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Linking anti-predator behaviour and habitat quality: group effect in nest defence of a passerine bird

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Abstract In habitats where the density of breeding individuals is higher, breeding success has been shown to increase with the number of close conspecific and heterospecific neighbours. However, the mechanisms linking habitat quality, group size of prey individuals and offspring defence are poorly known. In this field study, we examined the relationships between habitat quality and parental nest defence behaviour in the pied flycatcher (*Ficedula hypoleuca*). We found that mobbing is more intense in unmanaged forests where birds breed in more dense and diverse communities than in heavily managed young forests where heterospecific densities are lower. We also found that the mobbing activities of pied flycatchers breeding in unmanaged mature boreal forests attracted more neighbouring prey individuals than in nearby managed forests. This study shows that habitat quality-mediated effects might be responsible for the decreased group size of mobbing birds in managed forests, which may lead to less effective communal defence.

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Introduction

Understanding the importance of habitat quality for animals is crucial since reproductive success, survival and abundance of any species differ among habitats. Habitat quality can affect fitness through environmental characteristics, including predation risk (Caro 2005; Lima 2009). Studies have shown that, outside the breeding season, reducing the area of a high-quality patch significantly reduces the size of heterospecific foraging groups (Beauchamp 2008; Siffczyk et al. 2003), which decreases the probability of an approaching predator being detected (Beauchamp 2008; Griesser 2009). During the reproductive season, breeding success may increase with the number of close neighbours including heterospecifics (Alatalo and Lundberg 1984; Berg et al. 1992; Fuchs 1977; Haas 1985; Johnsson 1994; Patterson 1965; Wiklund and Andersson 1994), which, in turn, is higher in high-quality habitats. In some bird species, there is a strong association between egg and nestling survival in groups as opposed to nesting alone (Götmark and Andersson 1984). Some studies show that heterospecific neighbours may have a positive effect on breeding success (Forsman et al. 2002; Krams and Krama 2002; Seppänen et al. 2011) because they compete less for resources and provide more benefits in terms of anti-predator protection (Ekman 1989).

The density of birds can directly affect breeding success by increasing the efficacy of their anti-predator behaviours. Prey individuals can decrease the probability of being attacked by cooperating with surrounding individuals (Caro

2005; Krause and Ruxton 2002). Mobbing is an anti-predator behaviour that prey individuals use to harass a predator or brood parasite by cooperatively attacking it (Curio 1978; Welbergen and Davies 2009). During mobbing, the predator is usually unable to attack the individual that initiated the mob (Curio 1978). Mobbing behaviour is frequently seen in birds (Curio 1978; Griesser 2009; Griesser and Ekman 2005; Krams and Krama 2002; McLean and Rhodes 1991; Nocera et al. 2008; Nolen and Lucas 2009; Olendorf et al. 2004; Templeton et al. 2005), though it is also known to occur in other social animals such as mammals (Blumstein 2007; Solórzano-Filho 2006), fish (Hein 1996) and some invertebrates (Ken et al. 2005). Although mobbing has several overlapping functions (Curio 1978; Welbergen and Davies 2009), assemblies of mobbing prey individuals often cause a predator to vacate its immediate foraging area (Flasskamp 1994; Pettifor 1990).

Several studies have shown that the number of prey individuals mobbing a predator increases with group and colony size (Graw and Manser 2007; Hoogland and Sherman 1976). The number of birds mobbing a predator is greater during unsuccessful predatory attacks than during successful attacks, suggesting that bird numbers might be instrumental in reducing a predator's success (Palestis 2009; Wiklund and Andersson 1994). It has been recently demonstrated that individuals mob a predator more intensely when they are part of a larger mob, suggesting a direct link between group size and the individual safety of group members (Griesser and Ekman 2005; Krams et al. 2009). Curio (1978) has stated that should a predator leave an area sooner, the more intensely it is molested. Prey individuals in smaller groups must mob predators longer to achieve success, which might increase the prey individuals' exposure to predation (Dugatkin and Godin 1992) and entice more predators to areas of longer-lasting and less intense mobbing (Krama and Krams 2005; Krams et al. 2007). As a result, anti-predator behaviours should be more efficient and less costly to individual mobbers when they breed in higher density. Since breeding birds rely on mobbing to drive predators away, evaluating the factors that lead to larger more successful mobs is critical to a wider understanding of anti-predator behaviour.

