COMMUNITY ECOLOGY - ORIGINAL RESEARCH

Higher nest predation risk in association with a top predator: mesopredator attraction?

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Abstract Breeding close to top predators is a widespread reproductive strategy. Breeding animals may gain indirect benefits if proximity to top predators results in a reduction of predation due to suppression of mesopredators. We tested if passerine birds gain protection from mesopredators by nesting within territories of a top predator, the Ural owl (*Strix uralensis*). We placed nest boxes for pied flycatchers (*Ficedula hypoleuca*) in Ural owl nest sites and in control sites (currently unoccupied by owls). The nest boxes were designed so that nest predation risk could be altered (experimentally increased) after flycatcher settlement; we considered predation rate as a proxy of mesopredator abundance. Overall, we found higher nest predation rates in treatment than in control sites. Flycatcher laying date did not differ between sites, but smaller clutches were laid in treatment sites compared to controls, suggesting a response to perceived predation risk. Relative nest predation rate varied between years, being higher in owl nest sites in 2 years but similar in another; this variation might be indirectly influenced by vole abundance. Proximity to Ural owl nests might represent a risky habitat for passerines. High predation rates within owl territories could be because small mesopredators that do not directly threaten owl nests are attracted to owl nest sites. This could be explained if some mesopredators use owl territories to gain protection from their own predators, or if top predators and mesopredators independently seek similar habitats.

Introduction

Territory choice is vital in determining reproductive output and survival of breeding animals. When selecting a territory, an animal will gather information not only on habitat characteristics and resource availability but also on the presence of other individuals which might affect habitat quality through direct interspecific interactions (Morris 2003; Seppänen et al. 2007; Lima 2009). Also, individuals which share the same habitat, but do not directly interact with the settling individual, can be an important source of information on habitat quality (Seppänen et al. 2007). This indirect source of information can be particularly important when environmental conditions that alter species interactions change rapidly (Elmhagen et al. 2010).

For prey, interactions with predators cause both lethal and non-lethal costs (Caro 2005). During breeding, when predation costs are incurred to both the prey individual and its offspring, prey alter their territory location decisions relative to predator proximity or abundance (Caro 2005; Lima 2009) and make fine-tuned decisions relative to predator threat (Morosinotto et al. 2010). Some predators, however, may be inconspicuous and their presence may be difficult to assess directly. In these circumstances, prey may rely on the principle of "an enemy of my enemy is my friend" when making habitat selection decisions, using cues provided by species which might not directly interact with the

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prey but which negatively affect the predator species (Haemig 2001).

A common strategy to gain antipredator benefits during breeding is to actively select a territory close to a species that preys on predators, or to aggressive species that actively defend their territory from intruders. These protective nesting associations are a widespread phenomenon among birds and mammals, and may also involve invertebrates (Haemig 2001; Quinn and Ueta 2008). In these associations, the protected species benefits from a reduction of other predators on the site (Ritchie and Johnson 2009). The abundance of apex predators is generally negatively correlated with mesopredators because of the threat to mesopredators; top predators, therefore, frequently fit the role of protector species. The reduction of mesopredator density due to top predator presence is generally known as "mesopredator suppression" and can occur through direct killing, so-called intraguild predation (Polis and Holt 1992; Sergio and Hiraldo 2008), or through a change in mesopredator behaviour (Sergio et al. 2007a; Salo et al. 2008; Mukherjee et al. 2009).

