

Low light reflectance may explain the attraction of birds to defoliated trees

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Plants use volatile organic compounds to attract invertebrate predators and parasitoids of their herbivore pests. Recently, it has been suggested that plants, either through visual or olfactory cues, may also “cry for help” from vertebrate predators such as birds. We show that in a laboratory choice test, passerine birds (*Parus major* and *Cyanistes caeruleus*) were attracted to the intact branches of trees (*Betula pendula*) suffering from foliar damage caused by herbivore larvae (*Epirrita autumnata*) in nontest branches. Species, age, or sex of the experimental bird or lighting (ultraviolet [UV] or non-UV) did not affect the preference. However, the birds made a clear choice between the treatments when the trees came from a forest patch receiving more sunlight, whereas no obvious choice was observed when the trees came from a shadier forest patch. Results of the choice test were supported by the spectral reflectance of tree leaves. In the sunnier forest patch, control trees reflected more visible light than the herbivore trees, whereas no such difference was found in the shadier forest patch trees. We suggest that avian predators use their vision within visible wavelengths to find insect-rich plants even when they do not see the prey items or damaged leaves. *Key words:* induced plant defenses, insect herbivory, tritrophic interactions, vertebrate predators, vision. [*Behav Ecol*]

Plants suffering from herbivory can reduce the number of herbivorous insects. For example, plants can invest in secondary compounds that are harmful to insects or indirectly attract the predators and parasitoids of herbivores (Vet and Dicke 1992; Karban and Baldwin 1997; Van Bael et al. 2003). The mutualistic relationships observed between plants and the predators of herbivores have opened new insights into trophic level interactions. A phenomenon named “crying for help” is a tritrophic interaction, where the plant is adapted to attract predators and parasitoids in order to reduce herbivory. A number of studies have shown that plants can attract invertebrate predators and parasitoids actively with volatile organic compounds (Price et al. 1980; Vet and Dicke 1992; De Moraes et al. 1998; Tentelier et al. 2005; Kost and Heil 2006). There have also been some studies about the competence of avian predators in finding insect herbivores from plant individuals, which differ in quality (Heinrich and Collins 1983; Marquis and Whelan 1994; Mols and Visser 2002; Boege and Marquis 2006; Müller et al. 2006). However, in a first study concerning a possible crying-for-help system with vertebrate predators, Mäntylä et al. (2004) showed that willow warblers (*Phylloscopus trochilus*) were attracted to the intact branches cut from mountain birches (*Betula pubescens* ssp. *czerepanovii*) that had herbivores (*Arge fuscineris*, sawfly larvae) on adjacent branches. The birds clearly preferred those branches over the branches taken from a control tree without herbivores. This suggested that the mountain birch could be “crying for help” by producing inducible defense compounds that the birds perceive. However, the exact mechanism behind the attraction remained unclear (Mäntylä et al. 2004).

The attraction of birds to defoliated trees could either be through visual or olfactory cues. In addition to their broad range of vision (315–700 nm), diurnal birds can distinguish a large scale of chromatic variation, and thus, they see colors differently and with more shades than humans. This is because birds have 4 cone cell types and color vision-enhancing

oil droplets in their eyes and thus a tetrachromatic vision where every seen color consists of red, green, blue, and ultraviolet (UV, 320–400 nm) parts. In comparison, humans have only 3 cone cell types and a trichromatic vision lacking the UV part visible to birds (Cuthill 2006; Jones et al. 2007). The UV vision of birds is a good candidate for the mechanism behind the attraction of birds to plants suffering from herbivore defoliation as several bird species are known to use it, for example, during foraging (e.g., Viitala et al. 1995; Church et al. 1998; Honkavaara et al. 2002). Additionally, in the case of the birch, insect herbivory induces the production of defense chemicals (Haukioja 2003), such as flavonoids that are visible in UV wavelengths (Valkama et al. 2003). In contrast, the olfactory ability of most birds, including passerines, was long thought to be negligible (Roper 1999). Recent studies have, however, shown that passerines can use their olfaction in many situations (e.g., in foraging and aromatizing nests) (Roper 1999; Petit et al. 2002; Mennerat et al. 2005). Many invertebrate predators in tritrophic systems use volatile organic compounds produced by plants to smell and locate their prey (Turlings et al. 1990; Dudareva et al. 2006), so it is possible that such a mechanism could work in birds as well.