We examined the relationship between habitat quality, group size and mobbing intensity in the pied flycatcher. Although mobbing behaviour has been studied principally in birds, the evolutionary forces shaping nest defence may be applied equally well to any other taxa where parents defend their offspring. The aim of this field study was to find out whether the mobbing response of the pied flycatcher is more intense in old growth unmanaged forests where birds are breeding in higher densities than in heavily managed young forests where birds stay in less dense and less diverse communities (Schultz and De Santo 2006; Virkkala and Rajasärkkä 2006). We predicted that the mobbing activities of pied flycatchers breeding in unmanaged mature boreal forests would attract more neighbouring conspecific and heterospecific prey individuals than the pied flycatchers mobbing predators in nearby managed forests. Our understanding of the effects of habitat quality on nest defence behaviour is still in its infancy. Although this study does not represent a real manipulative experiment, it took advantage of natural variation in the composition of bird communities in two different habitats to investigate how environmental change caused by forestry affects group size and, thus, parental nest defence behaviour.

Methods

Study site

The field work was performed in June 2003 and 2007–2010 near Krāslava, southeastern Latvia (54°58′ N, 27°10′ E). The pied flycatcher, a small semi-colonially breeding migratory bird, is among the best-studied birds in the world (Lundberg and Alatalo 1992). To attract pied flycatchers, we used wooden board nest boxes. The nest boxes were placed in pairs about 210–240 m apart from each other along the border between two contrasting habitats. One of the nest boxes was placed in a mature boreal coniferous forest (95–145 years old), whilst the other nest box was placed in young (36–53 years old) plantations of Scots pine (*Pinus sylvestris*). The mature boreal forests have not been managed for at least for 65 years, whereas the young pine forests were managed twice during the last 30 years. The mature forests consisted of several tree species dominated by Norway spruce (*Picea abies*) and contained a thick understory. The young forests represented a monoculture of Scots pine with no understory. Thus, the identification of the forest types was based on the age and the management status. We selected the study plots so that there were no clear-cuts or sapling stands within 500 m of the nests.

To evaluate the density of breeding birds, we counted all birds observed singing, foraging or resting within the radii of 100 m around each nest box ($n=64$) 3–5 days before the experimental trials. Each site was visited twice, and the duration of each census was at least 40 min (58.20 ± 4.80 min of mean census time, SD). The mean density of breeding passerine birds was significantly higher in unmanaged forests (mean±SD=207.73 ± 31.22 pairs/km^2) than in managed young forests (31.26 ± 14.62 pairs/km^2; paired t test, $t=43.70$, $df=30$, $p<0.001$). Since we did not find any significant differences between the number of heterospecific neighbours observed at each of 64 sites during mobbing trials and during the estimation of the density of local passerine birds in both the mature forest (paired *t* test, $t=1.68$, $df=31$, $p=0.10$) and the young forest (paired *t* test, $t=1.36$, $df=31$, $p=0.18$), the number of heterospecific individuals was used as the group size covariate in further analysis. All of the spatial data were collected using a handheld GPS receiver. As pied flycatchers nested only in the nest boxes provided during this study, the density of breeding pied flycatchers did not differ between two habitats.

Nest defence experiment

The distance to the closest pairs of other nest boxes was at least 800 m. This distance between the two pairs of nest boxes was sufficient not to attract the neighbouring pair of pied flycatchers. Our first inclusion criterion for the nest defence experiment was that both nest boxes of a box pair were occupied by pied flycatchers. The age of nestlings was the next requirement for inclusion. Since parents are predicted to take higher risks whilst defending larger and older broods (Bogliani et al. 1999; Curio 1987; Lambrechts et al. 2000), we included in the study only nest boxes containing six nestlings which were at least 9 days old. The chicks of pied flycatchers fledge within 14–16 days of hatching (Lundberg and Alatalo 1992). Therefore, we included into the study the nest box pairs where the maximum difference in the age of nestlings in the two nest boxes was 4 days (mean±SD=2.00±0.16 days). The age of nestlings did not differ between habitats (two-tailed paired *t* test, $t=-0.80$, $df=31$, $p=0.43$). A total of 32 pairs of nest boxes (64 individual nest boxes) met these requirements.

