

Territory Choice of Pied Flycatchers is Not Based on Induced Cues of Herbivore Damaged Trees

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Abstract: Passerine birds use a variety of indirect cues to make territory location decisions. These birds can also distinguish herbivore-damaged plants from undamaged ones during foraging, even when they cannot see the herbivorous larvae or damaged leaves. To test the possibility that also the territory choice of passerines is affected by herbivore-induced plant cues, we established territories with and without indirect cues of herbivore presence for migratory pied flycatchers (*Ficedula hypoleuca*) at the time of their arrival. Half of the territories had folivorous moth larvae hidden inside mesh bags to defoliate small trees (*Betula* spp.) and half had only empty mesh bags on trees. Hidden herbivory on the trees did not affect the mean date of territory choice by either male or female birds. Nonetheless, there was a trend that females, but not males, chose the territories in the same order in two consecutive years. Thus, it seems that pied flycatchers do not use indirect cues of larval presence as a basis for their choice of territory, but possibly some more general environmental cues.

Keywords: Female choice, foraging, habitat choice, inducible plant responses, nest-site, territory quality, tritrophic interactions.

INTRODUCTION

Migratory passerines arriving to northern breeding grounds are time-limited and they need to quickly select good-quality territories as their reproductive success can decline if the start of breeding is delayed [1-3]. Recent evidence shows that these birds use a variety of indirect and direct cues to make quick but reliable territory location decisions, including the presence of individuals of their own species [4-6], of resident species [7, 8] and of predators [9]. A vital aspect of a good territory is that it contains sufficient food resources for both the breeding pair and their nestlings, e.g. during egg-laying or when nestlings need most food [1, 10].

One untested hypothesis for the mechanism of territory location selection is that birds can use herbivore-induced cues to recognise trees which have plenty of herbivorous larvae and favour nesting in their vicinity. When attacked by invertebrate herbivores, plants emit an assemblage of chemical signals, which attract predators and parasitoids of the herbivores, thus reducing the herbivore load on the plants [11-13]. Behavioural experiments have shown that insectivorous birds may also locate their prey using the chemical cues of plants, even if the insect herbivores or defoliated plant parts are not visible [14-16]. Birds might be able to detect herbivore-damaged trees visually, as suggested by differences in light reflection of silver birch (*Betula pendula* Roth.) leaves between defoliated and intact trees [16]. They might also use olfaction, as suggested by significant differences in volatile organic compound (VOC) emissions

between herbivore-damaged and intact mountain birches (*Betula pubescens* ssp. *czerepanovii* (Orlova) Hämet-Ahti) and by the correlation between VOC emission and avian predation on birches [15].

Herbivore-induced responses of trees may thus act as a cue for territory choice so that the early-arriving individuals might be able to occupy the territories with the highest expected larval abundance. Using herbivore-damaged trees as territory location cues may also predict future food resources. Defence compounds and VOCs of the trees are induced already when herbivore larvae are small [12], and often it takes weeks before the larvae are fully grown and large enough to have a nutritional value to birds. A parallel phenomenon can be found from diurnal birds of prey which can assess vole abundance using their UV vision (e.g. at possible nesting areas) since the vole urine reflects UV light [17, 18].

To examine whether insectivorous migrant birds are attracted to territories with induced herbivory but no herbivores directly visible, we conducted an experiment with silver birch and downy birch (*Betula pubescens* Ehrh.), autumnal moth larvae (*Epirrita autumnata* Borkhausen) and a hole-nesting passerine, the pied flycatcher (*Ficedula hypoleuca* Pallas). We established territories of nest-boxes in which half of the territories had autumnal moth larvae hidden on birch branches close to the nest-boxes and half of the territories were controls with empty mesh bags (Fig. 1). We then documented the nest-site choice of birds to the territories. We predicted that if the birds would use indirect cues of herbivore larvae presence as basis for territory choice, the early-arriving pied flycatchers would choose territories with herbivore-damaged birches and later-arriving birds would be left to breed in intact territories.

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Fig. (1). A territory with two nest-boxes and two experimental birches with mesh bags on branches. Photo by Toni Nikkanen.