Protective nesting associations could also involve species in the same guild. Although not explicitly studied to date, small mesopredators may choose to breed near large or aggressive predators that represent a low risk of predation to avoid more dangerous predators. This type of nesting association could be called "mesopredator attraction". This has been indirectly suggested by four previous studies. Two corvid species, the azure-winged magpie (*Cyanopica cyana*) and the chough (*Pyrrhocorax pyrrhocorax*), both occasional predators of small vertebrates, have been shown to breed close to predators, the Japanese lesser sparrowhawk (*Accipiter gularis*) and lesser kestrel (*Falco naumanni*), respectively, to reduce their own nest predation risk (Ueta 1994; Blanco and Tella 1997). Moreover, indirect evidence suggests that pygmy owl (*Glaucidium passerinum*) and Tengmalm's owl (*Aegolius funereus*) may spatially associate, and thus gain fitness benefits, with goshawk (*Accipiter gentilis*) and eagle owl (*Bubo bubo*), respectively (Hakkarainen and Korpimäki 1996; Pakkala et al. 2006). Protective nesting associations where the protector species might represent a danger for the protected species, due to occasional predation, have been previously demonstrated (Quinn and Kokorev 2002).

Species appear able to adapt to changes in ambient predation risk, showing a stronger active association with a protector species only when predation risk is high (Haemig 1999). Furthermore, these species may even associate with different species as the interactions between the protector and enemy species (the predator) change due to environmental factors (Larsen and Grundetjern 1997). In addition, the benefits accrued by associating with a protector species are likely to vary as environmental conditions change and can sometimes even become harmful (Bêty et al. 2002; Smith et al. 2007); however, these changes in protection benefits remain largely unstudied.

We investigate the protection provided by the Ural owl (*Strix uralensis*) to passerine nests (Häkkilä et al. 2011), here represented by pied flycatcher (*Ficedula hypoleuca*) nests in experimentally altered nest sites. We consider flycatcher nest predation rate as a proxy of the mesopredator abundance in the forest patch. We further examine if the outcome of this association is consistent across years, as environmental conditions change due to fluctuation in the population density of microtine rodents, which are the main prey of Ural owls and many other mesopredators in the landscape (Korpimäki et al. 2005). Ural owls are aggressive nest defenders (Kontiainen et al. 2009) and prey on several mesopredator species that represent a danger to songbirds nests. Ural owls, in contrast, only rarely prey on small songbirds, and even more rarely (or never) on their nests (Korpimäki and Sulkava 1987; Hannu Pietiäinen, personal communication).

We use a unique nest box manipulation approach on real pied flycatcher nests to simulate the high nest predation risk experienced by birds breeding in open cup nests and natural cavities. These boxes initially appear normal, but the entrance hole can be experimentally enlarged to closer mimic the high risk of natural nests (Fig. 1). The nest box manipulation is needed because passerines breeding in nest boxes with small entrance holes generally experience low nest predation rates (Lundberg and Alatalo 1992; Purcell et al. 1997; Mitrus 2003). This novel technique avoids the potential bias of using artificial nests (Weidinger 2002; Zanette 2004), and allows a fully experimental approach to study protective benefits.