During the study period, the average clutch size was similar between the habitats (*t* test, $t=1.03$, $df=31$, $p=0.30$), and pied flycatchers did not lay more eggs in unmanaged forests (mean±SD=6.42±0.64 eggs) than in managed forests (mean±SD=6.35±0.62 eggs). There was no significant effect of habitat on the number of fledglings between unmanaged forests (mean±SD=5.43±1.19 fledglings) and managed forests (5.56±1.13 fledglings; paired *t* test, $t=0.48$, $df=31$, $p=0.64$). This result suggests that both managed forests and unmanaged forests may be of similar quality for breeding pied flycatchers with regard to food resources. This is usually explained by the lower competition (Kilgas et al. 2006, 2007) in young and less populated forests. Moreover, in this study, pied flycatchers were often observed collecting food in both habitats. The observed reproductive success across habitats was not found to be dependent on the presence of the pine marten (*Martes martes*) either. The density of martens in the study area was generally high (Lindström et al. 1995; Krams et al. 2007). Although the predators usually prefer older forests, they were often seen by day in pine plantations within 200–300 m away from the old forest. These observations led us to conclude that the level of predation risk was supposedly similar near the edge of both habitats. Finally, we noticed that some nest boxes were attacked by martens (14 nest boxes in the old forest, 12 nest boxes in the young forest, $\chi^2=0.065$, $p=0.799$). However, the predators did not succeed because they were not able to open the nest boxes and the nest boxes were deep enough to prevent reaching nests, nestlings or females through the nest box entrance.

As soon as one of the paired nest box nestlings was at least 9 days old, we presented a stuffed tawny owl (*Strix aluco*) as a predator stimulus. This is a common predator of forest passerines (Glue 1972; Mikkola 1983) whose presence strongly affects their behaviour (e.g. Bautista and Lane 2000; Hendrichsen et al. 2006; Krams et al. 2008, 2010a, b. Although only one owl model was used, previous studies have found little or no difference in birds' responses to different models of the same species (Welbergen and Davies 2009).

The predator was mounted on a small platform 1.2 m above the ground, about 1.5 m from the focal nest box and facing the nest. As soon as the owl was discovered by nest owners, we began documenting the mobbing response of the nest owners, the number of neighbours arriving to mob and the behaviour of neighbours during a 10-min period. The trial was repeated at the other nest box the next day. By showing the predator only once at each nest box, we minimized the risk of the birds habituating to the stuffed owl (Knight and Temple 1986; Listoen et al. 2000). The trials were done mainly during morning hours (0500–0900 hours) in calm, warm and dry weather. We recorded the behaviour of the adult pied flycatchers from a hide placed about 30 m from the nest box. Only one experimental trial was done in each type of the habitat at each study site.

Our scale of pied flycatcher mobbing response consisted of four categories of displays and vocalizations: (1) no response to the dummy predator (0 points)—birds investigating the predator from a distance (>10 m) usually without alarm calls whilst continuing activities such as foraging or singing; (2) weak response (1 point)—with frequent approaching to and retreating from the predator within 5–10 m; (3) medium response (2 points)—birds close to the predator (3–5 m) and moving restlessly around it by bowing, pivoting, tail flicking or hovering in the air in front of it; and (4) strong response (3 points)—intense movements and display close to the predator (0.5–3 m), including dive attacks at the predator (Krams et al. 2006, 2008). Although we do not know whether our ranking system is linear in terms of risk and energy expenditure, it corresponds to the species-specific, step-by-step, increasing intensity of mobbing behaviour observed in other species under field conditions (Creutz 1955; Curio 1959; Shalter 1978).

The boldness of birds defending their offspring was measured by how closely the adult flycatchers approached the predator. During trials, we measured the minimum distance from the predator, which was defined as the shortest distance of the focal bird to the stuffed owl during each trial. Before conducting the trials, we marked nearby tree trunks and braches, which allowed us to accurately measure the birds' approach distances. Within each of the 32 areas, the experimental trials were performed only once.

As soon as the trial was completed, we captured all of adult birds by mist nets (Ecotone, http://www.ecotone.pl) to determine their age and colour morphs. We recaptured two females banded a year ago in unmanaged forests and three females banded a year ago in highly managed young forests. The rest of the birds were yearling individuals.