METHODS

The study was conducted in 2008-2009. The study area consisted of three different-sized forest areas north-east of Turku, SW Finland (60°27' N, 22°16' E). The mixed forests contained mainly Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* (L.) H. Karst.) with smaller numbers of silver birch, downy birch and aspen (*Populus tremula* L.). We had chosen locations for the experimental territories in all forests prior to the breeding season. The first forest had 10 territories, the second 20 and the third 30 territories, and the distances between the forests were from 2.5 to 4.3 km. In 2009 we used 28 territories only from the largest forest. Each territory, defined to cover ca. 30 m from the nest-boxes, had at least two small (height 1.5-4 m) birches (either silver or downy birch) close to the nest-boxes (max. distance ca. 5 m) and no tall birches (Fig. 1). In 2009, the average number of birches (over 1.5 m tall) in the territories was 23.4 ($SE = 2.2$, range 6-47, $N = 28$; data were not recorded for 2008). The minimum distance between neighbouring territories was 50 m. On each territory, two nest-boxes were placed in a standardised way on trees a maximum of 10 m from each other (Fig. 1). We used two nest-boxes in order to reduce variation in nest site quality. The diameter of the entrance hole was 32 mm and the nest-box was hung on ca. 120-140 cm height. Only few natural

holes in trees and no other nest-boxes existed in the forests at the time of the experiment. Pied flycatcher males usually defend a rather small area around the nest-box, median 10 m [19], so they can breed quite close to each other. Nest-boxes were erected at sites on 7th May (2008) and 10th May (2009); chosen so that the herbivory could be induced before any birds claimed territories (see below). At this time, the first pied flycatcher males had just arrived to southern Finland, and most other hole-nesting passerines (mainly tits) had already started their nesting and they would thus not compete much for nest-boxes anymore. If tits managed to occupy a nest-box first, we brought a third nest-box to the territory and moved the tit box each day a bit further away (5-10 m) from the remaining two boxes. Thus, the pied flycatchers had always two free nest-boxes to choose from on each territory.

Autumnal moth larvae were used as herbivores to induce chemical signalling of birches in each treatment (herbivore) territory, as in [15, 16]. Neonate larvae were reared in laboratory with young leaves of birch until they were in their 2nd instar (out of 5 instars) for the experiment in 2008. Experimental larvae were offspring of a parental generation collected as larvae in the previous spring from south-western Finland. Females had been mated with males in the autumn, and the eggs that they produced overwintered in outdoor

storage. On 7th May (2008) the autumnal moth larvae were brought to the territories at the same time when the nest-boxes were introduced to the birds. In 2009 we inserted the autumnal moths already as eggs (just before the larvae hatched from the eggs) on 6th May (2009). Territories alternated between treatment and control. In 2009 half of the herbivore territories had been herbivore and half control territories in 2008, and similarly for the control territories. This could be done as different sets of trees were used in territories in 2008 and 2009. In herbivore territories in 2008 ($N = 30$), we placed mesh bags (ca. 80 × 35 cm, mesh 0.3 mm) invariably on two branches of the two small birches we had chosen as the experimental trees. In 2009, we used two or three small birches per herbivore territory ($N = 14$) in a similar manner, thus representing, on average, ca. 10% of available birches in a territory. In 2008 we released inside each bag 15 or 20 larvae (depending on the size of the birch, more larvae were released on the taller trees). The amount of eggs per mesh bag in 2009 was 30-50, as usually approximately 50% of the eggs manage to hatch a larva that finds a leaf and starts to eat it (Kai Ruohomäki, pers. comm.). Since the larvae were inside the mesh bags, the birds could not see or catch the larvae, only see or smell the cues of the birches, and presumably also smell cues from the larvae [15]. In control territories (2008: $N = 30$, 2009: $N = 14$) mesh bags were placed in the same way but without larvae inside. There were no signs of other herbivory in either herbivore or control territories when the larvae were brought outdoors in the spring, and in mid-June (11th–18th June 2008) the missing leaf area (ca. 40 random leaves examined per tree) was low in all experimental birch branches outside the mesh bags (herbivore: $mean = 3.3\%$, $SE = 5.6\%$; control: $mean = 3.5\%$, $SE = 3.7\%$). The larvae and mesh bags were removed on 26th or 27th May 2008 and on 2nd June 2009 when most of the birds had arrived and the larvae were on their ultimate or penultimate instar. At that time the defoliation percentage of the leaves was high inside the mesh bags of herbivore trees (2008: $mean = 80.8\%$, $SE = 20.0\%$; 2009: $mean = 37.6\%$, $SE = 25.6\%$).