Our aim is to test the costs or benefits of proximity to a breeding top predator to passerine nests. If Ural owls provide protection, we expect nest predation rates in proximity to active Ural owl nests to be lower compared to nests in control forest patches. Furthermore, if the strength of the protection benefits for passerine nests varies as Ural owl interactions with other predators/prey change across years, we expect protection benefits to be higher when predation risk for mesopredators is higher. If, instead, a process of mesopredator attraction occurs, we would expect that small mesopredators would actively select sites close to Ural owls with consequent higher predation risk for passerines breeding in these sites. We would also expect that fluctuations in Ural owl main prey might increase the predation risk for small mesopredators, which might affect their presence at short distance from Ural owl nests in different years. We also test if pied flycatchers actively seek protective nesting associations with breeding Ural owls and, if this is the case, we predict earlier settlement and greater reproductive investment by flycatchers breeding in Ural owl patches
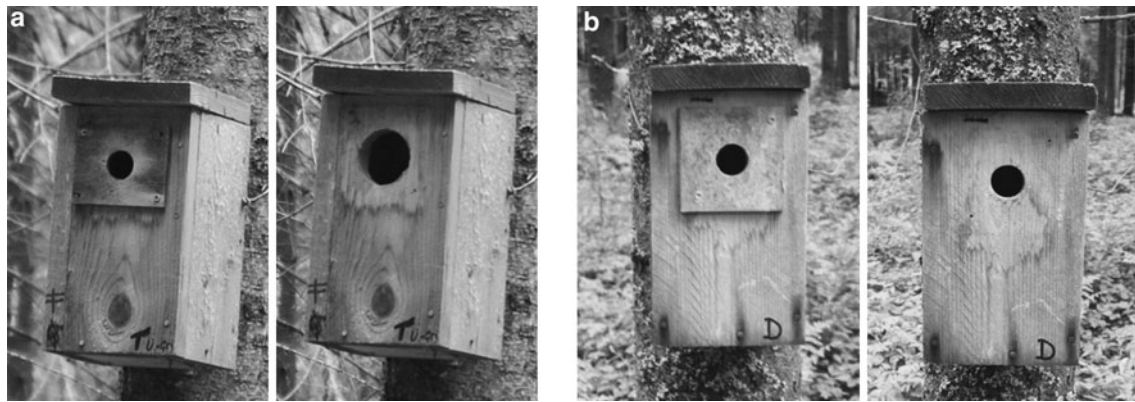
Fig. 1 a Treatment boxes for pied flycatchers (*Ficedula hypoleuca*) appear normal during habitat choice and laying, but a panel is removed during incubation revealing an enlarged entrance hole increasing nest predation risk. **b** Control boxes appear normal; a panel is also removed but it reveals a normal-sized entrance hole underneath and not altering nest predation risk. (Photos by CM)

compared to controls, since early birds generally have higher reproductive success (Sergio et al. 2007b; Verhulst and Nilsson 2008).

Materials and methods

Experimental design

This study was conducted in the Kauhava region, western Finland (63ºN, 23ºE), during 2008–2010. The three study years covered the three phases of vole cycle, the amplitude of which, in the boreal environment, can vary from 50 to 500 fold (Korpimäki et al. 2005). We studied pied flycatcher habitat selection, reproductive investment and nest predation rate in forest patches with Ural owl nests and in control patches, defined as sites where Ural owls bred in previous years but that were currently unoccupied by owls during the study year (see Morosinotto et al. 2010). In our experiment, we used 41 forest patches: 22 were Ural owl nest sites and 19 were controls (respectively 7 vs. 5 in 2008, 9 vs. 6 in 2009, and 6 vs. 8 in 2010). Ural owls bred in nest boxes in all study sites, except for one where the Ural owl pair bred in a natural cavity.

We attempted to use each forest patch only once, but this was not possible due to a limited number of Ural owl territories (our study area is ~1,500 km²). In 2008 and 2009, 27 experimental patches were used, 25 of which were different sites and spatial overlap was minimal. In 2010, our site choice was largely exhausted and we "reused" patches from both previous years, except for 1 new control site (in total, 13 "reused" patches and 1 new patch). The majority of these "reused" patches were of opposite treatment to previous years (10 of 13), and therefore spatial pseudoreplication of sites remained minimal.

We placed five pied flycatcher nest boxes in each site at a distance of 80–100 m from the Ural owl nest box. In each

site, three enlarged and two normal boxes were placed. The so-called "enlarged" boxes appeared normal, with a small entrance hole (3.2 cm), during settlement and egg laying, but a panel was removed during incubation revealing an enlarged entrance hole (5.5–6.0 cm; Fig. 1a). Our aim with the enlarged entrance was to increase nest predation risk. The "normal" boxes initially appeared normal with the small entrance hole, but during incubation a panel was removed revealing an entrance hole of the same size, not altering nest predation risk (Fig. 1b). The front panel was removed from all boxes on the 6–8th day of incubation (incubation lasts on average 13 days) and was replaced when chicks were 2–3 days old. Nests in treatment boxes were exposed to nest predators approximately for 8–9 days. Predation events were checked after cover removal and predator type was identified whenever possible by tracks, hair, teeth marks or scent. The nest box manipulation method was approved by the Finnish Environmental centre (permission number: LSU-2009-L-497).