We checked nest boxes to record clutch size and nestling age three to five times before the experimental trials. Since we checked the nest boxes mainly in the absence of adult birds, our activities did not cause any significant disturbance leading to desertion or abnormal behaviour.

Statistical analysis

The variation in mobbing behaviour in relation to habitat type and group size was studied using multinomial logistic regression analysis (function mlogit in R 2.12.0; R Development Core Team 2010). The analysis is practical where the response variable is categorical (as mobbing scores mostly are). We tested whether the mobbing birds choose different mobbing scores (in relation to a reference category) in different habitats and whether the choice is related to group size. The ratio of the probability of choosing one outcome category over the probability of choosing the reference category is often referred to as relative risk, exp(*b*). Descriptive data were analysed using SPSS 11.0 statistical package for Windows (SPSS Inc., Chicago, IL). The level of significance was set at 0.05, and all tests were two-tailed.

Results

The mobbing intensity of males and females was similar both in the mature forest (Wilcoxon matched-pairs signed-ranks test, $Z=-0.58$, $N=32$, $p=0.68$) and young forest (Wilcoxon matched-pairs signed-ranks test, $Z=-0.82$, $N=32$, $p=0.41$). Therefore, we calculated the mean value and assigned it to each pair of adult pied flycatchers. The mobbing intensity was higher in unmanaged forest (mean±SE=2.34±1.12, Fig. 1) than in managed young forest (mean±SE=1.59±0.14; Wilcoxon matched-pairs signed-ranks test, $Z=-3.93$, $N=32$, $p<0.001$; Fig. 1).

In the unmanaged forest, alarm calls of parent flycatchers attracted significantly more neighbouring heterospecific passerines (5.75±1.55 individuals, min=4, max=9; Fig. 2) to mob the predator than in the young forest (2.03±1.62 individuals, min=0, max=5; paired *t* test, $t=-10.67$, $df=31$, $p<0.001$; Fig. 2). No neighbouring pied flycatchers arrived to assist the mobbing individuals in either forest types. Although all of the neighbouring heterospecifics uttered alarm calls, none of them approached the predator closer than 4 m, and they never attacked the predator. Even the most active neighbours finished their mobbing significantly sooner than the nest owners (5.22±0.20 vs. 8.40±217 min; paired *t* test, $t=13.46$, $df=63$, $p<0.001$).

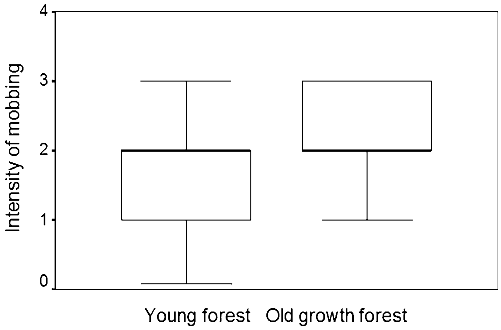

Fig. 1 Box and whisker plot (*thick bar*, median; *box*, interquartile range; *whiskers*, full value range) of the intensity of mobbing of parent pied flycatchers in young highly managed forests ($N=32$) and old growth forests ($N=32$)

The results of the multinomial logistic regression analysis are shown in Table 1. The mobbing scores were significantly related to group size (Fig. 2), and as indicated by the large positive exp(*p*) values, the more intensive scores (2 vs. 1 and 3 vs. 1) were more probable with increasing group size. The habitat type did not affect the intensity of mobbing within the group size of 0–5 heterospecific neighbours since greater mobbing scores (2 vs. 1 and 3 vs. 1) were equally probable in both forest types (Table 1).

The minimum distance of males from the stuffed owl was 0.64±0.44 m (mean±SD) and that of females was 0.59±0.35 m in unmanaged forests. In the young managed forest,

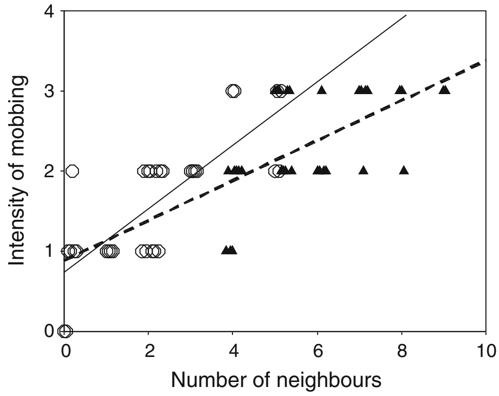

Fig. 2 Positive relationship between the number of heterospecific neighbours and the intensity of mobbing in young highly managed forests (*circle* and *continuous line*, $N=32$) and old growth forests (*triangle* and *dotted line*, $N=32$)