In present day behavioral ecology, the replication of tests of novel ideas across studies is not commonly done (Owens 2006). This leads to many plausible hypotheses on adaptive animal behavior in single species but generates few generalizations over other taxa and ecosystems. In this paper, our goal was to readdress our earlier findings about the attraction of passerine birds to herbivore-damaged trees (Mäntylä et al. 2004) but in a different system consisting of a new suite of species (silver birch—autumnal moth—tits). We also aimed to find out more about the mechanisms that birds might use to locate the insect-rich trees. Specifically, we tested whether the attraction could be explained by reflectance in UV wavelengths by conducting choice tests with and without UV illumination. Also, in order to find out whether there is any difference in light reflectance between the damaged and control trees either in the UV or human-visible spectrum, we measured the reflectance spectrum from the tree leaves with a spectrophotometer.

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MATERIALS AND METHODS

Study site and design

The experiment was carried out during May and June 2006 at the Botanical Gardens of the University of Turku on the island of Ruissalo (60°26'N, 25°01'E), Southwestern Finland. At the Botanical Gardens, there were 2 patches of 10-m tall silver birches (*Betula pendula* Roth) planted as 3-year-old saplings in 1994. The larger forest patch contained birches in a 44 × 5 grid (total 162 trees), and the smaller forest patch in a 15 × 5 grid (total 54 trees). In both patches, some trees had been cut down earlier. The small forest patch was on the northern side of the large patch and partly shaded by its trees. A narrow footpath separated the patches. The birches were from a total of 10 clones originating from the southern and middle parts of Finland (Poteri et al. 2001).

For this experiment, we chose a total of 38 tree individuals from 3 clones because none of the clones alone had enough trees. For practical reasons, the main selection criterion was that the selected birches were to have branches also in the lower part of their stem. From each chosen clone, we selected 12 or 14 birches that were organized in pairs. There were thus a total of 19 pairs of trees, 6 or 7 per clone. Two pairs per clone were always from the small and 4 or 5 pairs from the large forest patch. One pair of trees in the small forest patch had to be left out from the experiment because there were no longer birds available for choice tests (see below). Accordingly, we used 18 pairs of trees in the experiment (6 per clone). The trees in each pair were alike in genotype and in phenotype (i.e., similar height and structure) and were growing close (<10 m) to each other without obvious herbivore damage. Three mesh bags (ca. 80 × 35 cm, mesh 0.4 mm) were placed on 3 branches in the lower part of each experimental tree. The tree that was left as a control in each tree pair and the one exposed to herbivory by autumnal moth larvae (*Epirrita autumnata* Borkhausen, Lepidoptera, Geometridae) were chosen by randomization. The autumnal moth is a common species in Southern Finland but it does not usually cause visible damage to trees like it does in Northern Fennoscandia (Haukioja et al. 1988). Twenty laboratory-hatched autumnal moth larvae in their early instar (second out of 5) were placed in each of the 3 mesh bags on the treatment (herbivore) trees on 4th May at the time of leafing. The mesh bags in the control trees were left empty of larvae. In addition, the 2 biggest birches had an extra (fourth) bag with 15 larvae, and also their control trees had an extra empty bag.

