Attraction of willow warblers to sawfly-damaged mountain birches: novel function of inducible plant defences?

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Abstract
Plants wounded by invertebrate herbivores emit volatile compounds which invertebrate predators and parasitoids can utilize in locating herbivore prey or hosts. We studied the possibility that an analogical phenomenon might operate between plants and avian insectivores. We show that foliar damage by sawfly larvae on the mountain birch led a passerine bird (willow warbler) to prefer intact branches from trees with introduced larvae over intact branches from control trees. Besides olfaction, the UV vision of birds offers a possible mechanism, as some herbivore-inducible leaf compounds, e.g. surface flavonoids, have UV spectral maxima well within the range of birds’ UV vision.

Keywords
Betula, chemical signalling, defoliation, indirect plant defences, insect herbivores, mutualism, olfaction, Phylloscopus, sawflies, tritrophic interactions, UV vision.


INTRODUCTION
During the last 2 decades, it has become clear that plants communicate with both co-specific and inter-specific plants and animals (Price et al. 1980; Vet & Dicke 1992; Takabayashi & Dicke 1996; Karban & Baldwin 1997; Dicke et al. 2003; Karban et al. 2003). The phenomenon known as ‘crying for help’ describes interactions between herbivore-damaged plants, insect herbivores and parasitic wasps attacking larvae of the herbivore (Turlings et al. 1990; De Moraes et al. 1998; Hoballah & Turlings 2001), as well as between plants, spider mites and predatory mites (Vet & Dicke 1992; Takabayashi & Dicke 1996). Inter-specific communication in these cases is based on inducible volatile compounds emitted by plants and acting as chemical attractants to parasitic or predatory invertebrates (Takabayashi & Dicke 1996; Kessler & Baldwin 2001).

Birds, too, can reduce densities of leaf-chewing insects, leading to increased growth of trees (Marquis & Whelan 1994; Sipura 1999). To the best of our knowledge, no one has studied whether an attacked plant can ‘cry for help’ to insectivorous birds, analogously to the tritrophic interactions between plants, herbivores and invertebrate carnivores. Birds have the necessary senses for this task; they utilise their olfactory capability and UV vision for multiple functions (reviewed in Bennett & Cuthill 1994; Roper 1999; Honkavaara et al. 2002), including hunting and foraging (e.g. Nevitt et al. 1995; Viitala et al. 1995; Church et al. 1998; Koivula & Viitala 1999; Siitari et al. 2002; Roper 2003).

In this note we present the results of an experiment designed to study whether damage by the larvae of a herbivorous insect on mountain birch (Betula pubescens ssp. czerepanovii (Orlova) Hämöt-Ahti) foliage could make these trees preferred by the willow warbler (Phylloscopus trochilus L.), an insectivorous passerine. Willow warblers forage in the canopies of trees and take a broad spectrum of insect prey, including lepidopteran and sawfly larvae (Glutz von Blotzheim & Bauer 1991; Nystrom 1991). Earlier studies have demonstrated that the feeding of herbivore larvae on a single mountain birch branch can cause rapid systemic inducible responses (i.e. leaf quality alters in intact leaves close to damaged leaves as well as in the whole tree) within a few hours or days (Haukioja & Niemelä 1979; Haukioja & Hanhimäki 1985; Hanhimäki & Senn 1992; Kaitaniemi & Ruohomäki 2001). Hence, we tested whether willow warblers prefer intact branches from trees with larvae over intact branches from control trees.

METHODS
The study was carried out at the Kevo Subarctic Research Station (69°45′ N, 27° E), northernmost Finland, during late July and early August in 2003. From the mountain birch
The two trees in each pair were alike in phenotype, without obvious herbivore damage and situated close to each other (maximum distance \(\leq 10\) m). Two mesh bags (\(c. 80 \times 35\) cm, mesh 0.4 mm) were placed on two branches (in the lower third of the crown) of each experimental tree. We randomized which tree in each tree pair was exposed to herbivory by sawfly (\(Arge\) fuscinervis Lindqvist; Hymenoptera, Symphyta) larvae, and which was left as a control. In each pair, 15 sawfly larvae in their penultimate or ultimate instars were placed in mesh bags on the treatment (herbivory) tree, while the mesh bags in the control trees were left empty as sawflies.

The sawfly larvae in the bags were allowed to feed on the birches a week or more until the test with willow warblers. At testing, at least 20% loss of foliage was observed in the birches. A new pair of branches was tested every day, with the order randomized. In all the test procedure took 2 weeks; thus the trees tested last suffered from the heaviest branch-wide defoliation (\(\geq 50\)% within the bags). The first tree pair was used only to practice the methods of observing the willow warblers (three individuals), and the data were excluded from all analyses.

In each test day, one non-bagged branch (length \(\leq 1\) m) from a tree exposed to larvae and one from a control tree was tested with several willow warblers (four to 12 individuals per day). Two persons participated in the process. One of them cut off the branches close to the bags, whether containing larvae (herbivory tree) or empty (control tree), and coded the test branches with a strip of paper. The other person (E.M. in each case) recorded bird behaviour. She did not know the origin of the branches, making it a blind test. Inside the observation booth (depth: 118 cm, height: 97 cm, width: 75 cm; window in the door: 10 \(\times\) 10 cm), the two branches were placed in bottles filled with water on the left and right side of the booth; the placement was made randomly, by flipping a coin. No other branches or perches were available for the birds, but they sometimes rested on the narrow wall shelf or the floor of the booth. The light in the booth was made as natural as possible, using a True-Light 20 W lamp (Importer: AD-Lux Oy, Turku, Finland). The light covered a wide spectrum, including UV wavelengths, and was non-vibrating.