We visited every territory daily from 8th to 23rd May in 2008 and from 10th to 25th May in 2009, and recorded the presence of any pied flycatchers. Males arrive to the breeding area first and occupy a nest-hole which they defend against competitors. A male was recorded as present if it sang or otherwise defended the territory. In our experimental areas, some early males were seen to occupy several nest-boxes and sing on neighbouring territories [1], but when more males arrived they had to give up the extra territories. If the same male was seen on several territories its choice was determined by which territory it was defending in the following days. Most males can be identified individually on the basis of the highly variable plumage traits [1]. The arrival of females was determined mainly by the start of nest-building which begins typically as soon as the female has paired with a male. After 23rd May in 2008 and 25th May in 2009 the nest-boxes were checked ca. every third day since all males had arrived by then, and it was possible to estimate the start of female nest-building with this interval.

Some great tits (*Parus major* L.) and blue tits (*Cyanistes caeruleus* L.) tried to occupy territories but in most cases the pied flycatchers drove them away. In some cases pied flycatchers and tits shared a territory by nesting in the two (if

the tit arrived after pied flycatcher) or three (if tit arrived before pied flycatcher) nest-boxes. The nesting attempts by tits were easy to record from the moss gathered in the nest-box (pied flycatchers do not use moss in their nests). We considered territories to have tit presence if the tits were there before the pied flycatchers but this did not significantly affect the mean arrival date to the territory in either 2008 or 2009 by either male (2008: N (tits) = 14, N (no tits) = 43, 2009: N (tits) = 14, N (no tits) = 14; tits: $F_{1,81} = 0.50$, $p = 0.48$, year: $F_{1,81} = 1.35$, $p = 0.25$, tits×year: $F_{1,81} = 1.15$, $p = 0.29$) or female pied flycatchers (2008: N (tits) = 17, N (no tits) = 40, 2009: N (tits) = 16, N (no tits) = 11; tits: $F_{1,80} = 0.81$, $p = 0.37$, year: $F_{1,80} = 0.57$, $p = 0.59$, tits×year: $F_{1,80} = 0.46$, $p = 0.50$). The sample size is different for males and females because to some territories arrived a pied flycatcher male first, then a tit and then a pied flycatcher female.

Statistical Analyses

We tested with general linear mixed model (MIXED procedure of the SAS statistical software, version 9.2) whether the treatment, study year or their interaction affected the mean date in which pied flycatcher males and females chose the territories. The site of the territory (three forests in 2008 and one forest in 2009) nested within the study year was used as a random effect to control for possible differences in arrival times among the forests. The method for computing the denominator df (option KENWARDROGER) performed a general Kenward-Roger approximation for the denominator df. A similar test was used to analyse if there was a difference between herbivore and control territories in how quickly pied flycatcher males acquired females (i.e. female arrival date - male arrival date), and for the presence of the tits in the territories.

RESULTS

Pied flycatchers nested in 2008 in 28 herbivore and in 29 control territories (three territories were left empty), and in 2009 in 14 herbivore and 14 control territories; thus there were no differences between these groups in occupancy rate of the territories.

The treatment did not affect the territory choice of either males or females, as there were no differences in the dates when the territories became occupied (male, treatment: $F_{1,81} = 0.09$, $p = 0.77$, year: $F_{1,81} = 2.84$, $p = 0.10$, treatment×year: $F_{1,81} = 0.07$, $p = 0.79$; female, treatment: $F_{1,80} = 0.08$, $p = 0.78$, year: $F_{1,80} = 0.27$, $p = 0.70$, treatment×year: $F_{1,80} = 0.17$, $p = 0.68$) (Fig. 2).

