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**MUTUALISTIC INTERACTIONS
BETWEEN PLANTS AND BIRDS:
BEHAVIOURAL MECHANISMS AND
ECOLOGICAL IMPORTANCE**

by

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*There is nothing like looking, if you want to find something.
You certainly usually find something, if you look,
but it is not always quite the something you were after.*

Thorin Oakenshield
(J.R.R. Tolkien: The Hobbit)

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LIST OF ORIGINAL PAPERS

This thesis is based on the following articles and manuscripts, referred to in the text by their Roman numerals:

- I** Mäntylä E, Klemola T & Haukioja E. 2004. Attraction of willow warblers to sawfly-damaged mountain birches: novel function of inducible plant defenses? *Ecology Letters* 7: 915–918.
- II** Mäntylä E, Klemola T, Sirkiä P & Laaksonen T. 2008. Low light reflectance may explain the attraction of birds to defoliated trees. *Behavioral Ecology* 19: 325–330.
- III** Mäntylä E, Alessio GA, Blande JD, Heijari J, Holopainen JK, Laaksonen T, Piirtola P & Klemola T. 2008. From plants to birds: higher avian predation rates in trees responding to insect herbivory. *PLoS ONE* 3(7): 2832.
- IV** Mäntylä E, Sirkiä PM, Klemola T & Laaksonen T. Territory choice of pied flycatchers is not based on induced cues of herbivore-damaged trees. *Submitted manuscript*.
- V** Mäntylä E, Klemola T & Laaksonen T. Birds help plants – a meta-analysis of top-down trophic cascades caused by avian predators. *Submitted manuscript*.

Articles **I**, **II** and **III** are reprinted with permissions from Blackwell Publishing, Oxford University Press and Public Library of Science, respectively.

1. INTRODUCTION

Ecosystems consist of trophic levels (e.g. producers, consumers and decomposers) and interactions among species of the same or different trophic levels (Price et al. 1980). These interactions are often depicted as food chains (as in Fig. 1). The base of the food chain is typically a plant, which is eaten by herbivores. Naturally this interaction is negative for the plant (Nykänen & Koricheva 2004), which tries to defend itself against herbivores in several ways (see section 1.1.). Herbivores are themselves preyed on by carnivores of the next trophic level. At the other extreme of the food chain are the top predators, which eat lower-level carnivores. Even though trophic interactions almost always involve species from more than two trophic levels (Oksanen & Oksanen 2000), many intensive ecosystem studies in the past have nevertheless dealt with only two trophic levels at a time. One example of tritrophic interaction is the trophic cascade, which usually consists of a predator, an herbivore and a plant, and where the effect of predation on the herbivore has a positive impact on the plant (Persson 1999; Schmitz et al. 2004). When herbivore-eating predators remove herbivores from plants, the result can thus be an indirect mutualistic interaction between plant and predator (both species benefit from each other via the herbivore; Fig. 1) (e.g. Marquis & Whelan 1994; De Moraes et al. 1998; Mols & Visser 2002; Kalka et al. 2008). During the past couple of decades, the mechanisms of multitrophic interactions have become a popular research subject (e.g. Dicke et al. 1990; Turlings et al. 1990; Holopainen 2004; Kost & Heil 2006; Halitschke et al. 2008).

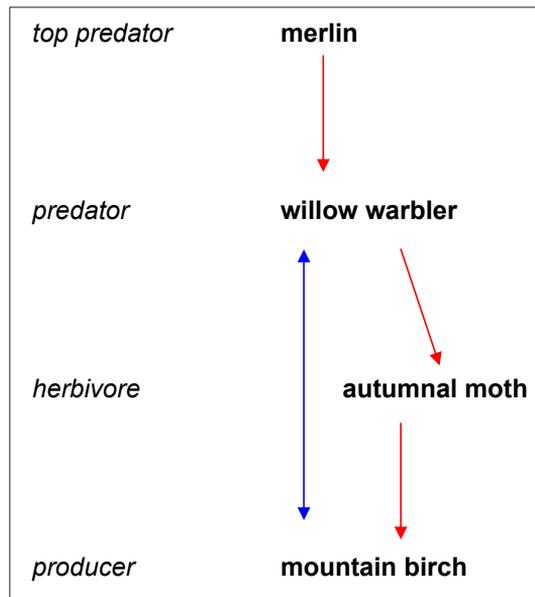


Figure 1. Example of a food chain in northern Finland, with merlin (*Falco columbarius*), willow warbler (*Phylloscopus trochilus*), autumnal moth (*Epirrita autumnata*) and mountain birch (*Betula pubescens* ssp. *czerepanovii*). Red arrows show predatory interactions (beneficial for one species, harmful for the other); blue arrow shows mutualistic interaction (beneficial for both species).

