Coexistence of two Sympatric Ant Species, Pheidole pallidula and Tetramorium semilaeve (Hymenoptera: Formicidae)

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Pheidole pallidula (Nylander 1848) and Tetramorium semilaeve André 1883 are 2 sympatric ant species that coexist in the same habitat in many places of their widely overlapping distribution. These are their main ecological features: They are 2 small-sized ants that collect animal and plant remains in a similar proportion and that have a similar prey-size range. When they find big prey, they follow the same mass recruitment mechanism, bringing a large number of workers to the baits and defending them against other ant species, by means of their aggressive behaviour. Both are crepuscular and nocturnal species and concur outside the nests during the greater part of their activity period, although their peaks of activity are dissimilar in time. Coexistence of these 2 ecologically similar species is discussed.

Key words: Ants — Pheidole pallidula — Tetramorium semilaeve — coexistence — interspecific competition.

1 Introduction

Ecological theory predicts that resource partitioning is necessary for the coexistence of competing species [MacArthur & Levins 1967, Schoener 1974]. Assuming that most of the renewable resources in an area are utilized, the number of species that can coexist on these resources should be related to the range available, the range of resources taken by each species and how similar the different species are in their use of these resources [Bernstein 1979]. The question is not whether or not organisms are competing, but the emphasis should be on the way in which competition influences the interaction of species and the degree to which it structures communities. The starting point should thus be to analyze the specific methods of resource exploitation as a means of elucidating intra-community relationships [Price 1986].

Pheidole pallidula (Nylander 1848) and Tetramorium semilaeve André 1883 are 2 Myrmicinae ants, with small size, omnivorous diet and crepuscular and nocturnal habits. P. pallidula is a species of great ecological plasticity that can tolerate many variable environmental factors, in such a manner that, being one of the typical species of the Iberian Peninsula holm-oak grove [Acosta et al 1983b], it is also abundant in heaths and zones with scarce vegetation. On the other hand, T. semilaeve is the most abundant species.
of the peninsular holm-oak grove and related habitats [Acosta et al 1983b], but it is also found in pine and oak forests [Martínez 1984] and in moorland and other degraded areas [Acosta et al 1983b].

*P. pallidula* and *T. semilaeve* have a broad Mediterranean distribution [Bernard 1968, 1983] and have been frequently found together in the Iberian Peninsula [Titant 1981, Acosta et al 1983a, Martínez 1984, Pascual 1986, Espadaler 1986], and also in other Mediterranean countries such as France [Bernard 1983] or Malta [Baroni Urbani 1968]. They also coexist in Canet de Mar, a location of the Mediterranean coast which has been the subject of many studies in recent years [Retana et al 1988, 1991, Cerdá et al 1988, 1989a, 1989b]. It is therefore interesting to analyze the parameters that could explain the usual sympatry of both species. Since single factor comparisons of ecologically similar species may be insufficient to explain their coexistence [Quinn & Dunham 1983], in this study different biological features of both species have been analyzed, such as ♀ size distribution, resource exploitation, feeding behaviour and foraging periods.

2 Material and Methods

Field study was carried out between 1985–1989 in Canet de Mar (40 km NE of Barcelona, on the Mediterranean coast) in a grassland of *Hyparrhenia birta* at 50 m NN and 750 m away from the coastline [described in Cerdá & Retana 1988]. Samples of ♀♀ of both species were collected for the study of biometry by excavating nests in the study area. Two measurements were taken in the laboratory under a stereoscopic microscope:

- Total body length of ants was measured from tip of mandibular to tip of gaster, with the ant in an extended position.
- Maximum caput width was measured at the interocular line.

In order to analyze the solid diet of each species, items brought to the nest by ♀♀ were taken for later identification in the laboratory.

Pairwise species overlap of carried forage was calculated as a proportional similarity index: \( PS = 1 - 0.5 \left( \sum |p_{ib} - p_{yb}| \right) \), where \( p_{ib} \) and \( p_{yb} \) are the respective proportions of resource \( i \) in the diet of species \( x \) and species \( y \) [Colwell & Futuyma 1971].