In 2008 the first pied flycatcher male arrived on 8th May and last one on 19th May. For females the dates were 11th May and 1st June, respectively. The mean difference between the male and female arrival to the territory was 6.4 days (from 0 to 16 days). In 2009 the first males arrived on 10th May and last ones on 19th May. Female arrival dates were 12th and 28th May, respectively. On average the males acquired a territory 5.8 days before the female arrived (from 1 to 12 days). There were no significant differences between treatments or years in how quickly males acquired females to their territories (treatment: $F_{1,80} = 0.44$, $p = 0.51$, year: $F_{1,80} = 0.54$, $p = 0.46$, treatment×year: $F_{1,80} < 0.01$, $p = 0.95$).

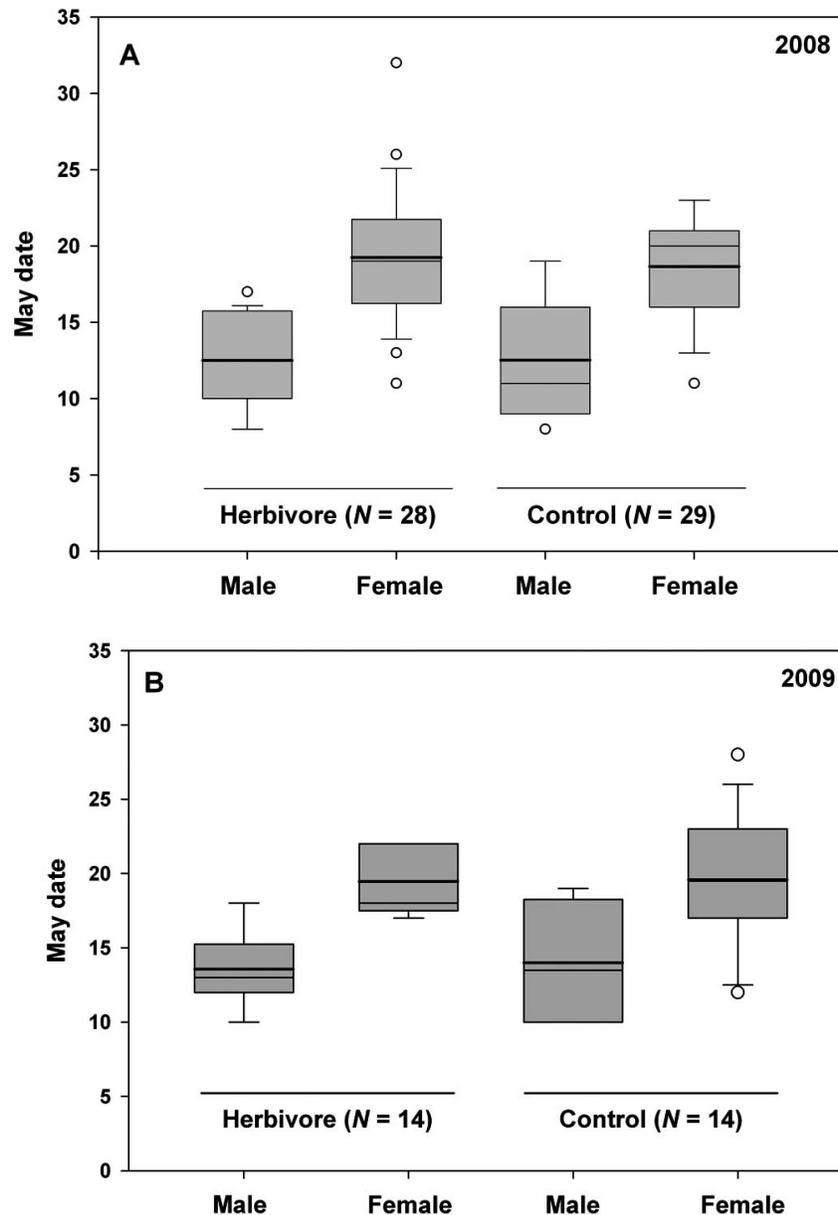


Fig. (2). The box-plot shows the arrival of male and female pied flycatchers to the herbivore and control territories in 2008 (A) and in 2009 (B). Inside the box, the thin line is median and the thick line is mean. The Y axis is dates of May, i.e. '10' is 10th May etc.

