Paul D. Haemig

Interference from ants alters foraging ecology of great tits

Received: 10 March 1995/Accepted after revision: 9 September 1995

Abstract In a field experiment, great tits Parus major foraged on a pair of artificial trees that were supplied with equal amounts of food. Wood ants Formica aquilonia were excluded from one tree, but foraged on the other. Great tits visited the tree without ants more frequently, and for longer periods of time, than the tree with ants. The time of foraging visits by tits in the tree with ants decreased as ant activity there increased. These results are the first to show that interference competition from ants can influence a bird’s choice of microhabitat in which to forage, as well as alter the time it spends foraging there.

Key words Competition · Interference · Ants · Birds · Parus major

Introduction

Ants are abundant and widespread insects that play influential roles in many ecological communities (Holling and Wilson 1990). In European forests, for example, territorial wood ants (Formica rufa group) alter the distribution and abundance of a wide variety of arthropod taxa (Fowler and Macgarvin 1985; Warrington and Whittaker 1985a, b; Savolainen and Vepsäläinen 1988, 1989; Ito and Higashi 1991; Olofsson 1992), as well as the growth, reproduction and survival of trees (Lane and Niemela 1980; Whittaker and Warrington 1985; Whittaker 1991).

Catzeflis (1979) proposed that ants also alter the distribution and abundance of birds. At a study site in Switzerland, he found an exceptionally low density and diversity of birds in a forest inhabited by a huge supercolony of the wood ant F. lugubris (Cherix 1980; Cherix and Bourne 1980). He hypothesized that this reduced diversity and abundance of birds was the result of the wood ants consuming large amounts of arthropods upon which the birds depended for food, thus decreasing the capacity of the forest to support birds.

I recently tested Catzeflis’ hypothesis with a field experiment, and found support for it (Haemig 1992, 1994). In a northern Swedish forest, I observed that foliage-gleaning birds increased foraging activity in trees from which wood ants had been excluded. In addition, the arthropods upon which the birds fed were significantly more abundant in trees from which ants were excluded.

Catzeflis proposed that ants exclude birds by exploitation competition, an interaction where species compete indirectly with each other by consuming the same limited resources (Keddy 1989). However, interference competition could also explain the results that Catzeflis and I obtained. Interference competition differs from exploitation competition in that one species directly competes with the other through physical or chemical attacks, threat behavior, or territoriality, thus limiting the other’s access to resources (Schoener 1983; Keddy 1989). Interference from one species can negatively alter the foraging behavior of the other species. For example, Savolainen (1991) found that interference from the wood ant F. polyctena caused a subordinate ant F. fusca to discover prey less often, to select smaller-sized prey, and to decrease the rate at which it retrieved prey. Interference from F. polyctena also caused other subordinate ant species to shift their foraging to different times of day and to different microhabitats (Savolainen and Vepsäläinen 1988, 1989; Vepsäläinen and Savolainen 1990).

Despite such studies, comparatively little is known about the effects of interference competition on the foraging behavior of distantly-related taxa, for example those of different phyla and kingdoms (Hochberg and Lawton 1990). One exception is Gill et al. (1982), who found that colonial Trigona bees chased hermit
hummingbirds Phaethornis superciliosus away from flowers, and prevented the birds from feeding at one-third of the flowers they approached.

In this study, I examine experimentally whether ants interfere with the foraging behavior of birds. I set up a pair of identical artificial trees (hereafter called trees), near eight different wood ant Formica aquilonia mounds, and compared the foraging of great tits Parus major on these trees. I supplied both trees in a pair with equal amounts of bird food and equal amounts of ant food, to attract both great tits and wood ants. This food was placed in plain sight for the birds to see. The two trees differed by only one factor: the presence or absence of ants (ants were excluded from one tree of the pair by a ring of glue around the tree trunk). The interference competition hypothesis predicted that great tits would prefer foraging on the tree without ants.