Prey length was measured with a micrometer under a stereo microscope. Proportional similarity index for food size was calculated as for food type. To establish the maximum weight that each species can carry individually, differently sized prey (weighed previously in the laboratory with a 0.1 mg sample scale) were offered to the ♀♀ to evaluate if they could transport them or not.

To ascertain whether or not there existed some food preferences on the part of the ♀♀ of both species, they were offered different types of items they could easily find in the field: hard arthropod corpses (such as Hymenoptera or Coleoptera), soft arthropod corpses (such as Diptera or Homoptera-Aphidinae), snails, pieces of vertebrates, plant remains and seeds. Responses were considered positive when the ant seized the item and tried to carry it to the nest, and negative when, after encountering the item, the ant abandoned it without having made any attempt to collect it.

To complete the study of the dietary spectrum of both species, every 2 h throughout every sampling day (12 days of observation from March to November 1985), the exploitation of liquid food sources was analyzed, counting the number of ants of both species that were gathering nectar on flowers and tending Homoptera on previously marked plants.

Recruitment behaviour of each species was studied by means of big prey that could not be carried to the nest by individual ♀♀. Crickets weighting 1.0–1.2 g and previously killed by freezing in the laboratory were placed 50 cm away from a *P. pallidula* or *T. semilaeve* nest. From the moment that a ♀ of the nest found the prey, the number of ♀♀ in contact with the cricket was counted every minute for the next 1/2 h. During each observation period, ♀♀ of other species or other nests of the same species were not allowed to approach and touch the cricket, in order to avoid interference in recruitment behaviour. Ten observations were done with each species.
To obtain data about the type of recruitment of both species, in 12 sampling days (from III–XI 1985) 30 plastic discs with different food baits (honey, biscuit, sausage, cheese, ham and bacon) that could not be transported to the nest by individual ♀♀♀ were laid randomly over the entire study area. Every hour, the number of ants of each species feeding at each bait was noted.

Interactions at baits between P. pallidula and T. semilaeve and the other ant species of the area were also recorded, and 3 types of interactions were considered: (a) pacific coexistence, when ♀♀♀ of different species occupy the same bait without showing aggressive behaviour; (b) expulsion, when one species drives another one away and occupies the bait; (c) escape, when one species is attacked and forced to abandon the bait.

Although baits represent an exceptionally rich food source, a fact that may, somehow, modify the normal activity of ants [Whitford et al 1980], the variations of the number of ants counted at baits every hour and every day were used as a way of measuring daily activity rhythms of both species. Together with the hourly measurement of activity at baits, the following environmental factors were recorded: ground surface temperatures in the sun and in the shade, relative humidity, and light intensity. Seasonal activity of each species has been estimated from the number of ♀♀♀ collected at pitfall traps in the different periods of the year. Each day of measurement 16 pitfall traps containing alcohol, detergent and water were distributed during 24 h in the study area. Their contents were later analyzed at the laboratory to the species level.

3 Results

3.1 Biometrical study of workers

As is shown in Fig 1, ♀ size distribution in both species is completely different:

- Caput width distribution of T. semilaeve ♀♀♀ is clearly monomorphic, with a mean (± standard deviation) of 0.718 ± 0.030 mm.
- On the other hand, P. pallidula has a dimorphic distribution, with 2 discrete classes without intermediate values between them: minors, with a mean caput width (± SD) of 0.555 ± 0.016 mm, and majors or soldiers, with a head width of 1.249 ± 0.082 mm and greater variability.

![Fig 1: Distribution of caput width of ♀♀♀ of: A Tetramorium semilaeve André 1883; B Pheidole pallidula (Nylander 1848) Y-axis: % of ♀♀♀ in each size class. X-axis: caput width (mm). [Hymenoptera: Formicidae].](image)

Minor ♀♀♀ of P. pallidula represent the main force of ♀♀♀ in the nests (92.5% of ♀♀♀ in Fig 1), while soldiers are much less frequent (7.5% of ♀♀♀ in Fig 1). Nevertheless, soldiers are of
great importance for *P. pallidula* colonies, because they have strong mandibula and are very aggressive, these features allowing them to have an active role in interspecific encounters.