The autumnal moth larvae in the bags were allowed to feed on the birch leaves for the rest of May until the bird choice tests began on 4th June (i.e., practically their whole larval stage: some even pupated during the tests). During the experiment, the degree of defoliation was visually estimated (Kaitaniemi et al. 1999) and the loss of foliage was estimated between 10% and 100% in the larval bags (mean ± standard deviation [SD] was 64 ± 19%). The order of the birches in the experiment was randomized between and within the clones, and each test day we used from 1 to 3 pairs of trees. Altogether, the testing period with birds lasted 15 days.

In order to test for preference, the birds were allowed to make a choice between a branch from a tree exposed to larvae (herbivore tree) that had never been bagged (length ca. 1.5 m) and a similar branch from a control tree. The test was conducted in a booth with 2 bird species, the great tit (*Parus major* L.) and the blue tit (*Cyanistes caeruleus* L.). Autumnal moth larvae together with other related species are part of the normal summer diet of both bird species (Eeva et al. 2005). Five to eight bird individuals were tested per tree pair. Two persons

participated in the testing process. One of them (P.S. in each case) cut off the branches close to the bags, whether containing larvae (herbivore tree) or empty (control tree), and coded the test branches with a strip of paper. The other person (E.M. in each case) observed bird behavior on the spot and later from videotapes that were recorded through a hole in the booth ceiling. The observer did not know which branch was from an herbivore tree and which from a control tree, which made it a blind test. Inside the observation booth (height 1.76 m, depth 1.16 m, and width 1.16 m), the 2 branches were placed in bottles filled with water on the left and right sides of the booth; the placement was made randomly. No other branches or perches were available for the birds, but they sometimes rested on the floor of the booth. There were 2 different lights in the booth. One of them was made as natural as possible using a True-Light 14-W fluorescent lamp (importer: AD-Lux Oy, Turku, Finland). This light covered a wide spectrum, including UV wavelengths, and was nonflickering. The other one was a standard 14-W fluorescent lamp (Philips Master Super 80) with an initially narrower spectrum. Additionally, this lamp was enclosed with a tube-shaped protector that filters out UV wavelengths (importer: AD-Lux Oy). We alternated the tests in consecutive birds so that every other bird was tested with the light including UV wavelengths and every other with the non-UV light.

The great tits and blue tits used in the experiment were captured from nest-box populations surrounding the study site at the Botanical Gardens. The birds were captured from their nest-boxes while they were feeding 7- to 12-day-old nestlings. They were released unharmed back into their territories immediately after testing (always within 3 h from the capture). The birds were ringed, aged, and measured (Svensson 1992). In total, 112 birds were used in the experiment (78 great tits and 34 blue tits, 51 males and 61 females). A total of 50 individuals were 1-year-old and 62 individuals were 2-year-old birds or older. The study was performed under a license for animal research to use wild birds in the experiments (license number 1632/06), admitted by the Lab-Animal Care and Use Committee, administered by the University of Turku.

In the choice test, the bird was first released inside a small booth (height 18.5 cm, depth 28 cm, and width 18.5 cm) attached to the actual observation booth to let it calm down for a few minutes. Thereafter, the hatch between the booths was opened, and the bird was free to fly to the observation booth (mean waiting time ± SD at the habituation booth was 25 ± 26 s). It typically took a couple of minutes for the bird to calm down (i.e., to ruffle its feathers a little) and get interested in the branches of the observation booth. The first choice of the bird was defined to be the first branch the bird went to after it had calmed down. The choice was recorded during the experiment and later confirmed from a videotape. It was easy to see the bird calm down and make the first choice. The test duration for each individual was 10 min, but the birds quite quickly lost their interest in the branches when they could not find any food on them. Thus, we have used the first choice as a response variable in this experiment (as in Mäntylä et al. 2004).

Three leaves from each birch were measured for their light reflectance with a spectrophotometer at the end of the experiments in mid-June (Avaspec 2048 with an Avalight DH-S light source and WS-2 white standard). Small branches were cut close to the mesh bags and immediately used in reflectance measurements, which were performed indoors. The measurements were done from the upper side of the leaves at 90° to the surface, avoiding the leaf veins. The light reflectance could be above 100% because the spectrophotometer was calibrated with the white standard.

