their liquid diets have been calculated: Schoener's index of the pair *T. nigerrimum-C. sylvaticus* is 0.755; for the pair *T. nigerrimum-C. cruentatus* is 0.824, and for the pair *T. nigerrimum-C. foreli* is 0.125. Thus, the dietary spectrum of *T. nigerrimum* is quite similar to that of the two former species but not to that of *C. foreli.* Indeed, this species is essentially nectarivorous, and therefore no interactions for food between it and *T. nigerrimum* are likely to occur.

3. INTERACTIONS WITH OTHER ANT SPECIES AT FOOD SOURCES

T. nigerrimum cannot exploit all food sources with equal intensity throughout the season, since there are other ants also feeding on them. As far as animal

TABLE IV. — *Interactions between* Tapinoma nigerrimum *and other ant species at baits.* T. nigerrimum *may either drive away the other species and occupy the bait (first column), coexist pacifically with it (second column), or be forced to abandon the bait (third column).*

Species	Expulsion	Indifference	Escape
Aphaenogaster senilis	35	2	6
Pheidole pallidula	–	–	17
Cataglyphis cursor	1	5	–
Camponotus foreli	–	5	–
Camponotus sylvaticus	–	1	–
Messor capitatus	2	–	2
Messor bouvieri	1	–	–

remains are concerned, Table IV shows the interactions observed at baits between *T. nigerrimum* and other ant species. Apart from those species which rarely interfer with *T. nigerrimum*, three patterns of interactions are observed:

A. Concerning *Aphaenogaster senilis*, a larger ant that, thanks to its group recruitment system, is able to carry large items in cooperation (CERDA *et al.*, 1988), *T. nigerrimum* displays an aggressive behavior biting legs and antennae of its rivals, and occasionally killing them. Thus, in most cases, *A. senilis* abandons the bait and is substituted by *T. nigerrimum.* The opposite only occurs occasionally

(Table IV) and normally at midday, when *T. nigerrimum* cannot stand the high temperatures registered.

B. Concerning *Pheidole pallidula*, a very aggressive small species that recruits great numbers of workers to food sources, *T. nigerrimum* behaves in a completely different way: many workers of *P. pallidula*, and specially soldiers, attack *T. nigerrimum* workers, decapitating some of them and forcing the rest away.

C. Concerning unaggressive species that search for food individually (as *Camponotus foreli* or *Cataglyphis cursor*), *T. nigerrimum* workers show indifference, up to the point that we have observed them attacking workers of *A. senilis* but ignoring workers of *Camponotus foreli* that were feeding on the same bait.

These interactions between species are shown when succession at baits is analyzed. Figure 3 illustrates an example of what happens on a typical day in July:

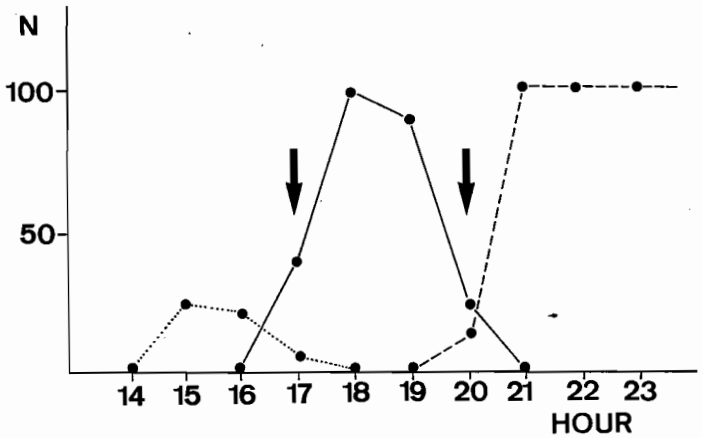

FIG. 3. – Fluctuations of numbers of *Tapinoma nigerrimum* (———); *Aphaenogaster senilis* (...) and *Pheidole pallidula* (– – –) workers at a cheese bait on July 13. Y-axis: number of workers of each species at the bait. X-axis: time of the day. Arrows indicate aggressive interactions between two species.

the bait is initially occupied by *A. senilis* early in the afternoon; when the temperature decreases, *T. nigerrimum* starts its activity and drives *A. senilis* away from the bait, but a few hours later, around 8.00 p.m., *P. pallidula* makes its appearance and, after attacking *T. nigerrimum* workers, occupies the bait for the whole night until the next morning, when it is unable to stay due to hot temperatures.