Total body length of *T. semilaeve* ♀ ♂ ranges between 2.0–3.2 mm, a little larger than that of minor ♀ ♂ of *P. pallidula* (1.2–2.6 mm), although much smaller than that of soldiers of this species (3.3–4.9 mm). According to their size, both species are the smallest species of this ant community except *Plagiolepis pygmaea*. Specifically, their main competitors for food resources (see below) are considerably bigger: *Tapinoma nigerrimum* (2.8–5.1 mm), *Aphaenogaster semilis* (6.4–7.7 mm), *Cataglyphis cursor* (4.3–7.2 mm), *Messor capitatus* (3.8–13.0 mm) and *Messor bouvieri* (4.0–8.5 mm).

### 3.2 Diet

*P. pallidula* and *T. semilaeve* are 2 omnivorous species whose ♀ ♂ carry solid items back to the nest. In Tab 1 the % of the different types of items in the diet of each species is given. Animal and plant remains are in similar proportion in both cases, although the detailed composition within each category can differ. The proportional similarity index of diet overlap for food type of *P. pallidula* and *T. semilaeve* is 0.678.

<table>
<thead>
<tr>
<th>Type of prey</th>
<th><em>P. pallidula</em></th>
<th><em>T. semilaeve</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Animal remains</td>
<td>57.9</td>
<td>48.1</td>
</tr>
<tr>
<td>+ Ants</td>
<td>41.3</td>
<td>20.8</td>
</tr>
<tr>
<td>+ Other Insects</td>
<td>3.9</td>
<td>12.2</td>
</tr>
<tr>
<td>+ Snails</td>
<td>2.3</td>
<td>3.8</td>
</tr>
<tr>
<td>+ Unidentified remains</td>
<td>10.4</td>
<td>11.3</td>
</tr>
<tr>
<td>Plant remains</td>
<td>42.1</td>
<td>51.9</td>
</tr>
<tr>
<td>+ Seeds</td>
<td>27.8</td>
<td>18.1</td>
</tr>
<tr>
<td>+ Ants</td>
<td>3.8</td>
<td>2.8</td>
</tr>
<tr>
<td>+ Flowers</td>
<td>2.3</td>
<td>0.0</td>
</tr>
<tr>
<td>+ Other plant remains</td>
<td>8.2</td>
<td>33.0</td>
</tr>
</tbody>
</table>

**Tab 1**: % of each type of item brought to the nest by *Pheidole pallidula* (Nylander 1848) (n = 133) and *Tetramorium semilaeve* André 1883 ♀ ♂ (n = 106) [Hymenoptera: Formicidae].

<table>
<thead>
<tr>
<th>Type of prey</th>
<th><em>P. pallidula</em></th>
<th><em>T. semilaeve</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>N</td>
<td>%A</td>
<td>N</td>
</tr>
<tr>
<td>Hard Arthropods</td>
<td>74</td>
<td>89</td>
</tr>
<tr>
<td>Soft Arthropods</td>
<td>40</td>
<td>100</td>
</tr>
<tr>
<td>Snails</td>
<td>10</td>
<td>100</td>
</tr>
<tr>
<td>Vegetarian leaves</td>
<td>20</td>
<td>70</td>
</tr>
<tr>
<td>Cenzoicous seeds</td>
<td>30</td>
<td>87</td>
</tr>
<tr>
<td>Other seeds</td>
<td>70</td>
<td>94</td>
</tr>
<tr>
<td>Feral flowers</td>
<td>10</td>
<td>100</td>
</tr>
<tr>
<td>Other plant remains</td>
<td>30</td>
<td>6</td>
</tr>
</tbody>
</table>

**Tab 2**: Items offered to *Pheidole pallidula* (Nylander 1848) and *Tetramorium semilaeve* André 1883. The number of items offered (N) and the % of acceptance (%A) of each type of item are indicated [Hymenoptera: Formicidae].