All nest boxes were checked once a week to determine laying date, clutch size and initiation of incubation. The occupation rate of pied flycatchers over the 3 years was similar between Ural owl sites and controls [77.3 % (85 of 110 nest boxes) in owl sites vs. 82.1 % (78 of 95) in control sites; $F_{1,164} = 0.68$ $P = 0.41$]. No pied flycatcher nests were abandoned due to our nest box manipulation during the 3 years of study. Overall, of the 205 nest boxes settled, 163 (79.5 %) were occupied by pied flycatchers: 63 nests were in normal boxes and 100 in enlarged boxes.

Study system

The Ural owl is a large boreal forest dwelling species that mainly subsists on two *Microtus* species (the field vole *M. agrestis* and the sibling vole *M. levis*) and bank voles (*Myodes glareolus*). Vole populations in boreal environments follow 3-year density cycles (Korpimäki et al. 2005).

During our study, 2008 was an increasing vole cycle phase; the density index of *Microtus* voles and bank voles rapidly increased from early spring until reaching high densities when Ural owls chicks fledged and became independent in late summer (from 8.6 to 25.1 voles per 100 trap nights); 2009 was a decreasing vole cycle phase with relatively high vole densities in early spring when owls settled in territories, but the densities decreased during the breeding season until reaching low densities when owl chicks fledged (from 5.0 to 1.2 voles per 100 trap nights); and 2010 was a low vole cycle phase where densities remained low throughout the owl breeding season (0.7 voles per 100 trap nights) (Korpimäki et al. 2005; and unpublished snap-trapping data). Ural owls are present in their territories all year round and might be present in the site despite not breeding due to scarcity of their main vole prey (Lundberg 1981; Pietiäinen 1989). During breeding, Ural owls are extremely aggressive and defend their nest and territory from intruders (Kontiainen et al. 2009).

The diet of Ural owls also includes mesopredators, in particular during decreasing and low vole cycle phase (Korpimäki and Sulkava 1987). Small mesopredators inhabiting boreal forests can be divided in two main groups depending on their main prey. First, small mustelids such as stoats (*Mustela erminea*) and least weasels (*M. nivalis*) that subsist mainly on *Microtus* and *Myodes* voles but shift to alternative prey, such as passerine nests, when vole density is low (Korpimäki et al. 1991). Secondly, there are generalist nest predators, such as the great spotted woodpecker (*Dendrocopos major*), the European Jay (*Garrulus glandarius*), the pine marten (*Martes martes*) and the red squirrel (*Sciurus vulgaris*); all are common predators of passerine nests (Weidinger and Kočvara 2010).

Mesopredators in our study area represent a small portion of Ural owl diet (red squirrel 0.5 % of total prey number, least weasels and stoats 0.9 %, woodpeckers 0.3 %, corvids 0.4 %; Korpimäki and Sulkava 1987). Similar results have been found for other areas of Finland (Jäderholm 1987). Mesopredators occurrence in Ural owl diet varies between years, being higher during decreasing and low vole phases (red squirrel 0–2.2 % and mustelids 0–2.3 %; Korpimäki and Sulkava 1987). These mesopredators, and indeed Ural owls, are also predated by others top predators in the area, like eagle owls (*Bubo bubo*) and goshawks (*Accipiter gentilis*). Data from our study area show that the proportion of mustelids in eagle owl diet was larger than in Ural owl diet (1.2 % in eagle owl vs. 0.9 % in Ural owl; Korpimäki et al. 1990), and both eagle owls and goshawks prey more frequently on red squirrels than Ural owls (respectively, 9.9 % in goshawk, 2.6 % in eagle owl and 1 % in Ural owl; Selonen et al. 2010).