1.1. Plant defences

Direct defences by plants against herbivores may be constitutive defences, e.g. thorns or spines, but they may also be certain chemicals that are always present in the plant (Agrawal 2006). However, chemical defences are often activated only following herbivore attack (e.g. Haukioja 1990; Heil et al. 2004). A wide range of these inducible chemicals have been identified in plants, including tannins, alkaloids, terpenoids and flavonoids. Some of those are highly species-specific (either to the plant or against a certain herbivore species), while others are more universal (Peñuelas & Llusà 2004). The chemicals in plants consumed by herbivores can harm the herbivore directly, for instance by slowing its growth or even killing it (e.g. Coley & Barone 1996; Kause et al. 1999; Haukioja 2003; Haviola et al. 2007). Some plant defences can be indirect, such as the volatile organic compounds (VOCs) of plants that attract the herbivore's natural enemies (Karban & Baldwin 1997; Turlings & Wäckers 2004). This phenomenon, known as “crying-for-help”, has previously been known only in invertebrate predators and in parasitoids that consume for instance herbivorous larvae (e.g. Turlings et al. 1990; Vet & Dicke 1992; Takabayashi & Dicke 1996; De Moraes et al. 1998; Hoballah & Turlings 2001).

1.2. Tritrophic interactions

The mutualistic relationships observed between plants and the predators of herbivores have opened up new insights into trophic level interactions. Inter-specific communication between plants and invertebrate predators and parasitoids is based on inducible VOCs that are emitted by plants and that act as chemical attractants (Price et al. 1980; Vet and Dicke 1992; Takabayashi & Dicke 1996; De Moraes et al. 1998; Kessler & Baldwin 2001, Tentelier et al. 2005; Kost and Heil 2006). The feeding of herbivore larvae on a single tree branch has been found to cause rapid systemic inducible responses (i.e. leaf quality alters in intact leaves close to the damaged ones as well as in the whole tree) within a few hours or days (e.g. Haukioja & Niemelä 1979; Haukioja & Hanhimäki 1985; Hanhimäki & Senn 1992; Kaitaniemi & Ruohomäki 2001). Thus predators and parasitoids are able to sense herbivore-damaged trees from a distance, before they actually see or smell the herbivores themselves (Frag & Paré 2002; Heil & Silva Bueno 2007; Staudt & Lhoutellier 2007).

There have been some studies on the competence of avian predators in finding insect herbivores on plant individuals of varying quality (Heinrich & Collins 1983; Marquis & Whelan 1994; Mols & Visser 2002; Boege & Marquis 2006; Müller et al. 2006). Avian predation can considerably reduce the herbivore load or damage to plants (e.g. Marquis & Whelan 1994; Van Bael et al. 2003); thus it may give plants an adaptive advantage to attract avian predators that reduce their herbivore

load. However, predators or parasitoids may have adapted to recognise cues from herbivore-damaged plants without the plants specifically adapting for this purpose (Janssen et al. 2002; Niinemets et al. 2004; Rosenstiel et al. 2004). Such cues may include for example the products or by-products of induced chemical defence, or other structural, physiological or chemical changes in the plant that are sensed by the natural enemies of the herbivores. It is therefore crucial to understand the mechanisms behind the attraction, before arriving at conclusions as to potential co-evolution between plants and the avian predators or the parasitoids of their herbivores (Peñuelas & Llusà 2004; Halitschke et al. 2008). Birds may also compete with invertebrate predators and parasitoids for the same prey or host (e.g. caterpillars). Additionally, it has been suggested that predators are more profitable to plants than parasitoids because they remove the herbivore immediately from the plant (Dicke & van Loon 2000; van der Meijden & Klinkhamer 2000).