With regard to food preferences of each species, Tab 2 shows that most of the animal remains offered to *P. pallidula* and *T. semilaeve* ♀ ♂ were collected (93.5 % for *P. pallidula* and 88.3 %
for *T. semilaeve*). The same is not true for plant remains: some of them, e.g., fennel flowers (*Foeniculum vulgare*) or *Centaura* seeds (with an elaiosome specially attractive to most species of ants, not only granivorous ones [Cerdà et al. 1989a], were mostly accepted, while the acceptance of the other seeds varied according to the type of seed offered. The comparison of results obtained for the 2 species confirms that their dietary spectrum is very similar, because they have similar % in almost all the types of items offered.

Another important food resource for many ant species is liquid food collected from plants. Nevertheless, ♀ ♂ of *P. pallidula* and *T. semilaeve* are very seldom found collecting nectar from flowers or tending aphids: in the study area, no ♀ of *T. semilaeve* was found on plants, and only at the end of the season, in X, a few *P. pallidula* ♀ ♂ were found on *Ivula viscosa* flowers and on fennel, tending *Aphis fabae* individuals.

### 3.3 Size of prey

Another factor that can affect interspecific competition is food size. Prey size distributions of both species are shown in Fig 2. Size of prey collected by *P. pallidula* and *T. semilaeve* is significatively different (chi square = 14.93, P = 0.005), those of *P. pallidula* (mean 2.18 ± 1.50 mm) being larger than those of *T. semilaeve* (mean 1.57 ± 0.92 mm). Nevertheless, diet overlap for food size is 0.782, a little higher than that of food type.

There also are some differences in the maximum weight that ♀ ♂ of both species can carry individually: *P. pallidula* can transport prey which weighs up to 3.5 mg approximately, while *T. semilaeve* only carries prey up to 2.5 mg.

![Fig 2](image)

**Fig 2**: Distribution of size (body length) of items brought to the nest by ♀ ♂ of (A) *Tetramorium semilaeve* André 1883; (B) *Pheidole pallidula* (Nylander 1848). Y-axis: % of items of each size. X-axis: length (mm). [Hymenoptera: Formicidae].

### 3.4 Recruitment to large prey

Fig 3 shows the whole activity period distribution of the total number of workers found at each bait for both species. The two histograms are not significantly different (chi square = 18.96, P = 0.05), their mode being the class fo 100 or more ♀ ♂.

Fig 4 represents the mean number of *P. pallidula* and *T. semilaeve* ♀ ♂ in contact with a big cricket offered as prey (n = 10 observations for each species). The whole process starts with a long phase in which the number of ♀ ♂ is very low; afterwards there is a second stage in

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3 Entomol. Gener. 17
which the number of ♀♀♀ in contact with the item grows progressively, but still insufficiently to defend it against other competitors; finally, the number of ♀♀♀ reaches a value that allows the species to monopolize the food. Both curves are similar although *P. pallidula* starts recruitment about 5 min before *T. semilaeve*. Behaviour of both species when they exploit this type of food source is also similar: ♀♀♀ do not cooperate in the transport of the whole item, but tear it and carry the pieces individually to the nest.

![Graph A](image1)

**Fig 3:** Percentage of baits occupied by different numbers of workers of **A** *Pheidole pallidula* (Nylander 1848) (*n* = 1,633) and **B** *Tetramorium semilaeve* André 1883 (*n* = 269), grouping all the data collected at the different hours and sampling days. X-axis, classes of ♀ number at baits: 1 1 ♀; 2 2–5 ♀♀♀; 3 6–10 ♀♀♀; 4 11–20 ♀♀♀; 5 21–30 ♀♀♀; 6 31–40 ♀♀♀; 7 41–50 ♀♀♀; 8 51–60 ♀♀♀; 9 61–70 ♀♀♀; 10 71–80 ♀♀♀; 11 81–90 ♀♀♀; 12 > 90 ♀♀♀. Y-axis: % of the total number of baits occupied by a different number of ♀♀♀. *(Hymenoptera: Formicidae).*

![Graph B](image2)