Pied flycatchers are migratory passerines that lay between five and eight eggs with biparental care of the young (Lundberg and Alatalo 1992). Flycatchers modify both their habitat selection and reproductive investment depending on perceived predation risk from predators that pose a direct threat to adults (Thomson et al. 2006; Morosinotto et al. 2010). Early arriving flycatchers are generally in good body condition, settle first in high quality patches and have higher reproductive success (Lundberg and Alatalo 1992). Pied flycatchers breed in cavity nests, either natural cavities or in nest boxes. Predation rate in natural nests is higher than in nest-boxes and depends mainly on entrance hole size and height of the nest (Lundberg and Alatalo 1992). The majority of studies comparing passerine predation risk among nest types found higher nest predation rates in natural cavities versus nest boxes (Purcell et al. 1997; Mitrus 2003; but see Czeszczewik 2004). Moreover, in this study, no nests in nest boxes with small entrance holes were predated (see "Results").

Ural owl breeding overlaps well past the median flycatcher fledgling time of 30 June in our study area, which is an important requirement for a protective nesting association (Quinn and Ueta 2008). Ural owl egg laying is initiated between mid-March and mid-April (Pietiäinen 1989); therefore, when flycatchers settled in mid-May, Ural owl nestlings were still in the nest. Owl chicks generally fledged before mid-June, after which parents feed and defend young for a further 3 months in the vicinity of the nest (Pietiäinen 1989), and therefore the potential protection of pied flycatcher nests continues after fledgling.

Statistical analyses

Forest patch (Ural owl nest or control site) was used as the sampling unit in all analyses ($n = 41$). We compared laying dates, clutch sizes and nest predation rates of pied flycatchers between Ural owl sites and control sites. Laying date was used as a proxy for flycatcher habitat choice; females start nest-building soon after arrival in the territory and lay the first egg within few days (Lundberg and Alatalo 1992). Clutch size was used as a proxy for parental investment. For laying date and clutch size variables, we used values of the earliest settled pied flycatcher nest in a forest patch only to avoid confounding effects of conspecific attraction on settlement and perceived habitat quality. In addition, this prevented us from including potential polygynous males in the variables.

Clutches contained six or seven eggs, with five egg clutches being infrequent (4 of 41) and did not fit either normal or Poisson distribution. We divided the variable in two classes: small (five to six eggs) and large clutches (seven eggs). This subdivision of clutch size data in two classes was possible without losing important biological information. We used a generalised linear model (PROC GENMOD in SAS/STAT software 9.2) to analyse the

difference in laying date (normal distribution, identity link) and clutch size (binomial distribution, logit link) between Ural owl and control sites. Year was also included in both models as independent variable. Laying date was entered as a continuous factor in clutch size models.

Each forest patch was classified as either predated or non-predated, based on the nest predation fate of the flycatcher nests. We considered only nests in treatment boxes (one to three nests per site) because no predation occurred in control boxes. If a patch contained even one predated nest in treatment box, it was classified as a predated patch. In a given site, when present, a mesopredator generally predated all available nests in treatment boxes; in only 6 of 41 sites was there a mix of predated and non-predated nests. Mixed patches can generally be explained by temporal separation in the reproductive phase of nests in a site. A binomial nest predation classification (predated or not) most accurately describes the presence or absence of mesopredators in a forest patch and the probability of nest survival.

We examined flycatchers nest predation in a patch using an exact conditional logistic regression (logit link; EXACT function; proc LOGISTIC in SAS 9.2) with owl presence (Ural owl nest site vs. controls), year and the interaction owl presence*year as independent variables. The method used is a special correction of the logistic regression, which adopts exact conditional inference, and solves the problem of quasi-separation of data points caused by small sample size and presence of zeros in the dataset (King and Ryan 2002; Heinze 2006).

We also compared the nest predation rate between Ural owl nest sites and control sites with a 2 × 2 contingency table using the two-tailed Barnard test to have confirmation of the results by year. The Barnard test is a powerful alternative to the Fisher's exact test for small and unbalanced data (Martin Andres and Tapia Garcia 1999); Barnard's test was performed using MATLAB 5.3 (code by Trujillo-Ortiz et al. 2004).