Methods

The experiment was conducted during 1993 and 1994 in boreal forest east and south of the city of Umeå, northern Sweden (63°50' N, 20°20' E). I began each trial of the experiment when the first great tit visited one of the trees, and continued the experiment until I had recorded 50 great tit visits for each replicate. After recording the first 25 visits at each site, I stopped the experiment and reversed the locations of the two trees. After the ants resumed foraging normally, I then recorded the final 25 great tit visits. Each time a great tit visited one of the trees, I recorded whether or not that tree had foraging ants, and the precise duration of the visit. At periodic intervals during each trial, I measured ant activity on the tree with ants by recording the number of ants going up and down the tree trunk per minute. High ant activity was thus caused either by greater numbers of ants moving up and down the trees, or by smaller numbers of ants moving faster. I recorded ant activity in order to see if great tits reduced their time spent foraging as numbers or movements of ants increased.

Great tit foraging records were not taken when animals other than tits were visiting the trees. When squirrels or woodpeckers were feeding on one of the trees, the great tits foraged on the other tree. However, if a great tit was foraging on the trees with willow tits P. montanus, coal tits P. ater, or blue tits P. caeruleus, I included these records, because the great tit dominates these smaller tits, and displaces them from preferred foraging sites (Morse 1978; Atalato 1981; Haftorn 1993). I also included all great tit foraging records with conspecifics.

The trees were constructed out of 2-m-long wooden poles. Near the top of each pole, two 37-cm-long wooden dowels were inserted to serve as branches. At the distal end of each branch, I tapped a plastic spoon to hold the ant food. Right next to each plastic spoon (in the direction of the tree trunk), I fastened a petri dish to each branch. A strip of paper was painted to resemble the ring of glue on the experimental tree, and then applied to the trunk of the control tree (tree with ants), so that both trees looked similar to the birds. The mean distance of each tree from a wood ant mound was 2.8 m ($\bar{x} = 1.80, n = 16$). The mean distance between each pair of trees was 1.3 m ($\bar{x} = 0.49, n = 8$).

For bird food, I placed sunflower seeds in the petri dishes, and wired a single suet ball to the trunk of each tree where the branches were inserted. The suet balls were commercially prepared mixtures of suet, sunflower seeds, and peanut bits, and were the favorite food of the tits. The food provided for ants varied with the season; syrup was used in the spring and fall, while a mixture of syrup and tunafish was used during summer. All ant food was placed in the plastic spoons. Before starting each trial, and at appropriate times during them, I added food to the trees to keep their food levels equal. However, each time I did so, I also added a little to the other tree, to continually advertise to the tits that an alternative food source was available. Before starting each experiment trial, I also removed any arthropods except wood ants that had fallen into the syrup, or were sitting on the trees. This was necessary in only two replicates. In both cases, only a small insect was found.

With one exception (see below), all statistical analyses used Wilcoxon's signed-rank test for matched pairs (one-tailed) (Lehmann 1975). This test was used because the data were pairwise dependent. Analysis of covariance (Montgomery 1984) was used to examine whether or not the foraging time of great tits in the trees with ants decreased as ant activity there increased. This test was appropriate because only independent, non-paired observations were analysed (only tits visiting the trees with ants were considered), and only those tits which foraged alone were considered (to eliminate the effects of intraspecific competition). The logarithms of the foraging time of (individual birds) were explained by the replicate and the ant activity.

Results

In all replicates of the experiment (Table 1), great tits visited the trees without ants more often than the trees with ants ($T = 0, n = 8, P = 0.007$), and spent more time foraging in the trees without ants ($T = 0, n = 8, P = 0.007$). In addition, the mean duration of a great tit visit to a tree without ants was longer than the average visit to a tree with ants ($T = 0, n = 8, P = 0.007$).

These results can be seen even at the lowest levels of ant activity (Table 2).