**Fig 4:** Mean number of ♀♀♀ of **A** *Pheidole pallidula* (Nylander 1848) and **B** *Tetramorium semilaeve* André 1883, in contact with a big prey (a cricket weighing 1.2 g), throughout the time (*n* = 10 observations for each species). Y-axis: number of ♀♀♀, X-axis: time in minutes. *(Hymenoptera: Formicidae).*

### 3.5 Aggressive behaviour

*P. pallidula* and *T. semilaeve* are able to defend their food sources once they have occupied them. This ability allows them to exploit the prey longer even if other species try to get it. Aggressive interactions between these 2 species and the others of the community have been studied at baits throughout the whole activity period, and are summarized in Tab 3. In the majority of cases, both species attempt to dominate the bait (83% of the interactions for
There is only one ant in the study area, *Camponotus sylvaticus*, that is more aggressive than *P. pallidula*, and always drives it away from baits when they meet (*T. semilaeve* was only found in one case with *C. sylvaticus*, and there was no fight). When *P. pallidula* and *T. semilaeve* were found together at the same bait *T. semilaeve* occupied it in three cases and *P. pallidula* in 2 cases.

3.6 Daily activity rhythms

Daily activity rhythms of *P. pallidula* and *T. semilaeve* at baits in 3 different seasons are represented in Fig 5. Activity of both species is mainly crepuscular and nocturnal during almost the whole period of activity. The correlation between daily activity curves of both species throughout the year is quite good (*R = 0.7085, P = 0.001*). However, there are some differences between them.

**Fig 5:** Daily activity curves of *Pheidole pallidula* (Nyländer 1848) (—) and *Tetramorium semilaeve* André 1883 (---) on 3 different sampling days: A March 19; B July 1; C August 21. Y-axis: left scale, activity expressed as the % of the number of ♀♀ found at the bait at each hour related to the maximum number of ♀♀ found this day at the bait; right scale, ground surface temperature in the sun (T), in °C (dotted line). X-axis: time of the day (local standard time). [Hymenoptera: Formicidae].
In cool months, _P. pallidula_ is active during the whole day (e.g. in III, as can be seen in fig 5A), while _T. semilaeve_ has a more or less prolonged interruption of activity at midday, when the temperature is higher.

Furthermore, in the morning _P. pallidula_ usually ceases its activity 1–2 h later than _T. semilaeve_, and also resumes some hours earlier in the afternoon (Fig 5B and 5C).

### 3.7 Influence of environmental factors

The linear correlation between foraging activity of both species and environmental factors is quite low, the greatest correlation (although negative) being that of light intensity (R = -0.546, P = 0.01 for _T. semilaeve_ and R = -0.346, P = 0.001 for _P. pallidula_). This agrees with the fact that both are mainly nocturnal species that reduce their exterior activity in daylight hours.

In Fig 6, mean activity of both species for the different temperature values is indicated. The range of T for both species is similar, although the upper thermal limit for _P. pallidula_ is about 3 °C higher than that of _T. semilaeve_ (35 °C versus 32 °C).

![Fig 6: Breakdown of ground surface temperature in the shade by activity of _Pheidole pallidula_ (Nylander 1848) (--) and _Tetramorium semilaeve_ André 1883 (---). X-axis: ground temperature in °C. Y-axis: mean number of ♀♂ occupying the bait (N). [Hymenoptera: Formicidae].](image)

### 3.8 Seasonal activity rhythms

Seasonal activity curves of _P. pallidula_ and _T. semilaeve_ show a certain degree of displacement (Fig 7): outside activity of _T. semilaeve_ is greatest in May, June and the beginning of VII, decreasing later progressively, while that of _P. pallidula_ increases during these months and reaches its maximum at the end of VIII. Nevertheless, although maximum activity periods are different, _P. pallidula_ and _T. semilaeve_ curves of seasonal activity greatly overlap, proving that both species concur outside the nests during the greater part of their activity period.