Results

Habitat selection and reproductive investment

Laying date of pied flycatchers did not differ between patches with Ural owl nests or controls ($n = 41$; $\chi^2 = 2.46$, $P = 0.12$; estimates of the model ±SE: Ural owl nest sites 27.63 ± 0.43; controls 26.63 ± 0.47; $1 = 1$ May), but differed between years ($\chi^2 = 7.93$, $P = 0.02$). Flycatchers therefore did not prefer either Ural owl or control patches during habitat selection. Flycatcher clutch size differed between Ural owl nest and control sites ($n = 41$; $\chi^2 = 3.90$, $P = 0.048$). In Ural owl nest sites the majority of the flycatcher nests had clutches of six eggs (17 small vs. 5

large clutches); whereas in control sites, there were almost no differences in the frequency of large and small clutches (9 vs. 10 nests with six and seven eggs, respectively). Year ($\chi^2 = 1.18$, $P = 0.55$) and laying date ($\chi^2 = 0.13$, $P = 0.75$) did not have a significant effect on clutch size.

Predation rate

Our nest box manipulations significantly increased nest predation risk. No nests in normal boxes were predated (0 of 62) whereas 34 of 99 (34.4 %) nests in enlarged boxes were predated. Considering only enlarged boxes, 67.7 % of nests predated were in Ural owl breeding sites and 32.3 % were in control sites.

Pied flycatcher nests showed a higher probability of nest predation in Ural owl nest sites (13 of 22 predated, 59 %), compared to control sites (5 of 19, 26 %; Barnard test: Wald statistic = 2.11, $\pi = 0.67$, $P = 0.02$). Our model showed a significant interaction owl presence*year, suggesting that nest predation probability differed among years (Exact logistic regression, owl presence*year: test statistic 8.46 $\beta = -0.64$ $P = 0.017$) (Fig. 2). In Ural owl sites, nest predation rate varied between 50 and 70 % in the three study years, whereas in control sites, nest predation only occurred during 1 year of study. In 2008 (increasing phase of the vole cycle), 71 % of Ural owl nest sites were predated whereas no control sites were predated (Exact logistic regression: test statistic 5.61 $\beta = 1.16$ $P = 0.028$; Barnard test: Wald statistic 2.47, $\pi = 0.46$, $P = 0.009$; Fig. 2). Similarly, in 2010 (low vole year), 50 % of Ural owl nest sites showed predation while no predation events were observed in control sites (exact logistic regression: test statistic 4.73 $\beta = 0.99$ $P = 0.055$; Barnard test: Wald statistic 2.26, $\pi = 0.63$, $P = 0.02$; Fig. 2). In contrast, in 2009 (decreasing phase of the vole cycle), predation events were recorded in
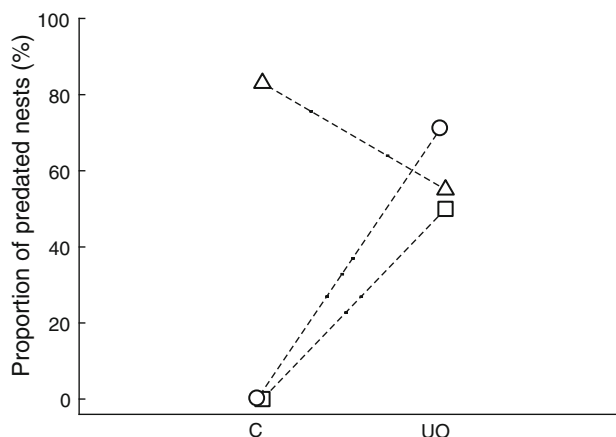

Fig. 2 Proportion of predated sites in controls (*C*) and Ural owl (*Strix uralensis*) nest sites (*UO*) during increasing (2008, *circle*), decreasing (2009, *triangle*) and low (2010, *square*) phases of the vole cycle

83 % of controls sites and in 55 % of Ural owl sites (exact logistic regression: test statistic 1.17 $\beta = -0.64$ $P = 0.58$; Barnard test: Wald statistic 1.12, $\pi = 0.12$, $P = 0.18$).