The time that great tits spent foraging on the tree with ants was inversely proportional to the ant activity there. As ant activity increased, tits spent less time per visit to the tree with ants [$F(1,105) = 13.34, n = 114, P = 0.000$]. The analysis of covariance revealed that the slopes of the function of ant activity and tit visit time were similar in all replicates [$F(7,98) = 1.58, n = 114, P = 0.150$], so an additive model was used for this analysis.

Discussion

Foraging animals must decide which food patches to feed in, which to avoid, and when to leave a patch and move to another (Stephens and Krebs 1986; Schoener 1987). Factors known to be important in making these decisions include the amount of food in the patch, or the net rate at which it can be harvested compared with the average for the environment (Krebs 1978), the presence of predators (Lima and Dill 1990), the proximity to or presence of refuges (Fraser and Cerri 1982; Ekman 1987; Hogstad 1988) and the presence of competitors (Ekman and Askemmo 1984; Milinski 1987).

The results of my experiment demonstrate that even distantly related competitors can be important. Although equal amounts of bird food were present in
Table 1  Number of visits, total foraging time, and the mean duration of individual visits by great tits to trees with ants, and to trees without ants. Numbers in parentheses are the standard errors of the means.

<table>
<thead>
<tr>
<th>Tree pair</th>
<th>Visits (n)</th>
<th>Foraging time (s)</th>
<th>Mean visit duration (s)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Ants</td>
<td>No ants</td>
<td>Ants</td>
</tr>
<tr>
<td>A</td>
<td>17</td>
<td>33</td>
<td>1587</td>
</tr>
<tr>
<td>B</td>
<td>12</td>
<td>38</td>
<td>57</td>
</tr>
<tr>
<td>C</td>
<td>13</td>
<td>37</td>
<td>60</td>
</tr>
<tr>
<td>D</td>
<td>12</td>
<td>38</td>
<td>252</td>
</tr>
<tr>
<td>E</td>
<td>20</td>
<td>30</td>
<td>140</td>
</tr>
<tr>
<td>F</td>
<td>21</td>
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<td>372</td>
</tr>
<tr>
<td>G</td>
<td>18</td>
<td>32</td>
<td>340</td>
</tr>
<tr>
<td>H</td>
<td>17</td>
<td>33</td>
<td>186</td>
</tr>
</tbody>
</table>

Table 2  Number of visits, total foraging time, and the mean duration of individual visits by great tits foraging during the lowest levels of wood ant activity (1-5 ants per minute). Numbers in parentheses are the standard errors of the means. Because n was different for most replicates, only the percentage of visit number and the mean visit time were analysed statistically (replicate D was omitted in the mean visit time analysis because no birds foraged on the tree with ants). The analysis showed that even at these lowest levels of ant activity, great tits visited the tree without ants more often (T = 0, n = 5, P = 0.03) and that the average time of such visits was significantly greater in the trees without ants than in the ant trees (T = 0, n = 6, P = 0.018).

<table>
<thead>
<tr>
<th>Tree pair</th>
<th>Ant activity (ants/minute)</th>
<th>Visits (n)</th>
<th>Foraging time (s)</th>
<th>Mean visit duration (s)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Ants</td>
<td>No ants</td>
<td>Ants</td>
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<tr>
<td>A</td>
<td>4.5</td>
<td>2</td>
<td>2</td>
<td>46</td>
</tr>
<tr>
<td>B</td>
<td>1</td>
<td>5</td>
<td>12</td>
<td>36</td>
</tr>
<tr>
<td>C</td>
<td>3</td>
<td>7</td>
<td>18</td>
<td>21</td>
</tr>
<tr>
<td>D</td>
<td>5</td>
<td>0</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>Total</td>
<td>12</td>
<td>31</td>
<td>57</td>
</tr>
<tr>
<td>D</td>
<td>4</td>
<td>0</td>
<td>5</td>
<td>0</td>
</tr>
<tr>
<td>E</td>
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<td>10</td>
<td>15</td>
<td>82</td>
</tr>
<tr>
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<td>10</td>
<td>15</td>
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</tr>
<tr>
<td>G</td>
<td>1</td>
<td>4</td>
<td>4</td>
<td>53</td>
</tr>
<tr>
<td>H</td>
<td>1.5</td>
<td>7</td>
<td>7</td>
<td>88</td>
</tr>
<tr>
<td></td>
<td>Total</td>
<td>14</td>
<td>21</td>
<td>161</td>
</tr>
</tbody>
</table>