Nevertheless, there was a trend that in the largest forest studied in both years the pied flycatcher females chose the territories in the same order in 2008 and in 2009 (Spearman rank-order correlation: $r_s = 0.387$, $N = 26$, $p = 0.051$), but this was not the same with the territory choice order of males ($r_s = 0.007$, $N = 27$, $p = 0.97$) (Fig. 3).

DISCUSSION

According to our results, pied flycatchers do not appear to prefer territories which have trees with hidden herbivory over territories which have undamaged trees close to the nest-box. There could be three reasons for why no herbivory treatment effect was found. The first is that the trees did not raise induced defences or production of VOCs that would

have been detectable by the birds. The second is that the pied flycatchers have not evolved to use such cues in their choice of territory. The third is that the scale of our experiment was not offering sufficiently large benefits for the birds (two or three trees manipulated in a territory).

We did not measure tree responses in this experiment, but it has been shown many times that birches have induced responses to herbivory, e.g. [20-22], and that these are detectable by birds [14-16]. We have therefore little doubt that the birches raised induced responses that could have been detected by the birds. In order to differentiate between the other two alternatives, we need to consider the potential importance of the moth larvae to birds.

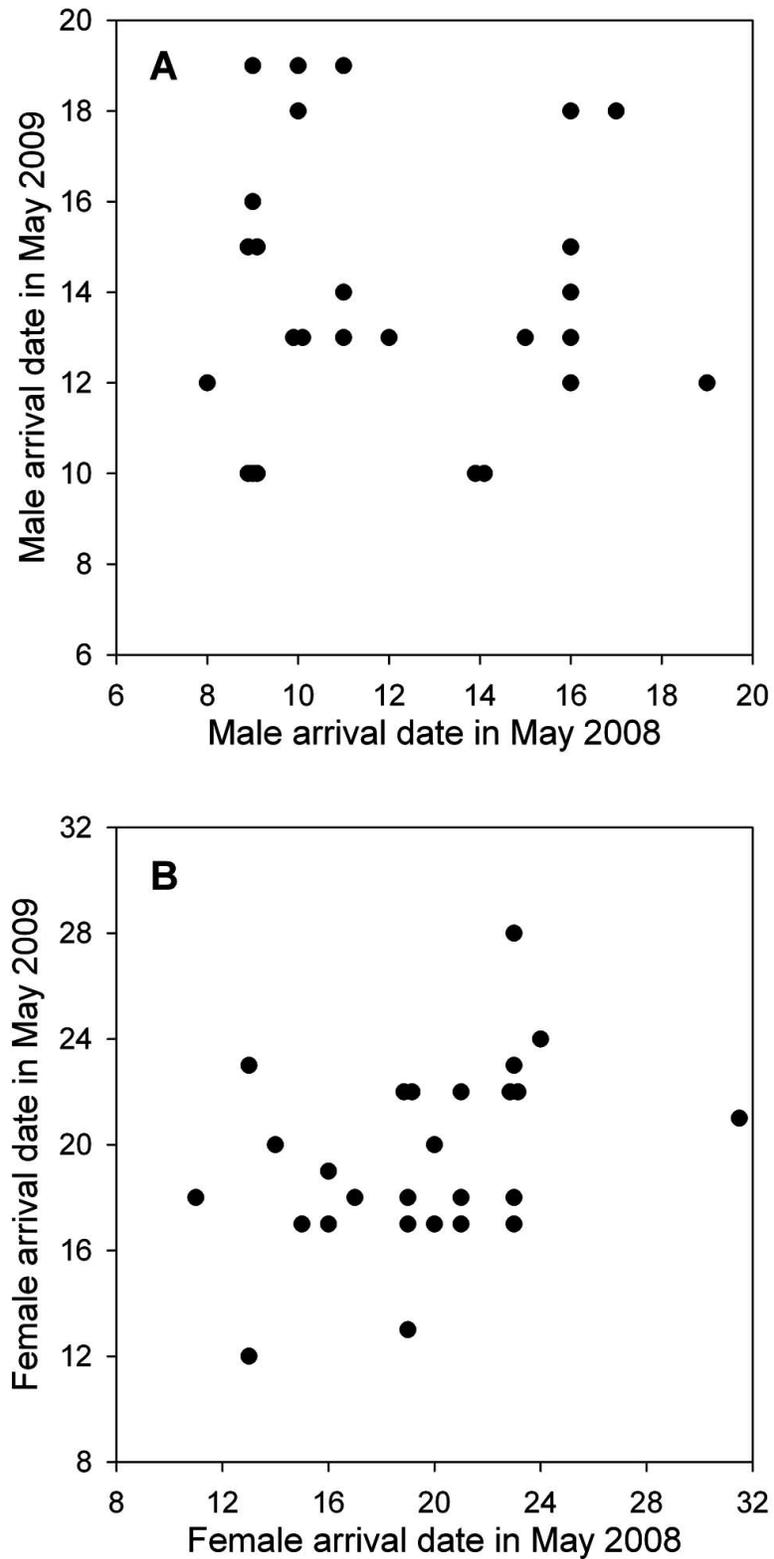


Fig. (3). The arrival dates of male (A) and female (B) pied flycatchers to the territories in 2008 and 2009. To prevent overlap, a few data points were slightly jittered in a horizontal direction. The original data were used for the analysis.

In southern Finland autumnal moth larvae reach their maximum size at the time when pied flycatchers are laying their eggs (late May – early June). Egg-laying is energetically demanding and food availability during egg-laying

typically has an effect on either timing of laying, clutch size or egg size [23, 24]. Also the quality of food during that time may have consequences for offspring quality and fitness. Green larvae are a major source of carotenoids to birds [25]

and there is evidence that carotenoids in the egg yolk are important for the developing offspring because they offer protection against oxidative stress [26-29]. For these reasons we suggest that being able to choose a larval rich territory should be beneficial for the birds even though we do not know how costly it is for the birds to find the best territory from a potentially large group of territories available.