### 4 Discussion

The main features of _P. pallidula_ and _T. semilaeve_ described in this paper are summarized in Tab 4. In spite of their coexistence in so many zones (see introduction), they have great similarities in almost all the factors analyzed. Concerning their dietary spectrum, _P. pallidula_ and _T. semilaeve_ are two omnivorous ants that collect animal and plant remains in a similar proportion and that rarely climb the plants to collect liquid food (the omnivorous diet of
Fig 7: Seasonal variations of the number of *Pheidole pallidula* (Nylander 1848) (---) and *Tetramorium semilaeve* André 1883 (---) ♀♂ collected at pitfall traps. Y-axis: left scale, relative abundance of each species at pitfall traps (RA), relating the number of ♀♂ found each sampling day to the maximum number found for the species throughout the year; right scale, mean daily temperature (T) in °C (dotted line). X-axis: months of the year. [Hymenoptera: Formicidae].

*P. pallidula* has also been described by Detrain [1990]. Although the detailed composition within each fraction can differ, both species have similar % of acceptance of all the types of items offered, thus confirming their similar food preferences. Diet overlap for food type of both species is PS = 0.678. Among temperate-zone ants, this high overlap in diet between sympatric generalist species is more common than dietary specialization [Levings & Traniello 1981, Lynch 1981, Fellers 1987, Rissing 1988].

**Tab 4:** Summary of the main features of *Pheidole pallidula* (Nylander 1848) and *Tetramorium semilaeve* André 1883 described in this paper [Hymenoptera: Formicidae].

<table>
<thead>
<tr>
<th>Ecological features</th>
<th><em>P. pallidula</em></th>
<th><em>T. semilaeve</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Total body length (minor)</td>
<td>1.2–2.6 mm</td>
<td>2.0–3.2 mm</td>
</tr>
<tr>
<td>Worker size distribution</td>
<td>dimorphic</td>
<td>monomorphic</td>
</tr>
<tr>
<td>Solitary diet</td>
<td>58% animal remains</td>
<td>48% animal remains</td>
</tr>
<tr>
<td>Liquid food collection</td>
<td>42% plant remains</td>
<td>62% plant remains</td>
</tr>
<tr>
<td>Prey size</td>
<td>2.18±1.50 mm</td>
<td>1.57±0.92 mm</td>
</tr>
<tr>
<td>Type of recruitment</td>
<td>mass recruitment</td>
<td>mass recruitment</td>
</tr>
<tr>
<td>Big prey exploitation</td>
<td>tearing and individual</td>
<td>tearing and individual transport</td>
</tr>
<tr>
<td>Dominance at baits</td>
<td>67%</td>
<td>83%</td>
</tr>
<tr>
<td>Daily activity</td>
<td>mainly crepuscular and</td>
<td>crepuscular and</td>
</tr>
<tr>
<td>and nocturnal</td>
<td></td>
<td>nocturnal</td>
</tr>
<tr>
<td>Range of temperatures</td>
<td>13–35°C</td>
<td>13–32°C</td>
</tr>
<tr>
<td>Maximum activity period</td>
<td>July–August</td>
<td>June–July</td>
</tr>
</tbody>
</table>

In most cases, ants are able to transport the majority of prey they find. Nevertheless, to do so, they employ different mechanisms, whether exploitation, namely finding and using limiting resources before other possible competitors, or interference, namely monopolizing available resources. Both *P. pallidula* and *T. semilaeve*, follow the latter mechanisms, accomplishing mass recruitment of ♀♂ to the baits, occupying them and fending off other species already present or later-arrived. From this point of view, this strategy confers similar advantages to both species in the occupation of large, hard-to-transport prey, but it also has similar disadvantages because there is a relatively long initial period (about 10–15 min) in which the prey stays in the field without being occupied. If we accept, according to Retana et al [1991], that the mean time lapse that the arthropod corpses stay in the field in the study zone at any
time of the day is very short (< 5 min), it is not really relevant that *P. pallidula* recruits a little faster than *T. semilaeve*, because there are other ants that find the items quicker, carry them back to their nest, and deprive both *P. pallidula* and *T. semilaeve* of them.

Comparing their competitive behaviour, the sole important difference between *P. pallidula* and *T. semilaeve* is that *P. pallidula* has another caste of ♀♂ — the soldiers — that provide additional defensive help for the colonies. Soldiers represent 7.5% of ♀♂ in our case, while Passera [1977] says that they are 3–5% of ♀ population in his *P. pallidula* nests. The *P. pallidula* soldiers are bad foragers, but are highly effective in tearing the prey or in fighting against other ants [Detrain et al 1988].