1.3. Possible ways for birds to detect herbivore-damaged plants

The two primary sensory mechanisms that birds may use to detect plants carrying herbivores are vision and olfaction. One hypothesis is that vision can be important in detecting herbivores at both long and short distances, while olfaction may be useful mainly closer to the damaged plants, especially under windy conditions.

1.3.1. Vision

Birds can naturally use visible feeding marks in leaves or qualitative structural differences among plant individuals as cues to find insect herbivores (Heinrich & Collins 1983; Mols & Visser 2002; Boege & Marquis 2006; Müller et al. 2006; but see Bergelson & Lawton 1988). In addition to their broad range of vision (315–700 nm), diurnal birds can distinguish a large scale of chromatic variation; thus they see colours differently and with more shades than humans (Cuthill 2006). This is because birds have four cone cell types and colour-vision-enhancing oil droplets in their eyes, giving rise to a tetrachromatic form of vision in which every perceived colour consists of red, green, blue and ultraviolet (UV, 315–400 nm) components. In comparison, humans have only three cone cell types and trichromatic vision, lacking the UV part visible to birds (Cuthill 2006; Jones et al. 2007).

The UV vision of birds may be 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 instance during foraging (e.g. Church et al. 1998; Honkavaara et al. 2002; Viitala et al. 1995). Additionally, in the case of the birch (*Betula* sp.), insect herbivory induces the production of defence chemicals (Haukioja 2003), such as flavonoids, which are visible in UV wavelengths (Valkama et al. 2003).

1.3.2. Olfaction

In contrast to vision, the olfactory ability of most birds, including passerines, was long thought to be negligible (Roper 1999). Recent studies, however, have shown that passerines can make use of olfaction in many situations, such as in aromatising nests (Petit et al. 2002; Mennerat et al. 2005; Gwinner & Berger 2008; Mennerat 2008) and in predator recognition (Amo et al. 2008; Roth et al. 2008). Many invertebrate predators in tritrophic systems use VOCs produced by plants to detect and locate their prey (Turlings et al. 1990; Dudareva et al. 2006). Novel VOCs emitted by herbivore-damaged plants may be the first indicators of herbivore presence to predators. It is therefore possible that olfaction may also be utilised by birds in receiving signals from plants.

Now there is also physiological and genetic evidence of the olfaction ability of birds. Steiger et al. (2008) studied nine bird species [blue tit (*Cyanistes caeruleus*), black coucal (*Centropus grillii*), brown kiwi (*Apteryx australis*), canary (*Serinus canaria*), galah (*Eolophus roseicapillus*), red jungle fowl (*Gallus gallus*), kakapo (*Strigops habroptilus*), mallard (*Anas platyrhynchos*), and snow petrel (*Pagodroma nivea*)] and found that they all had more active olfactory receptor (OR) genes than had previously been assumed. In vertebrates (especially in mammals and fish, which have been studied the most) the number of active OR genes generally correlates positively with the size of the olfactory bulb (i.e. the physiological capability to smell) (Niimura & Nei 2006). It thus seems that birds can detect smells much better than has previously been thought.

1.4. Ecological importance of insect-rich plants to birds

One question remains: how important is it to birds to know which plants have many herbivores? This can be especially beneficial for bird fitness if only some plants have large numbers of herbivores. Can birds, for example, choose their nesting sites close to herbivore-rich places? Quick choice of a breeding ground is especially important for migratory birds, which are time-limited and need to quickly select good-quality territories to ensure successful reproduction (Lundberg & Alatalo 1992; Siikamäki 1998; Sanz 1999). During the breeding season birds need to find food for both themselves and their offspring, so ample food resources close by should improve their breeding success (von Haartman 1982; Lundberg & Alatalo 1992). At least diurnal birds of prey can use their UV vision to assess the size of vole populations, since vole urine reflects UV light (Viitala et al. 1995; Koivula & Viitala 1999). Thus, assessing the size of prey populations, especially close the nesting sites may also be useful for other birds, such as insectivorous passerines.