Table 1 Results of the multinomial logistic regression analysis in which the probability of mobbing scores is analysed in relation to habitat type (0=young highly managed forest, 1=old growth forest) and heterospecific group size (range, 0–9)

	b	SE	*t*	*p* value	exp(*b*)
Mobbing score 2 vs. 1					
Intercept	−3.558	1.412	−2.597	0.009	
Habitat	−3.371	1.969	−1.902	0.061	0.03
Group size	1.928	0.663	2.983	0.004	6.85
Mobbing score 3 vs. 1					
Intercept	−7.828	1.86	−4.20	<0.001	
Habitat	−3.579	2.035	−2.251	0.058	0.028
Group size	3.125	0.735	3.631	<0.001	16.15

The term exp(*b*) is a ratio of the probability of choosing one outcome category over the probability of choosing the reference category

Log-likelihood=−40.241; McFadden R^2=0.3875; Likelihood ratio test: χ^2=55.771 (p=3.285e^{-11})

males approached the predator as close as 0.68±0.40 m, and 0.62±0.53 m (mean±SD) was the minimum distance of females from the predator. A GLM analysis revealed that the minimum distance from the predator was not affected by sex, habitat and the number of neighbouring heterospecifics and the interactions (all p>0.168).

Discussion

Our study was done at the end of the nestling phase when nest defence activity is predicted to be strongest and nestlings are most valuable because of their age (Andersson et al. 1980; Montgomerie and Weatherhead 1988). We found that the intensity of nest defence was significantly weaker in the highly managed forest than in the unmanaged forest. Since the reproductive success and age of the parent birds were similar across the habitats, the amount of food resources or age-related quality/experience of pied flycatchers could not be responsible for the lower intensity mobbing in highly managed young forest.

This study shows that the intensity of mobbing by flycatchers was significantly higher in the unmanaged forests where mobbing individuals attracted more neighbouring birds to mob the predator than in the managed forests. Mean bird densities in unmanaged forests are usually significantly higher than in a predominantly managed forest landscape (Schultz and De Santo 2006; Virkkala and Rajasärkkä 2006), and it was also supported by our results. It is important to note that the interaction between habitat type and group size did not show any effect related to the intensity of mobbing. This clearly shows that neither habitat factor is significant by itself, nor that any other characteristic of these particular study areas may explain the result. As the result, we conclude that the difference in the mobbing behaviour of parent pied flycatchers in the two habitats was due to the lower density of breeding birds in highly managed forests compared with unmanaged forests. This result is significant because several studies have demonstrated that larger groups of prey individuals are more effective at detecting approaching predators (Cresswell 1994; Eggers et al. 2008; Godin et al. 1988; Pulliam 1973). A bird mobbing alone stands little chance against a larger predator, but when mobbing as a part of a group, the risk to each group member can be reduced or diluted (Caro 2005; Curio 1978; Krams et al. 2010a, b; Krause and Ruxton 2002). The dilution effect proposed by Hamilton (1971) is a way to explain the benefits of cooperation by selfish individuals. In addition, members of larger groups have more chances of confusing the predator when they coordinate their behaviour (Driver and Humphries 1988; Hoogland and Sherman 1976). As a result, the observed habitat differences, which resulted in smaller mobs in lower quality habitat, are likely to have important survival consequences for breeding birds. Birds mobbing a predator tend to be highly conspicuous (Curio and Regelmann 1985; Ficken and Popp 1996), and predators do sometimes catch mobbers, which suggests both that engaging in mobbing behaviour carries real risks and that potential prey individuals should adapt the intensity of their behaviour to minimize such risks (reviewed by Curio and Regelmann 1985; McLean and Rhodes 1991; Pavey and Smyth 1998).