The willow warblers used in the experiment were captured with mist nets from the close vicinity of the research station and released unharmed back into nature after testing (always within 3 h from capture); the testing took place with the permission of the Lapland Regional Environment Centre (administered by the Finnish Ministry of the Environment).

The birds were ringed and aged and their wing length was measured. Wing length differentiates the genders in the willow warbler (Svensson 1992): 18 birds with a maximum wing length of 64 mm or less were undoubtedly females, while 42 with a maximum wing length of 67 mm or more were males; 12 birds could not be sexed with this method. Only two birds out of the total 72 captured were adults born in the previous year or before; the others were independent juveniles born in 2003. Thus the age of the bird was not among the variables analysed.

In the test trial, we released the willow warbler inside the booth. It typically took few minutes for the bird to calm down after fluttering around the booth, after which it usually started systematic searching of the cage, obviously for food. The first choice of the bird was recorded. Subsequently, the observer recorded when the bird moved from one branch to another or somewhere else in the booth (location \(\text{other}\) hereafter) until the bird lost interest to the branches (birds started either to flutter around or fell asleep). The mean (\(\pm SD\)) test duration (from bird’s first choice to the termination of the test) was 857 \(\pm\) 742 s.

The location (\(\text{herbivory tree, control tree or other}\)) of the bird in the test booth was an analysis variable in the statistical tests. We emphasised the birds’ first choice as a dependent variable, but also computed descriptive statistics for the mean number of visits and the proportion of total time spent in three different possible locations (excluding inactive birds). We used chi-square analysis of goodness-of-fit to test whether the birds’ first choice followed the expected ratio between location possibilities (1 : 1 : 1 between three possible locations; 1 : 1 between trees in restricted analyses excluding the possibility \(\text{other}\)). The effects of gender and side (left or right) of the booth on the dependent variable \(\text{first choice}\) were tested with generalized linear models (the GENMOD procedure of the SAS statistical software, version 8.02), using multinomial (test with three possible locations) or binomial (restricted test with two possible locations) distributions with cumulative logit or logit link functions, respectively. In order to assume complete independence across subjects, the tree pair was used as a subject effect in the repeated statement.

**Results**

Of the total 72 willow warblers used in the experiment, 57\% (41 individuals) flew or jumped first to the branch taken from a herbivory tree (Table 1, Fig. 1). The rest first chose the branch of a control tree (19 individuals) or some other place in the booth (12 individuals). This distribution deviated statistically from randomness: \(\chi^2 = 19.1, d.f. = 2, P < 0.0001\). Neither the bird’s gender nor the position of the branch in the booth had any effect on the birds’ first choice (generalized linear model: \(\chi^2 = 0.21, d.f. = 1, P = 0.64\) for gender, \(\chi^2 = 0.02, d.f. = 1, P = 0.90\) for side, \(\chi^2 = 0.01, d.f. = 1, P = 0.93\) for gender \(\times\) side). The results remained qualitatively similar when only birds choosing...
can react to induced changes of herbivore-damaged plants. Our study is the first one to suggest that insectivorous birds

**DISCUSSION**

(68%) first chose a herbivory tree and 19 a control tree

one of the two branches first were analysed (Fig. 1): 41

72 birds chose one of the test branches as their first choice, while

first choice of willow warblers in test trials (n = 72 birds, see also Fig. 1), mean (± 95% confidence limits) numbers of visits of willow warblers at each possible location in the booth (standardized for 10 min in the test trial) and mean (± 95% confidence limits) proportions (% of total time willow warblers spent on different locations during the test

![Figure 1](image)

**Table 1** First choice of willow warblers in test trials (n = 72 birds, see also Fig. 1), mean (± 95% confidence limits) numbers of visits of willow warblers at each possible location in the booth (standardized for 10 min in the test trial) and mean (± 95% confidence limits) proportions (% of total time willow warblers spent on different locations during the test

<table>
<thead>
<tr>
<th>Location</th>
<th>First choice (No. of individual)</th>
<th>No. of visit per 10 min</th>
<th>Total time (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Herbivory tree</td>
<td>41</td>
<td>7.2 ± 2.7</td>
<td>38.0 ± 22.4</td>
</tr>
<tr>
<td>Control tree</td>
<td>19</td>
<td>6.3 ± 3.6</td>
<td>24.7 ± 13.0</td>
</tr>
<tr>
<td>Other</td>
<td>12</td>
<td>9.7 ± 4.6</td>
<td>37.3 ± 16.3</td>
</tr>
</tbody>
</table>

Values for the latter variables are given for tree pair-specific means (n = 9 tree pairs, one to nine birds per pair) for the 38 birds considered sufficiently active after the first choice.

First choice of willow warblers in test trials for undamaged branches from trees with bagged larvae (shaded bars) and from control trees without bagged larvae (white bars). Sixty of 72 birds chose one of the test branches as their first choice, while the rest chose some other place in the booth.

The branch of an herbivory tree was preferred over the branch of a control tree seven times out of nine while equal preference was observed twice (Fig. 1). There were no obvious differences in the mean numbers of visits or the proportion of total time the willow warblers spent on different test branches (Table 1).

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**REFERENCES**


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