Statistical analyses

The first choice of the bird (branch of an herbivore tree or a control tree) was the response variable in the statistical tests. We made the tests with generalized linear mixed models (GLMM) using a residual pseudolikelihood estimation method, to see whether the first choice of the bird was affected by any of the following factors: sex, age, species, light treatment (UV or non-UV), mean defoliation percentage of the branches inside the mesh bags, running number of date (day 1 is the first test day and day 15 the last one) or forest patch (large or small). In this concept, the first choice was coded as a binary variable where 0 = control tree and 1 = herbivore tree. Thus, binomial distributions with logit link functions were used in the GLIMMIX procedure of the SAS statistical software, version 9.1. We also tested for the interactions age \times light and sex \times light in the first choice because the lack of the degrees of freedom (df) prevented us from using all possible pairwise or more complicated interactions and because these 2 interactions were seen as the most interesting biologically. In order to assume complete independence across the subjects, the tree pair nested within the birch clone was used as a subject and a random effect in the RANDOM statement. To compute the denominator df, we divided the residual df into between-subject and within-subject portions (option BETWITHIN).

For the spectral data, we used linear mixed model analyses (the restricted maximum-likelihood method of the MIXED procedure of the SAS) with total reflectance sum of 2 different parts of the spectrum as dependent variables (UV = 300–400 nm and human visible = 400–700 nm) (Montgomerie 2006). Forest patch (large or small), treatment (defoliated herbivore tree or control tree), and their interaction were included as independent variables. The identity of the tree nested within the birch clone was used as a clustering factor (REPEATED statement) to control the fact that the 3 measurements from the same tree were not independent observations. The method for computing the denominator df (option SATTERTHWAITE) performed a general Satterthwaite approximation for the denominator df.

RESULTS

The only statistically significant factor affecting the birds' first choice was forest patch (Table 1). The birds preferred branches of the herbivore trees as their first choice when the trees came from the large forest patch, but there was no preference between branches from the small forest patch. In the final model, with the birch individual (nested within the clone) included as a random factor (Table 1), the 95% confidence limits (CLs) of the least square mean for the probability of choosing the herbivore tree did not include the expected 0.50 value (1:1 ratio) in the large forest patch (least square mean = 0.731, lower 95% CL = 0.567, upper 95% CL = 0.849). On the contrary, in the small forest patch, the 95% CLs included 0.50, which did not provide clear support for the choice of either branch (least square mean = 0.340, lower 95% CL = 0.139, upper 95% CL = 0.621). This result can be best illustrated by plotting the distribution of first choices by tree pairs (Figure 1). Among the tree pairs from the large forest patch, the birds chose herbivore trees 43 times and control trees 16 times (Figure 1; $\chi^2 = 11.46$, df = 1, $P = 0.0007$), whereas among the tree pairs from the small forest patch, 7 individuals chose the herbivore tree and 14 individuals the control tree (Figure 1; $\chi^2 = 1.72$, df = 1, $P = 0.19$). The result can be confirmed using trees as replication units: herbivore trees were preferred 11 times and control trees 2 times (binomial probability is $P = 0.0095$) in the large forest patch (Figure 1), whereas the corresponding ratio was

Table 1

Results of the GLMMs on fixed factors affecting the first choice of birds

	Numerator df	Denominator df	<i>F</i>	<i>P</i>
Fixed effects—final model				
Forest patch	1	16	6.64	0.020
Removed fixed effects				
Defoliation percentage	1	15	3.46	0.082
Bird species	1	11	2.01	0.184
Light treatment	1	16	1.68	0.213
Bird age	1	11	0.07	0.803
Bird age \times light treatment	1	2	0.52	0.547
Bird sex	1	15	0.03	0.859
Day	1	61	0.03	0.858
Bird sex \times light treatment	1	1	0.01	0.946

The analysis was first based on a full model, from which fixed effects were dropped one by one in order of least significance. The final model is given with the only statistically significant ($P < 0.05$) variable (forest patch). Results for other factors are given when they were added alone to the final model (interaction variables were added together with the corresponding main factors).