Both trees, the great tits foraged less frequently in the tree with ants, spending less and less time there as ant activity increased. These results show that great tits make decisions about how long and how often to forage in a microhabitat based on the presence and activity level of wood ants. They provide support for the interference competition hypothesis.

Some of my observations may also shed light on the mechanisms of interference. The bites of wood ants are painful, and ants may drive away tits by biting them. On several occasions during the experiment, I saw great tits jump when a moving wood ant came in contact with one of their feet. In all cases when this occurred, the tit rapidly left the tree with ants, and began foraging on the tree without ants.

Wood ants also spray formic acid at enemies (Judson and Bennett 1992; Löfqvist 1976; Budavari 1989) and it is possible that tits avoid this toxic and corrosive chemical. During the course of studying wood ants, I have been sprayed in the eye by wood ants. It was painful and impaired my vision for several seconds.

Small birds, such as tits, have relatively large eyes, and may also find such chemical attacks by ants painful and momentarily debilitating.

Related evidence supporting this "ant toxin avoidance hypothesis" comes from research on the anting behavior of birds. Judson and Bennett (1992) studied this highly stereotyped behavior in starlings Sturnus vulgaris using the wood ant F. rufa, and found that anting occurred most often when a bird's stomach was empty. Their results supported the hypothesis that the function of anting is to remove formic acid from ants, so that ants can be safely eaten by birds (formic acid is less potent when the stomach is full of other food). Thus, Judson and Bennett's study, like my own, suggests that birds have evolved behaviors to reduce exposure to ant toxins.

My experiment created a situation where great tits could choose between foraging where there were many ants, or foraging where there were no ants. This design is a realistic simulation of nature because wood ants are unevenly distributed within their territories. For
example, wood ants generally decrease in abundance with distance from their mounds, and their densities also vary from tree to tree among trees equally distant from a mound (Lane and Niemela 1980; Skinner 1980). Also, wood ant colonies are usually scattered unevenly in the forest, and so there are usually many areas adjacent to wood ant territories which are free of wood ants (Adlung 1966; Lane and Niemela 1980; Skinner 1980).

My experimental setup was conservative in that it placed equal amounts of bird food in both trees. In reality, the biomass of arthropod prey for birds is greater in trees from which wood ants have been excluded (Haemig 1994; Skinner and Whittaker 1981; Adlung 1966), and also increases with distance from the ant mound, as wood ant density decreases (Lane and Niemela 1980). Perhaps the preference of the great tits for foraging in the tree without ants in my experiment would have been even greater if a larger amount of bird food had been placed in the tree without ants. Although great tits may also alter their foraging in response to exploitation competition (Haemig 1992, 1994), the results of this experiment demonstrate that there is an interference component to the competitive interaction between wood ants and great tits. Wood ants are not just another insect species passively inhabiting the habitat of the great tit, and only indirectly affecting birds through resource consumption. Rather, the entire ant colony is an active and dynamic competitor, the changing densities of whose foraging workers must often be avoided.

Acknowledgements Christian Otto, Arne Lundberg, and Sara Sjöstedt gave me helpful advice and critically read the manuscript. Gunnar Borgström, Göran Andersson and Stig-Ola Ivarsson helped build the artificial trees and erect them at the experiment sites.

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Communicated by M.A. Elgar