Differences in activity rhythms are another mechanism that allows ants to avoid competition from other similar resources-collecting species [Briese & Macauley 1980, Klotz 1984], but in this case they are not very great. Daily rhythms of *P. pallidula* and *T. semilaeve* are crepuscular and nocturnal during the main part of their activity period. Thermic overlap of both species is also very high, which indicates that they forage nearly at the same T. Only maximum seasonal activity periods differ but, nevertheless, *P. pallidula* and *T. semilaeve* concur in the field during the greater part of their activity season.

Globally, *P. pallidula* and *T. semilaeve* are much more similar to each other than to the other species of the study zone. In this community there are two other granivorous species, *Messor capitatus* and *Messor bowieri*, but they collect bigger seeds than *P. pallidula* and *T. semilaeve* and are active mainly during the daytime. Differences are also important with regards to the three species that collect arthropod corpses: *Cataglyphis cursor* is a highly thermophilic species whose greatest activity takes place when the T is highest [Cerdá et al 1989a]; *Aphaenogaster senilis* is also a strictly diurnal species with an exploitative strategy that allows it to find and carry the prey back to the nest by means of a well developed mechanism of group recruitment [Cerdá et al 1988]. On the other hand, *Tapinoma nigerrimum* resembles *P. pallidula* and *T. semilaeve* in that it has crepuscular and nocturnal activity and a similar mass recruitment strategy, but it can be clearly distinguished because its seasonal activity curve differs widely from that of *P. pallidula* and *T. semilaeve*, and because its main food is honeydew of aphids, although it also collects arthropod corpses [Cerdá et al 1989b]. The other abundant ants of this community (such as *Camponotus foreli* or *Camponotus sylvestris*) differ from *P. pallidula* and *T. semilaeve* in that they almost exclusively collect sugary liquids such as honeydew or nectar.

*P. pallidula* and *T. semilaeve* are strikingly similar in most aspects of their ecology, because they are broadly overlapping species in diet, foraging times and habitat requirements. This seems to show that competition between them is possible. Nevertheless, they coexist in sympatry without evident competitive interactions: in Canet de Mar, *P. pallidula* is much more abundant than *T. semilaeve* [Cerdá & Retana 1988: 40% versus 2% of ant nests of the study area] but, in the last 6 years at least, the proportions of nests of both species has remained more or less constant. This indicates that there is not, at least in the short term, a progressive displacement of one species by the other.

Coexistence of ecologically similar insect species in the same community is not uncommon in the literature, and has been described in so unrelated groups as herbivorous stem-boring insects [Rathcke 1976], similar proboscis length bumblebees [Ranta & Tiainen 1982] or taxonomically closely related carabid beetles [Den Boer 1980]. The question is, to what degree can 2 potentially competing species such as *P. pallidula* and *T. semilaeve* be similar and yet remain in the same community without one of them disappearing. In competition studies it is always uncertain whether all the important factors in niche segregation have been taken into account, and whether the measurement of variables reflects really what animals perceive
because human perception of resource classes may not correspond to what a species perceives [Petrakis 1979]. Competition in nature is usually imperfect and developed in a changing environment which, in spite of ecological theory [Murray 1986], enables ecologically related species to coexist.

On the other hand, beside competition there are a variety of alternative hypothesis that might account for the coexistence of species that are similar in their resource use: (a) species may partition microhabitats (e.g. depending on nest site availability) and overlap little spatially; (b) differential susceptibility to parasites or other natural enemies could allow coexistence, if the best competitor were selectively held in check [Feener 1981: study of the interaction of phorid fly parasitism regulating interspecific competition in Texas ants]; (c) life history differences among species may allow one species to be a better colonist and the other, a better competitor; (d) some environmental disturbance regime may keep ant densities too low for competition to play a role in shaping the community. In order to evaluate the different possibilities, in this case a removal experiment might suggest whether the 2 species compete at all.

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6 References


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