Foraging responses of the aphid tending ant *Lasius niger* to spatio-temporal changes in aphid colonies *Cinara cedri* *

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黑蚁对雪松长足大蚜集群时空变化的取食反应 *

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Most studies addressing how the aphid-tending ant *Lasius niger* assesses the characteristics of food, makes collective choices and engages nestmates in a efficient collective exploitation of resources (Beckers et al., 1992; Maillieux et al., 2000; Portha et al., 2002) were carried out in the laboratory. Ant colonies are known to favour the exploitation of the most profitable food sources in terms of amount of nectar or honeydew collected per time unit by the ants (Beckers et al., 1992; Sakata, 1995; Maillieux et al., 2000; Fischer et al., 2002; Portha et al., 2002) and in terms of quality with for instance a higher level of amino acids (Lanza and Krauss, 1984; Lanza, 1988, 1991) or a higher proportion in trisaccharides (Vökl et al., 1999). Furthermore, in *Lasius niger*, colonies manage the density of tended aphids by favouring or stabilising the growth of preferred aphid colonies while decreasing the growth of less productive homopteran species (Sakata, 1995, 1999). Hence, *Lasius niger* colonies are expected to preferentially exploit the most profitable feeding sites (Sakata, 1994) and adjust the number of tending foragers to the productivity in honeydew of the homopteran colonies or sugary resources such as nectar (Breed et al., 1987; Sudd, 1987b; Maillieux et al., 2003). Moreover one can assume that colonies should be able to collectively select close food sources in order to limit energetic expenditure due to transport costs and to maximise their individual reward (Schoener, 1971; Taylor, 1977; Orians and Pearson, 1979).

Here, we investigated whether the predicted adjustments of ant exploitation to the productivity and/or distance from the nest of aphid colonies are met under natural conditions. In this respect, we deliberately chose a rather simple situation where only one aphid species *Cinara cedri* and one colony of aphid-tending *Lasius niger* were present in order to avoid bias due to competitive interactions between aphid species (Addicott, 1978; Sakata, 1995, 1999; Fischer et al., 2001; Portha and Detrain, 2004). Over one branch of a cedar *Cedrus libani* foraged by ants, we made regular surveys of the spatial distribution of aphid colonies, of their demography as well as of the time evolution of their exploitation by ants. This al-

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lowed us to know how ants exploit multiple food resources differing by their distance from the nest and whether, at a local scale, the tending activity of ants was related to the growth of aphid populations and/or influence their spatial distribution.

1 Materials and methods

We observed the time evolution of aphid populations of *Cinara cedri* species as well as the global activity of one colony of *Lasius niger* over one branch of a cedar *Cedrus libani* growing as ornamental on the campus of the Brussels University. In order to avoid potential competition for tending between several aphid species, we paid attention to have only one in this tree before beginning our observations. We carefully checked the aphid belonging to *Cinara cedri* species but we did not carry out genetic analyses of aphid aggregates since, until now, there is not reported evidence of a differential tending behaviour of ants according to the strains of homopterans.

The chosen branch was positioned at only 70 cm height and this made ants and aphids easy to observe. The nest entrance of the ant colony was located close to the base of the trunk.

Observations were conducted once a week during seven weeks from 15 June 2001 until the 29 July 2001. The aphid population started to decrease slightly from the sixth week and fell to very low values at the seventh week, so we were forced to stop our observations and do not understand why this occurred. However, given a recent report about the life cycle of *Cinara cedri* in Turkey, the population could be between two peaks of growth at the end of July (Kaygın and Canakcioğlu, 2003).

One day each week, we counted the number of aphids over all the twigs along the whole branch. In this respect, we considered each aphid alone or a group of aphids as being a distinct food resource (and as a different aphid colony) when they were located on different twig sections (a section being spatially limited by a lower and an upper twig ramifications node). We noted whether ants were observed close to aphids or walking over them. Since an aphid colony that was actually exploited by ants had always one worker staying on it, we considered an aphid colony as being exploited as soon as we observed at least one ant foraging on it. Each week, we quantified the distance of each aphid resource by measuring with a graduated ruler over twigs and branches, the shortest path way followed by the ants from the food source until the ant nest entrance. Concurrently, we also measured the outgoing and incoming flows of ants during 15 minutes over each of the seven major ramifications of the branch. In most cases, the conditions of normality (checked with Kolmogorov-Smirnov’s test) and/or homoscedasticity (checked with Levene’s test) were not met; hence data were statistically compared using non-parametric tests. All *P* values given were one-tailed test values.