Existing non-experimental and experimental data suggest a direct link between group size and mobbing intensity (Becker 1984; Hoogland and Sherman 1976; Krams et al. 2009; Robinson 1985). Although being a member of a larger group might entail additional costs, such as being more conspicuous to surrounding predators, reduced group size is likely to lead to decreased offspring defence, as found in this study. Welbergen and Davies (2008, 2009) have recently shown that reed warblers (*Acrocephalus scirpaceus*) mob cuckoos (*Cuculus canorus*) and crows at their nests, but cooperative mobs rarely form, heterospecifics never join, and predators of adults such as hawks are not mobbed. This might be because potential mobbers are relatively spread out. Grim (2008) also did not find a relationship between the intensity of mobbing behaviour and the number of attracted birds. It is likely that Grim (2008) observed communities mostly consisting of migratory birds, whilst interspecific attraction in mobbing was found to be stronger in breeding communities consisting of sedentary birds (Krams and Krama 2002). Future experimental research is needed to show the role of community composition and whether there is an optimal group size in mobbing which could be dependent also on predator size and type (Templeton et al. 2005).

The observed difference in mobbing intensity might also be related to the uneven density of predators in both habitats. Since the density of potential prey species is higher in unmanaged forest, it might pay predators such as birds of prey and European pine martens to search for prey in this habitat rather than in the young forest. Previous studies have shown that martens usually live in unmanaged forests and rarely come into less productive pine plantations (Krama and Krams 2005; Krams et al. 2007). However, adult martens can be seen searching for their prey in either habitat as early as May and become even more active in June when their young begin to emerge out of their dens (Kronitis 1972). Therefore, it is not likely that more intense mobbing in the unmanaged forests is a result of the pied flycatchers breeding there being more familiar with predators and, thus, mobbing more intensely than birds in the young forests.

We did not find any difference in the minimum distance from the predator among flycatchers breeding in different habitats, whilst the birds approached and mobbed the predator from different perches in the two habitats. There are sufficient branches in the canopy of numerous sapling trees and bushes in an understory of unmanaged old forests that can be used as perches by mobbing birds, whereas branches are available only within the canopy of young pines in highly managed forests. The flycatchers usually perched on branches of sapling trees and bushes within 1–3 m above the ground level whilst mobbing the predator in unmanaged forests. In contrast, there was not any understory vegetation in young forest and the birds perched just on tree trunks above the predator whilst approaching it. The tree canopy and the forest understory have been observed to serve as the anti-predator cover to forest passerines (Krams 1996, 2000). Since it has been shown that the forest passerines are vulnerable when foraging outside the tree canopy, the prey individuals might be more vulnerable to attacks of their principal predators such as the pygmy owl (*Glaucidium passerinum*) and the sparrowhawk (*Accipiter nisus*; Ekman 1987; Kullberg 1995; Krams 1996, 2001; Andersson et al. 2008) whilst mobbing the predator in the young forest. However, the distance between the ground and the lowest part of the canopy is much shorter in the young forest than in the mature forest because trees are taller in the mature forest. Due to proximity of the protective canopy in the young forest and proximity to bushes and sapling trees in the mature forest, mobbing birds might be equally exposed to other predators whilst mobbing, which may explain their similar minimum approach distances from the predator.

The results of this study indicate that unmanaged forests containing more prey individuals can provide more safety because birds in unmanaged forests are parts of larger groups during predatory events. Unmanaged forests are typical of natural boreal forests, which have been logged in Northern Europe continuously. As a result of extensive ongoing clear-cutting and other logging procedures (Gil-Tena et al. 2009), their total area has been dramatically decreasing. In addition to habitat loss, old growth forests are becoming increasingly fragmented, i.e. old growth forest patches are becoming smaller and more isolated, which affects boreal biota, such as birds (Schmiegelow and Mönkkönen 2002). As a consequence of these factors, many forest bird species have declined during recent decades (Amar et al. 2008; Ludwig et al. 2009). Our study shows that among other factors, decreased group size might be responsible for the less effective communal defence of prey individuals because nest defence by mobbing heterospecific neighbours is reduced in low-quality habitats.

One of the most important findings of this study is that habitat quality can affect nest defence behaviour of mobbing heterospecifics. Mixed-species associations are a common phenomenon throughout the world which can be tight and can exist year round both in tropical (Munn and Terborgh 1979) and temperate areas (Ekman 1989). Our results show that birds in such heterospecific associations can engage in mutual cooperation to drive the predators out of their breeding territories. This suggests a link between the benefits of mobbing and clumped spatial associations of forest passerines often observed during the breeding season (Forsman et al. 1998a, b; Mönkkönen et al. 1997).

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