The last question is whether the magnitude of our treatment is realistic and whether it sufficiently mimics potential benefits for birds. Natural densities of autumnal moth larvae in SW Finland were slightly higher in summer 2008 than in other recent years (mean of 13 sites was 0.27 larvae per 100 birch short shoots), and in 2009 the densities were lower than in 2008 (mean of 12 sites was 0.09 per 100 birch short shoots) (Kai Ruohomäki, pers. comm.). 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, as was the observed foliar damage inside the mesh bags of our experimental trees in herbivore territories compared to typical foliar damage due to endemic herbivory in birches of SW Finland [30]. We thus consider that our treatment should have made a sufficiently large impact to mimic a territory rich with caterpillars. Moreover, there are several herbivore species feeding on birches that could be important prey items for pied flycatchers [30, 31]. Autumnal moth is only one of the species causing induced defences, and thus our experiment can be considered to mimic herbivore presence in more general terms than just mimicking the presence of autumnal moth larvae.

Despite the importance of the amount of food to the reproductive success of birds at all stages of breeding, surprisingly little is known about nest-site choice in relation to food abundance in the territory, [e.g. 32]. Often when researchers have studied the territory choice of birds they have focused on the amount of suitable nesting sites, vegetation characteristics or a full range of indirect cues of territory quality, e.g. [33-35], and not that much on the actual food available there.

When pied flycatcher females arrive to the breeding locations, they often have several singing males to choose from. A debated, but still unsolved question is whether females choose the best territory or the best male [36-39]. Our data show that the females tended to choose first the same territories in both study years (Fig. 3B). This suggests that the territories have some consistent quality differences also across the years. Our result is unlikely to be confounded by the same females making the choice in the two years (although it has been shown that two groups of females choose the territories in the same order during the same year, [39]), because only approximately 10 % of pied flycatcher females in south-western Finland return to the same breeding area in the following year, e.g. [40, 41]. The result is not explained by the males being the same either, as only ca. 20% of males returns to the same area and of these, only a small proportion (13%) breed in the same nest-box territory [41]. Despite our efforts, crucial traits for the territory choice of females remain still unclear. We however conclude that the presence of hidden herbivore larvae is not likely to be a sufficiently strong attraction in the territory choice of pied flycatchers.

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