1:4 ($P = 0.1563$) in the small forest patch (Figure 1). Some birds had to be excluded from the analysis because they did not calm down (16 individuals) or make any clear first choice (16 individuals).

The total reflectance (i.e., total brightness using nanometer sums) of leaves in the human-visible wavelengths (400–700 nm) was significantly higher in control trees than in herbivore trees and also in the trees of the small forest patch compared with the trees of the large forest patch (Figure 2; treatment: $F_{1,33.3} = 4.97$, $P = 0.033$; forest patch: $F_{1,33.7} = 8.15$, $P = 0.007$). In neither case did the total reflectance differ significantly in the UV wavelengths (300–400 nm) (Figure 2;

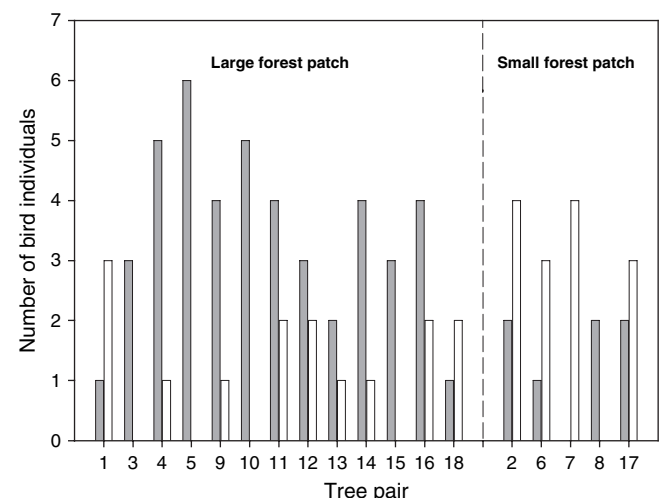


Figure 1

Number of bird individuals per tree pair that chose a branch of an herbivore tree (gray bar) or a branch of a control tree (white bar). The numbers of the tree pairs show the order in which they were used in the experiment. The 5 tree pairs on the right side of the figure are from the small forest patch and rest of the tree pairs from the large forest patch.

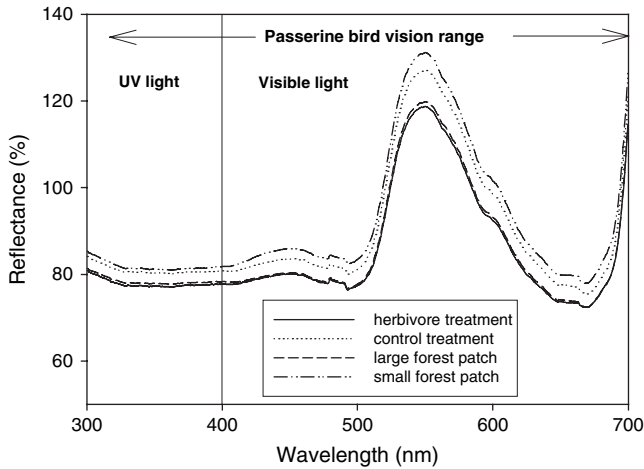


Figure 2

Spectrum curves of intact birch leaves of the control treatment and the herbivore treatment and the small forest patch and the large forest patch. Both statistically significant main effects are depicted.