2 Results

During our seven weeks of observation, we counted 2,814 aphids aggregated within 89 different aphid colonies. We considered a colony as being the same as that observed the week before when aphids were located at the same place (between the same two bifurcation nodes). The majority (75%) of aphid colonies was observed only once (Fig.1). Only 22 colonies were located at the same place during several successive weeks, the more persistent aphid colony remaining over the same branch for up to 5 weeks (Fig.1). Among these 22 persistent colonies, we found a higher percentage (63.6%) of tended colonies—that means being tended by ants at least once during the successive weeks—than unattended ones (36.4%) though this difference was not statistically significant (Fisher exact test, *n* = 22, NS).

We analysed whether this higher percentage of tended colonies resulted from a preferential exploitation by ants of persistent aphid colonies or from a higher sampling of persistent aphid aggregates. Therefore, we calculated the probability *P* for an aphid colony persisting during two successive weeks to be considered as unattended. Given the proportion of unattended colonies (70.1%) among the total number of one week colonies (Fig.1), the expected probability for an aphid colony to remain unattended during two successive weeks was *P* = 0.701² = 0.492. As a correlate, the expected probability to be tended at least one of the two weeks was equal to *Q* = 1 − *P* = 0.508. This expected value was very close to that actually observed as 53.85% (Fig.1, 7/13) showing that the higher percentage of tending on persistent colonies resulted from an increased sampling effort over two successive weeks. Thus, there was no preferential exploitation by ants of persistent colonies nor stabilizing effect of the presence of ants on the aphids.

Aphid colonies did not show a random spatial distribution over the cedar branch. Actually, the smallest colonies as well as isolated aphids were usually situated close to branch tips and hence further from the ant nest than larger aggregates. As a result, there was a significant negative correlation between the colony distance and its number of aphid individuals (all colonies pooled: Spearman’s correlation: *r* = −0.38, *n* = 124: *P* < 0.001). Such correlation still occurred when we took into account separately either exploited colonies (*r* = −0.35, *n* = 51: *P* < 0.05) or unattended ones (*r* = −0.27, *n* = 73: *P* < 0.05).
Therefore, the presence of ants did not seem to influence the spatial distribution of aphids at the scale of the branch.

We found, among the 125 observations of aphid colonies, a similar percentage were exploited by ants (41.6%) or remained unattended (58.7%) (Fisher exact test, \( n = 125 \), NS). However, those two types of colonies (tended vs. unattended) differed by their size (Table 1). Indeed, the average size of colonies exploited by ants was three times higher than that of unattended colonies (Table 1: \( U = 1338.5, P < 0.01 \)). This larger size of exploited colonies of aphids was observed for every week excepting the first and the last one (Fig. 2).

Due to their lower honeydew production, it is less likely to see one ant foraging on small aphid colonies and this could lead us to underestimate the proportion of small-sized colonies being exploited by ants. To minimize colony size related bias, we analysed our results taking into account only large colonies with more than 10 aphids. This did not lead to different conclusions and confirmed that exploited homopteran colonies were on average significantly more populous (Table 1).

The proportion of ants’ flow foraging on a twig was strongly correlated to the proportion of exploited aphids located on this ramification (Fig. 3). Hence, when faced with multiple food sources, ant workers were not distributed at random or homogeneously over all available paths but they focused their foraging activity on colonies with more numerous aphids and hence with a potentially higher productivity in honeydew. Besides, this also suggested that ants could protect and favour the growth of aphid colonies that they exploit.