1.5. Ecological importance of insectivorous birds to plants

Carnivorous birds are common in ecosystems throughout the world, and numerous studies have shown that they can affect the population sizes of insects and other small herbivores (e.g. Holmes 1979; Fowler et al. 1991; Williams-Guillén et al. 2008). An increasing number of studies have also examined the effect of bird predation cascading down to plants. A recent review has assessed the importance of birds in reducing plant damage mainly in forests and agricultural environments in the tropics (Van Bael et al. 2008). One question is to what extent this phenomenon varies among climatic areas, or between natural and agricultural environments. Recent studies (Sekercioglu 2006; Van Bael et al. 2008; Whelan et al. 2008) have shown that birds are beneficial to plants and constitute an important part of ecosystems, and that the removal of herbivores from harvested plants is certainly a potential ecosystem service of economic value (Sekercioglu 2006; Whelan et al. 2008).

2. AIMS OF THE THESIS

In this thesis I studied whether passerine birds are attracted to herbivore-damaged trees even if they do not see the larvae or damaged leaves (**I, II, III, IV**). The purpose of study **I** was to find out whether this occurs; studies **II** and **III** repeated the first study with different species and examined the possible mechanisms birds might use to find insect-rich plants. I approached these questions both in controlled laboratory aviaries (**I, II**) and in nature (**III, IV**), carrying out experiments in the northern subarctic (Kevo Research Station, Finland) (**I, III**) and in hemiboreal conditions (Turku, Finland) (**II, IV**) (Fig. 2). In addition to bird attraction, I also used measures from herbivore-damaged and undamaged birch leaves: light reflectance (**II**), net photosynthesis rate (**III**) and VOC emissions (**III**). In addition, I investigated whether passerine birds were able to use cues from herbivore-damaged plants in their territory choice (**IV**). Finally, in order to obtain a broader view of mutualistic interactions between birds and plants, I conducted meta-analyses of published articles on this topic (**V**).



Figure 2. Map showing the experimental study sites: Turku (60°27' N, 22°16' E) and Kevo (69°45' N, 27°01' E). Original map is from Wikimedia Commons (commons.wikimedia.org).

3. MATERIAL AND METHODS

In this chapter I briefly introduce the species and methods used in the experimental studies (studies **I** – **IV**). More detailed accounts of the methods can be found in the original articles. Studies **I** and **III** were carried out in the subarctic birch zone at the Kevo Research Station at Utsjoki, Finland (69°45' N, 27°01' E). Study **II** was carried out at the Botanical Gardens of the University of Turku on the island of Ruissalo, close to the city of Turku (60°27' N, 22°16' E). Study **IV** was carried out in three forests close to the city of Turku. They are typical Finnish mixed forests, with Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* (L.) H. Karst.) as the main tree species. Both study sites in Turku (**II**, **IV**) belong to the hemiboreal zone.

3.1. Experimental study set-ups

Studies **I**, **II**, **III** and **IV** were experimental studies, with varying species and methods (Table 1). In all four of these studies, half of the birches (*Betula* sp.) had larvae in mesh bags (herbivore trees); the other half (control trees) had empty mesh bags, with no herbivores. For the aviary studies (**I**, **II**), I always had another person cut a branch from both an herbivore tree and a control tree. The branches were from outside the mesh bags, and contained no larvae, damaged leaves or larval faeces. Thus I did not know which branch was from which tree (i.e. a double blind experiment). The birds were released in the aviary individually; I observed their behaviour and recorded which branch the bird first visited after calming down. The birds could not see the larvae in any of the studies. The plant, herbivore and bird species used in the experimental studies, the methods used to monitor birds' attraction to plants, and the plant variables measured in addition to bird attraction are shown in Table 1.

3.2. Species studied

In this section I introduce the species shown in Table 1. In all experimental studies I used common species of deciduous trees, herbivore larvae and passerine birds, in either the south (**II**, **IV**) or the north (**I**, **III**) of Finland. Thus these species have had a long period of coevolution and may already have been interacting mutualistically prior to the experiments. The species were chosen mainly for practical reasons. In study **I**, for instance, willow warblers were not accessible before the end of their breeding season in late July; I therefore had to use sawfly larvae as herbivores, as they feed on mature birch leaves at that time.

Table 1. Species used in the experimental studies, methods used to monitor birds' attraction to plants, and plant variables measured in addition to bird attraction.