treatment: $F_{1,33.3} = 1.95$, $P = 0.17$; forest patch: $F_{1,33.8} = 1.90$, $P = 0.18$). The interaction term forest patch \times treatment was nonsignificant in both visible ($F_{1,32.7} = 0.79$, $P = 0.38$) and UV wavelengths ($F_{1,32.7} = 0.34$, $P = 0.57$), and it was excluded from the final models. However, because a single bird could only choose between branches taken from the same forest patch, it was relevant to test how strong the treatment effects were within the forest patches. Therefore, we performed separate one-way models for both forest patches. The total reflectance of leaves in the human-visible wavelengths was significantly higher in control trees than in herbivore trees in the large forest patch ($F_{1,24} = 4.82$, $P = 0.038$) but not in the small forest patch ($F_{1,8.28} = 0.29$, $P = 0.60$) (Figure 3). This is in accordance with the birds making a clear choice

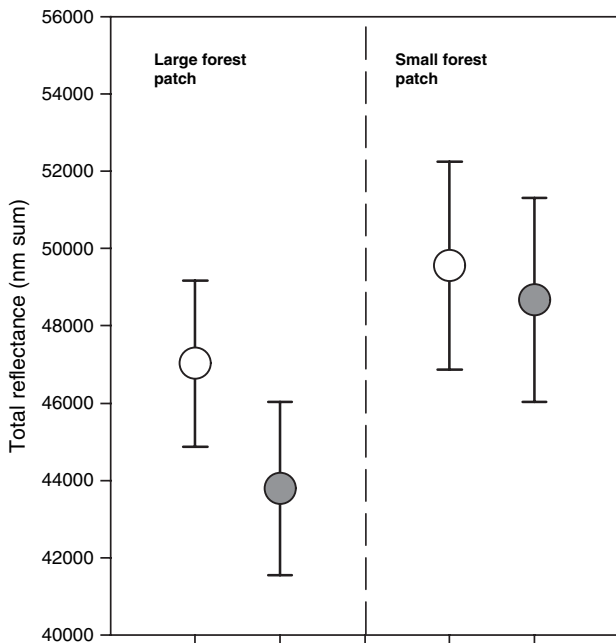


Figure 3

Least square means with 95% CLs of reflectance in the human-visible light range 400–700 nm of control trees (white dots) and herbivore trees (gray dots) of the large and small forest patches.

between the trees from the large forest patch but not between trees from the small forest patch (Figure 1). There were no significant differences inside the forest patches in the UV wavelengths (large forest patch: $F_{1,24} = 1.90$, $P = 0.18$; small forest patch: $F_{1,8.14} = 0.09$, $P = 0.77$). There was probably no variation in hue (the perceived color, Montgomerie 2006) because the wavelength with maximum reflectance (550 nm) was the same in all leaf measurements (Figure 2).

DISCUSSION

Our results with silver birches, autumnal moths, and tits confirm those obtained in another tritrophic system that included a completely different set of species (Mäntylä et al. 2004). In both tritrophic systems, the birds were attracted to trees that had herbivore defoliation on nontest branches. We also found a plausible candidate for the mechanism with which insectivorous birds can find trees carrying insect herbivores. The herbivore-damaged birches reflected less light in the passerine bird (and human) visual range than the control birches, offering a vision-based mechanism for the observed phenomenon. It seems that the birds can see the difference in brightness and behave accordingly. In contrast, our earlier working hypothesis about the role of birds' UV vision was not supported because no difference in choice was found between the light treatments (UV and non-UV) (Table 1). It rather seems that birds use their entire range of vision (315–700 nm) to identify branches of insect-rich trees even in the absence of visible prey items or damaged leaves. However, our results do not rule out the possibility of olfaction contributing to the attraction together with vision.