At aphid colonies on pine trees, these interactions do not take place: neither *A. senilis* nor *P. pallidula* collect honeydew, and as far as the three above-mentioned species of *Camponotus* are concerned, no interactions have been observed, although *C. cruentatus* and *C. sylvaticus* are also territorial species. *T. nigerrimum* dominates the pine trees at the beginning of the season when other ants are little-active; in June-July *C. cruentatus and C. sylvaticus* appear and they partition the unoccupied pine trees; at the end of July *T. nigerrimum* activity diminishes while that of *C. sylvaticus* increases to dominate all pine trees up to the end of the season.

DISCUSSION

T. nigerrimum may be regarded as an opportunistic nester (according to HÖLLDOBLER & WILSON, 1977), that lives in unstable areas and may readily change its nesting site when the old one is disturbed. Its polygynic colonies are typically divided into subunits connected by chemical trails. This endows it with a great ecological plasticity and the ability to colonize degradated areas (ACOSTA, 1980; ACOSTA *et al.*, 1983) with scanty slope and little arboreal stratum. BERNARD (1980) considers it to be the least typical of forest environments of all the Mediterranean ants. Therefore, it is particularly abundant in man-influenced areas (PASSERA, 1977; COMIN & DE HARO, 1980; ESPADALER, 1986), such as our study zone in Canet de Mar.

T. nigerrimum is active when air temperatures vary between 10 and 30°C, normally at night or in the early morning. Its activity decreases at midday and in the hottest months.

Its diet in Canet de Mar is omnivorous: workers collect dead arthropods, but honeydew of aphids (mainly *Cinara maritimae*) is their main food source, something that has already been cited elsewhere (BERNARD, 1977, 1983; ESPADALER, 1986) and is typical of the Dolichoderinae (BERNARD, 1951).

T. nigerrimum uses a combined foraging system in which different strategies are carried out according to the type of food exploited, and similar to the one described for other ant species (CHERIX & ROSENGREN, 1980; BREED & BENNETT, 1985). When they collect insect corpses, they follow an individual strategy typical of primitive species (FRESNEAU, 1985), but when they find an item that is too big they recruit a great number of nestmates that tear and carry the prey to the nest. However, when the food source is abundant, stable and continuous, the strategy followed is predictible, with permanent chemical trails between the nest and the food source, and avoiding interference with neighbour colonies (HÖLLDOBLER & LUMSDEN, 1980). The fact that the foraging strategy is not rigidly determined allows for a high degree of flexibility and variability in the exploitation of ressources which is important in view of the considerable overlap that exists, as we have seen, between the diet of *T. nigerrimum* and other ants in the study area.

Interference between *T. nigerrimum* and other ants for animal remains is avoided in different ways according to the species. The mean size of items collected by the species is much lower than that of the insectivorous *Cataglyphis cursor* and *Aphaenogaster senilis*, since these larger species are able to carry considerably heavier remains. However, as already said, *T. nigerrimum* can also exploit large items by recruiting nestmates and defending food sources against other ants.

In the case of *C. cursor*, interference is avoided because this species forages at the hottest times of the day, when other ants are not active (CERDA *et al.*, in press). *A. senilis*, on the other hand, follows an opportunistic strategy, spotting items before other ants and rapidly carrying them to the nest (CERDA *et al.*, 1988). The substitution between species with different foraging strategies (group recruitment and cooperative transport in the case of *A. senilis*, and mass recruitment and dissection of items in the case of *T. nigerrimum*) is a phenomenon commonly found in ants (HÖLLDOBLER *et al.*, 1978; LYNCH *et al.*, 1980; TRANIELLO, 1983), although it does not always involve aggressive interactions (DE VROEY, 1980).

P. pallidula is another ant competing with *T. nigerrimum* for the exploitation of food sources. Both species are abundant in the area, with nocturnal activity and similar recruitment strategies. However, *P. pallidula* is more aggressive and attacks its rivals more efficiently thus driving *T. nigerrimum* away from baits. Nevertheless there exists a marked seasonal partitioning between both species: *T. nigerrimum* being most active in spring and early summer (that is, in the temperate months of the year when mean temperatures do not exceed 20°C), and *P. pallidula* from late summer to November (when mean temperatures are higher) (*see* fig. 2).

There is also a spatial and temporal partitioning in the exploitation of honeydew of aphids on pine trees between *T. nigerrimum* and other ant species, specially *C. sylvaticus* (*C. cruentatus* also exploits this type of food but is much less abundant). As we have seen, their diets overlap considerably but any given pine tree is exploited by only one species at a time. Furthermore, *T. nigerrimum* is specially abundant at the beginning of the season, whereas *C. sylvaticus* forages in summer and autumn (RETANA *et al.*, 1988). This spatial and temporal partitioning for the exploitation of important food sources is frequent between ecologically dominant ants (HÖLLDOBLER, 1979; BARONI URBANI, 1980; MABELIS, 1984) since it diminishes the likelihood of aggressive encounters and subsequent loss of individuals of competing colonies.

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