	Study I	Study II	Study III	Study IV
Plant species				
- mountain birch	X		X	
- silver birch		X		X
- downy birch				X
Herbivore species				
- autumnal moth		X	X	X
- sawfly	X			
Bird species				
- willow warbler	X			
- great tit		X		
- blue tit		X		
- pied flycatcher				X
- passerine birds			X	
Response variable				
- choice in aviary	X	X		
- predation of plasticine larvae			X	
- territory choice				X
Plant cues measured				
- light reflectance		X		
- photosynthesis rate			X	
- VOC emissions			X	

3.2.1. Plants

Mountain birch (*Betula pubescens* ssp. *czerepanovii* (Orlova) Hämet-Ahti) is the tree-line species in northern Fennoscandia (Hämet-Ahti 1963). All mountain birches represent some level of hybridisation of downy birch (*B. pubescens* Ehrh.) and dwarf birch (*B. nana* L.). In northern Finnish Lapland they are typically poly-cormic, i.e. bush-like formations with multiple stems (ramets) (Kallio & Mäkinen 1978). Silver birch (*B. pendula* Roth) and downy birch are common tree species in Europe and Asia (Atkinson 1992). Silver birches mainly grow on dry and sandy soils, while downy birch can also grow in wetter ground. Downy birch is usually smaller than silver birch. There are no major genetic differences between these three birch species, all of which can hybridise with each other (Elkington 1968; Wilsey et al. 1998).

3.2.2. Herbivores

The autumnal moth (*Epirrita autumnata* Borkhausen; Lepidoptera, Geometridae) is the main herbivore of mountain birch in northern Finnish Lapland (Tenow 1972) but is also relatively common in southern Finland (Ruohomäki et al. 2000). Its population cycle is ca. 9–11 years, and at its peak phase it can cause large-scale forest defoliation in northern Fennoscandia (Haukioja et al. 1988). It overwinters in the form of eggs; the larvae hatch at the time of birch budbreak (Kevo, late May – early June; Turku, early May). The larvae

can feed on several woody plants, but are usually found on birch leaves since birch is often the most common deciduous tree. The autumnal moth has five larval instars, after which it pupates in the soil (Kevo, late June – early July; Turku, early June). Adult moths emerge and fly from August to October. Autumnal moth larvae, pupae and adults are common prey for e.g. insectivorous birds (Tanhuanpää et al. 2001), small mammals (Tanhuanpää et al. 1999) and invertebrate predators (Karhu & Neuvonen 1998), and eggs, larvae and pupae common hosts for several parasitoids (Ruohomäki et al. 2000; Klemola et al. 2008).

The sawfly used in study I (*Arge fuscinervis* Lindqvist; Hymenoptera, Symphyta) is one of many sawfly species found in Finnish Lapland (Kouki et al. 1994). *A. fuscinervis* overwinters as a prepupa; the adults emerge in spring. Females oviposit their eggs on birch leaves. The larvae hatch in June – July and eat mature birch leaves before pupating in late July – early August. The predators of *A. fuscinervis* are mainly ants (Punttila et al. 2004; Petre et al. 2007) and birds, which eat also adult sawflies (Wilson et al. 1999). The sawflies also have parasitoids (K. Ruohomäki et al., unpublished data) but there has been no detailed research of those.

3.2.3. Birds

The willow warbler (*Phylloscopus trochilus* L.) is the most common bird species in Finland (especially in Lapland), and breeds throughout northern and temperate Europe and Asia (Väisänen et al. 1998). It is a migratory bird, wintering mainly in sub-Saharan Africa. Willow warblers forage in the canopies of trees and eat various insects, such as lepidopteran and sawfly larvae (Nyström 1991). They build their nests of grasses on the ground; the fledglings leave the nest between mid-July and early August.

The pied flycatcher (*Ficedula hypoleuca* Pallas) is also a migratory bird, wintering in western Africa. It is a common insectivorous bird species in many parts of Europe, including Finland. It breeds in natural holes and in nest-boxes. Although pied flycatchers are often thought to catch insects mainly in the air, they actually also forage to a considerable extent on the ground and on tree branches (Lundberg & Alatalo 1992). They arrive in Finland in May and leave in late summer – early autumn.