The only variable explicitly explaining the birds' first choice in the experiment was the forest patch in which the tree pair grew. The birds exhibited a clear choice between the treatments when the trees came from the large forest patch, whereas no obvious choice was observed when the trees came from the small forest patch. In accordance, there was a difference in the light reflectance of leaves between the treatments in the large forest patch but not in the small one. In the large forest patch, the control trees reflected more light than the herbivore trees. This difference was apparent particularly in the human-visible range of the spectrum. Both the herbivore treatment and the forest patch had an overall effect on light reflectance: the birches of the small forest patch reflected more light than the birches of the large forest patch, and the control trees reflected overall more than the herbivore trees. In all cases, the largest differences were seen in wavelengths corresponding to green and yellow (ca. 500–600 nm). Because there was a difference between the light reflection of control birches and herbivore birches of the large forest patch and because birds clearly differed in their preference between the 2 alternatives, we suggest that birds perceive this difference. At least physiologically, due to their tetrachromatic vision and oil droplets, the birds are able to differentiate more shades of a particular color (e.g., green) than humans (Cuthill 2006; Jones et al. 2007).

In our opinion, the most likely explanation for the difference in light reflectance between the forest patches is shading. The small forest patch is on the northern side of the large one and because the distance between the patches is only 6 m, the 10-m tall birches cast a shadow over the birches of the small forest patch. In addition, branches from the small forest patch were sampled from trees throughout the patch, whereas in the large forest patch, the majority of branches were sampled from trees growing at the southern edge of the patch that is exposed to direct sunlight throughout the day.

However, the proximate reason for the reflection difference in the shaded and nonshaded leaves is not easily identified.

It seems likely that shading caused a colder microclimate around the birches of the small forest patch. In addition, shading reduces the allocation of nutrients to secondary defense chemicals in mountain birches that are closely related to silver birches (Henriksson et al. 2003). At least, the leaf water content and the amounts of both protein-bound and free amino acids are higher in shaded trees or branches than in nonshaded ones (Henriksson et al. 2003). On the other hand, the levels of leaf sugars, total phenolics, and soluble proanthocyanidins together with leaf toughness are lower in the shade (Henriksson et al. 2003). In general, plants are known to respond to solar radiation (especially to harmful UV-B radiation) with several defense and repair mechanisms (Julkunen-Tiitto et al. 2005). Some inducible secondary products (especially phenolics) protect plants against photodamage as antioxidants (Close and McArthur 2002; Julkunen-Tiitto et al. 2005). Because these same compounds also deter herbivores, it may well be possible that resources in defoliated trees growing in sunny conditions are allocated differently than in nondefoliated trees and in trees growing in the shade. However, the detailed mechanism of how birds could sense these hypothetical differences remains open.

There are obvious benefits for birds to find food easily and it is no surprise that they use any available cues, whether active or passive, from plants and herbivores to find it (Heinrich and Collins 1983; Mäntylä et al. 2004; Müller et al. 2006). However, it remains to be investigated whether the chemical or structural changes in plant leaves in response to herbivory evolve as a direct consequence of the benefit arising from attracting birds to forage on the herbivores. It is nevertheless known that avian predation of herbivores can have substantial fitness benefits for plants (Atlegrim 1989; Strong et al. 2000); it can, for example, increase growth in trees (Marquis and Whelan 1994; Sipura 1999) and yield in apple orchards (Mols and Visser 2002). The high benefits of reduced herbivory suggest that there should be selection for the induced mechanisms that specifically aim to attract birds. With our results in mind, it seems that birds find the insect herbivores best when the trees are not in shade, and thereby, the plants produce enough constitutive or inducible defense compounds against photodamage and/or herbivores (see Close and McArthur 2002). The plants can either attract predators actively with, for example, volatile organic compounds, which are energy costly for them, or rely on predators finding the herbivores without any active cues. The mechanism attracting birds has interesting implications also for the herbivore evolution, as they need to evolve crypsis against the predators.

In conclusion, our results strengthen the evidence that passerine birds are attracted, at least in some conditions, to herbivore-damaged trees even when they do not see the physical damage caused by the herbivores. Furthermore, we found the first evidence of how the mechanism may operate. It appears that the birds can detect the herbivore-rich trees with their vision.

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