On average, all the observed aphid colonies were located at 296 cm [± 73 (SD), \( n = 125 \)] from Lasius niger nest entrance. The average distance of exploited aphid colonies was significantly lower than that of non-exploited ones (Table 1). Such distance

![Fig. 1 Relative distribution of aphid colonies tended or not by ants as a function of their persistence](image)

The percentages are calculated over the total number of aphid colonies observed (\( n = 89 \)). The absolute number of colonies is given on the top of histograms.

<table>
<thead>
<tr>
<th>Table 1</th>
<th>Size and ant nest distance of aphids colonies (Mean ± SD)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Exploited</td>
</tr>
<tr>
<td>Number of aphids</td>
<td>38.4 ± 66.3</td>
</tr>
<tr>
<td>(All colonies)</td>
<td>( n = 52 )</td>
</tr>
<tr>
<td>Number of aphids</td>
<td>64.2 ± 79</td>
</tr>
<tr>
<td>(Colonies with &gt;10 aphids)</td>
<td>( n = 29 )</td>
</tr>
<tr>
<td>Distance (cm) from ant nest</td>
<td>257.4 ± 70.7</td>
</tr>
<tr>
<td>(All colonies)</td>
<td>( n = 52 )</td>
</tr>
<tr>
<td>Distance (cm) from ant nest</td>
<td>167.7 ± 56.7</td>
</tr>
<tr>
<td>(Colonies with &gt;10 aphids)</td>
<td>( n = 29 )</td>
</tr>
</tbody>
</table>
difference between exploited and non exploited colonies was observed every week (Fig. 4) and for aphid colonies of similar size (less or more than 10 aphids, Table 1). Therefore, ant colonies faced with multiple choices in the field selected closer food sources. Though ants are able to preferentially forage on near food sites, they seemed to be unable to remove aphid colonies and bring them closer to the nest. Indeed, throughout our period of observation, we noticed a slight increase of distance of food resources (Fig. 4: Kruskal-Wallis’ test KW = 26.85 and KW = 14.03 for non-exploited and exploited colonies respectively, $P < 0.001$ and $P < 0.05$).

3 Discussion
We studied under natural conditions, the collective foraging behaviour of *Lasius niger* faced with a multiple choice of aphid resources. We observed that ants focus their foraging on colonies with more numerous aphids and a probably higher productivity in honeydew (Cushman and Addicott, 1989, 1991; Fischer et al., 2002). This result confirms predictions about an adjustment of the number of tending ants to the productivity and quality of food sources (Crawford and Rissing, 1983; Cushman, 1991; Cushman and Addicott, 1991; Mailleux et al.,
While the location of aphid populations is quite stable across the season at the scale of a tree (Addicott, 1979), we show that at the local scale of twigs, the spatial stability of aphid colonies is very weak since they scarcely stay more than two weeks at the same place. Aphids are known to exhibit geotactic and phototactic responses to environmental changes, to move according to the quality of their host (Walters and Dixon, 1982) or to wander as they grow older (El-Ziady, 1960). Our observations confirm that aphid colonies regularly move most probably to colonise plant parts on which they can achieve the highest growth and developmental rates (Ibbotson and Kennedy, 1950; Kennedy et al., 1950; Johnson, 1958; Harrington and Taylor, 1990; Dixon, 1998). We suggest that the smallest aphid colonies situated at the end of cedar branches consisted in younger aphids which prefer tender twigs (Dixon and Logan, 1973; Dixon, 1998). These aphids could move towards more ligneous parts of branches during their growth.

In contrast with other studies (Banks, 1962; Way, 1963; Sudd, 1987a), we observed that there is no preferential tending of persistent aphid colonies by ants. The rather high mobility of aphid colonies (Taylor and Taylor, 1983; Harrington and Taylor, 1990) suggests that ants have to frequently re-direct their exploitation during the season. In this respect, we show that ant colonies are able to select proximal food sources. However, they are unable to make an active displacement of Cimara cedri aphids towards closer sites since distance between nest and aphid colonies slightly increased during our period of observation. The relocation of aphids by ant workers could be specific since Lasius niger does not transport Aphis fabae (El-Ziady and Kennedy, 1956) while it can actively carry Pierocnemus salicis towards non-colonised host plants (Collins and Leather, 2002).

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