In contrast to the above two bird species, tits are mainly residents in Finland; after successful breeding years, however, there may be short-distance partial migrations (Väisänen et al. 1998). The great tit (*Parus major* L.) is one of the most common bird species in Eurasia. It breeds in holes, nowadays often in nest-boxes. The great tit is omnivorous, but during the summer its diet consists mainly of insects (Eeva et al. 2005). The blue tit (*P. caeruleus* L.; also *Cyanistes caeruleus*) likewise occurs in many parts of Eurasia; the Finnish population is found in the southern half of the country (Väisänen et al. 1998). Breeding and foraging habits are similar to those of the great tit.

In study **III**, the birds used belonged to the local passerine bird fauna. Species observed in the study area were the pied flycatcher, the willow warbler, the brambling (*Fringilla montifringilla* L.), the great tit, the Siberian tit (*Parus cinctus* Boddaert; also *Poecile cinctus*), the common redpoll (*Carduelis flammea* L.), the yellow wagtail (*Motacilla flava* L.), the bohemian waxwing (*Bombycilla garrulus* L.), the bluethroat (*Luscinia svecica* L.) and the fieldfare (*Turdus pilaris* L.).

3.3. Observation methods

The aviary (or booth) used in study **I** was 118 cm deep, 97 cm high and 75 cm wide. I observed bird behaviour through a window (10 × 10 cm) in the door. The light in the booth was made as natural as possible, covering a wide spectrum (with UV wavelengths), and non-flickering. The aviary used in study **II** was slightly larger (height 176 cm, depth 116 cm, width 116 cm) than in the first study. It too had a small window in the door; the main form of observation, however, was with a video camera filming through a hole in the ceiling. This aviary had two different light conditions: UV light (non-flickering fluorescent light with a wide spectrum) and non-UV (normal fluorescent light with a UV filter).

In study **III**, artificial larvae were used to measure the bird predation rate in the experimental trees. The larvae were made of light green plasticine (close to the colour of for instance the autumnal moth larva) and were attached to the branches with thin metal wire. As the plasticine remained soft for several days (despite rain or cold weather), it was easy to check the artificial larvae daily and record whether they had been pecked at by birds (see also Brodie 1993).

Study **IV** dealt with the territorial choices of pied flycatchers. All territories had two nest-boxes, with two small birches growing close to the boxes. Half of the territories contained autumnal moth larvae on birch branches inside mesh bags, while the other half contained only empty mesh bags. The arrival date of both male and female pied flycatchers in the territories in spring was recorded daily. I also observed whether the birds preferred territories with hidden larvae over control territories.

3.4. Plant cues studied

Birds most likely receive cues from herbivore-damaged plants through sight and/or olfaction. To study these cues I used several methods. In study **II** half of the birds were tested in UV light, the other half in non-UV light. If the birds were interested in herbivore-damaged branches only in UV light, they were probably using their UV vision to find these trees. In study **II**, the light reflectance of the leaves of the experimental silver birches was measured with a spectrophotometer to obtain more information as

to whether birds were able to use their vision to recognise herbivore-damaged birches. In study **III** the plant cues of mountain birches measured were VOC emissions and net photosynthesis rate. A total of 15 different VOCs (mono-, homo- and sesquiterpenes and green leaf volatiles) were measured. The differences between the herbivore and control trees in the composition and quantities of these VOCs, and the correlations between VOC emissions and avian predation on the birches, would indicate whether birds could use olfaction in detecting herbivores. The net photosynthesis rate is generally correlated with the light reflectance of the leaves; undamaged plants can photosynthesise more than damaged ones and are therefore greener (Zangerl et al. 2002; Peñuelas et al. 2004; Louis et al. 2005). This is another way to determine whether birds are able to use vision to search for insect-rich trees.

3.5. Meta-analysis

To obtain the studies for the meta-analyses in my study **V**, I searched online databases with different combinations of keywords, as well as references in already found articles, to find all studies of tritrophic interactions among birds, herbivores and plants. To qualify for use in the meta-analysis, an article had to fulfill the following requirements: 1) at least one of the predators in the system studied had to be a bird species; 2) the experiment had to include a group with either no birds at all or significantly fewer of them than in the second group, in which bird predation was allowed; 3) there had to be at least one plant response measured, such as the extent of leaf damage or changes in biomass, growth, or mortality; 4) sample sizes and means, with their deviation terms, had to be stated in the article text or in a table or figure, for both experimental and control groups. I calculated an effect size [log response ratio, $\ln R = \ln(\text{control mean}) - \ln(\text{experimental mean})$] and its confidence interval for all experiments in the articles found. I used those values to compare studies performed in different environments and climatic areas, and different plant responses in plants of different ages.

4. MAIN RESULTS AND DISCUSSION

The first experiment (**I**) showed that willow warblers were more attracted to the intact branches of herbivore-damaged trees than to those of the control trees. The experiment was designed to reveal the possible attraction of herbivore-induced trees, not the mechanism behind the hypothetical phenomenon. In the subsequent experiments I tested how the birds were able to find the herbivore-damaged trees. I therefore used in study **II** two different light conditions in the aviary, with half of the birds tested in light with UV wavelengths and half in non-UV light, but this did not affect the birds' attraction. I also measured the light reflectance of the trees with a spectrophotometer. The control trees reflected significantly more light throughout the visible spectrum than the herbivore-damaged trees. Thus we could rule out the possibility of UV cues alone being important in attracting birds. It seems more likely that light reflectance across the whole spectrum visible to birds (315–700 nm) is relevant. Another finding in study **II** was that birds were attracted to herbivore-damaged birches only if the branches were from trees growing in the sunnier forest patch. Likewise in the case of the light reflectance of the leaves, a difference was found between treatment and control trees only in the sunnier forest patch but not in the shadier one. This was an unexpected finding; I can only speculate as to why the birds could not distinguish between the branches or why the difference in light reflectance is absent in the shadier forest patch. Shaded plants photosynthesise less than plants in sunshine, and their chemistry is thus different (Henriksson et al. 2003); possibly they cannot invest as much in defence chemicals as plants in sunnier places.

In study **III** significantly more pecked artificial plasticine larvae were found in herbivore-damaged birches than in undamaged control trees; thus the same phenomenon as observed in studies **I** and **II** in aviaries was also observed in nature. To find potential cues the birds might use, we measured emissions of several VOCs and the net photosynthesis rate in the same experimental trees. There were significant differences in VOC emissions between herbivore-damaged and control birches, and a correlation was found between the emission of three VOCs [(*E*)-DMNT, β -ocimene and linalool] and avian predation on the birches. The same three VOCs are also among the key compounds in the attraction of insect parasitoids and predatory mites to herbivore-damaged plants (Dicke et al. 1990; De Moraes et al. 1998; Kappers et al. 2005; Shimoda et al. 2005). This suggests that birds, invertebrate predators and parasitoids may be taking the same cues from foliage, and plants may thus possess a more universal signalling system, functioning for all predators and parasitoids. The net photosynthesis rate was also significantly higher in control than in herbivore-damaged trees, suggesting that birds may use olfaction, vision or both as cues for finding insect-rich trees.

My studies (**I**, **II**, **III**) are the first to suggest that insectivorous birds may react to induced changes in herbivore-damaged plants, as the birds were more attracted to the intact branches of herbivore-damaged birches than to the intact branches of the controls. Because of the systemic nature of inducible responses (e.g. Haukioja & Niemelä 1979; Haukioja & Hanhimäki 1985; Hanhimäki & Senn 1992; Kaitaniemi & Ruohomäki 2001; Farag & Paré 2002), the test branches from herbivore trees probably differed in chemical composition from those of the control trees. The birds were somehow able to sense this difference and adjust their behaviour accordingly. Studies in behavioural ecology are rarely replicated nowadays, which can make it difficult to generalise over other taxa and ecosystems (Owens 2006). Thus these three separate studies on the attraction of passerine birds to herbivore-damaged trees, using different combinations of species and different methods, provide strong support for the existence of this phenomenon (**I**, **II**, **III**).

Study **IV** showed that induced cues from herbivore-damaged birches did not affect the order in which pied flycatchers occupied the territories. There are several potential explanations for this. One is that the birches did not raise induced defences or production of VOCs that would have been detectable by the birds. We did not measure tree responses in this experiment, but it has been shown repeatedly that birches have induced responses to herbivory (e.g. Kauser et al. 1999, Haukioja 2005, Vuorinen et al. 2007), and that these are detectable by birds (**I**, **II**, **III**). Another explanation could be that the pied flycatchers have not evolved to use such cues in their choice of territory. The autumnal moth larvae reach their final instar during the time of pied flycatcher egg-laying which is energetically demanding and food availability affects the fitness of the birds (e.g. Visser & Lessells 2001; Moreno et al. 2008). Thus, an ability to choose a larval rich territory should be beneficial for the birds. Yet another reason may be that the scale of our treatment (two small defoliated or control birches per territory) was too small to influence the birds' decisions. But still the amount of larvae in our treatment (60–80 larvae in two small trees per territory) was at least tenfold higher than natural larval densities in the area (0.27 larvae per 100 birch short shoots, Kai Ruohomäki, pers. comm.). It is still not known what pied flycatchers' main criteria are in choosing a territory (Alatalo et al. 1986; Slagsvold 1986). So far it is known that pied flycatchers prefer to nest in deciduous over coniferous forest (Lundberg et al. 1981), probably since the former tend to have more caterpillars (Gibb & Betts 1963; Royama 1970), and that they first choose territories in larger forest patches (Huhta et al. 1998). Pied flycatchers also avoid nesting too close to their avian predators, sparrowhawks (*Accipiter nisus*) (Thomson et al. 2006) or pygmy owls (*Glaucidium passerinum*) (C. Morosinotto et al., unpublished data). They are also attracted to the presence of resident species (e.g. tits) close to the territories (Forsman et al. 2002, 2007). Nonetheless, these aspects were not examined in study **IV**, as the main interest was the role of herbivore larvae which evidently needs more research.

The set of meta-analyses in study **V** (a review study) revealed that plants in all environments (natural and agricultural) and climates (boreal, temperate and tropical) benefit from the presence of birds that remove herbivorous insects and other arthropods feeding on the plants. There is thus a trophic cascade, from birds via herbivores to plants. The results do not support the general notion that trophic cascades can only occur in simple ecosystems, such as agricultural environments, or in colder climatic areas (Polis & Strong 1996). The strongest effects were usually found in measuring plant leaf damage, biomass or mortality. Leaf damage is the first sign of herbivory and is usually rather easy to measure, but it does not always reveal the degree of damage to the fitness of the plant over time. Thus the study by Mols & Visser (2002) is a notable exception; they found that the presence of birds increased the amount of fruit produced by apple trees (*Malus domestica*). Studies with mature plants showed stronger effects than studies with saplings. This result may derive from higher bird abundances in mature forests (e.g. Rice & Greenberg 2000), or from the tendency of saplings to be controlled more by bottom-up effects (e.g. inorganic resources) than top-down ones (e.g. predation). Study **V**, along with some other recent studies (Sekercioglu 2006; Van Bael et al. 2008; Whelan et al. 2008) have shown that birds are beneficial to plants and form an integral part of ecosystems.

5. CONCLUSIONS

What general conclusions can be drawn from the studies presented in this PhD thesis? First of all, I can say that birds recognise herbivore-damaged trees and are attracted to them (**I**, **II**, **III**). I succeeded in showing this preference under both aviary (**I**, **II**) and natural conditions (**III**). I examined the possible cues emitted by herbivore-damaged birches that birds could sense either visually, i.e. differences in light reflection (**II**) and net photosynthesis rate (**III**), or by olfaction, i.e. differences in VOC emissions (**III**). To study the importance of herbivore-damaged plants for birds, I examined the territory choices made by pied flycatchers between territories with herbivore-damaged and undamaged birches (**IV**). I found no differences, even though plants with abundant herbivores are most likely important to birds. My review of trophic cascades from birds to plants showed that plants do better in the presence of birds (**V**). It thus seems that the interaction is mutually beneficial to both birds and plants. These five studies have opened up opportunities for future research on the role for instance of vision and olfaction in this mutualistic interaction between birds and plants. The next steps in this field should focus on the details of birds' sensory mechanisms (vision and olfaction), and on the ecological importance of the tritrophic interaction to both birds and plants on a broader scale (e.g. more species in an experiment or a longer study time).

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