We were able to confirm the predator identity in six sites; this represents 33 % of total predated ones (four in Ural owl nest sites and two control sites). In five sites, the predators were mammalian, four were mustelids and one was by red squirrel (confirmed by odor, hairs or tracks). The other site was predated by Eurasian jay (identified by feathers). In addition, indirect predator signs in the vicinity of predated nests suggested that another three sites were predated by mammals and two by woodpeckers; however, the identity of the predator could not be confirmed due to lack of clear signs at the site (like hairs or feathers).

Discussion

Overall, we found higher predation rates on pied flycatcher nests at Ural owl sites than at control sites. Ural owls did not protect pied flycatcher nests from predation, but instead appeared to attract mesopredators resulting in higher passerine nest predation rates in Ural owl sites. Therefore, our results suggest that breeding in the vicinity of top predators may result in costs of increased predation and thus not entail protective benefits.

Our results suggest that, for birds breeding in predator-susceptible nest sites, such as open cup nesters, the association with Ural owls can be disadvantageous, at least at the distances (80–100 m) considered in this study. Nest box manipulations were successful in simulating the higher nest predation risk site that is characteristic of open cup nests, since the nest cup can be easily accessed by medium-size mesopredators. Mönkkönen et al. (2007) and Häkkilä et al. (2011) found lower nest predation rates close to goshawk and Ural owl nests, respectively. Furthermore, nest predation rates were suggested to vary between years, being lower near Ural owls in years of decrease vole abundance (Häkkilä et al. 2011). But these studies used artificial nests, which might bias results (Weidinger 2002; Zanette 2004). Furthermore, the main focus of previous studies was on ground-nesting species which are more susceptible to larger mesopredators like the red fox (*Vulpes vulpes*) and the raccoon dog (*Nyctereutes procyonoides*). We can expect Ural owl aggressiveness to be especially strong against these large mammalian intruders because, during the breeding season, they represent a danger for the Ural owl offspring, which leave their nests when still unable to fly and stay defenceless in the surrounding of the nest for a few weeks after fledgling (Kontiainen et al. 2009). Our study suggests that some mesopredators (like great spotted woodpeckers, Eurasian jays, red squirrels and mustelids) may be attracted to top predator sites rendering them more abundant there.

When nest predator identification was possible, it was mainly due to mammals (red squirrel or mustelids: least weasel, stoat or pine marten) or birds (woodpeckers and jays). These species, except for larger mustelids, do not predate ground nests but mainly passerine nests. This may explain contrasting results with earlier studies.

Mesopredators may actively choose the proximity of a top predator to gain protection from their own predators. Similar associations between prey and predator occur when benefits of protection are higher than costs (Norrdahl et al. 1995; Haemig 2001; Quinn and Kokorev 2002; Thomson et al. 2006). Small mesopredators, such as red squirrels and mustelids, could occur close to Ural owls, despite being occasional prey. Mesopredators may associate with Ural owls to gain protection against bigger predators, like goshawk and eagle owl that represent a higher risk (Korpimäki et al. 1990; Selonen et al. 2010). Ural owls are smaller than goshawks and eagle owls but are highly aggressive, especially during breeding, which should limit the occurrence of other top predators in the vicinity of their nests. For example, lesser kestrel can protect choughs from a large array of predators, because of its strong nest defense, although kestrels are also occasionally victims of those predators (Blanco and Tella 1997). In addition, it is possible that the benefits of associating with Ural owls vary between mesopredator species and might also depend on environmental fluctuating characteristics (see Bêty et al. 2001, 2002; Smith et al. 2007), especially for those mesopredators, like mustelids, that mainly prey on voles.

Mesopredator attraction to top predator nest sites has been suggested in boreal forests. Pakkala et al. (2006) suggested that pygmy owls and three-toed woodpeckers (*Picoides tridactylus*) actively select to breed close to goshawk nests, whereas great spotted woodpeckers do not. Preliminary census data from our study area suggests that great spotted woodpeckers are not attracted to Ural owl nest sites (R.L. Thomson, unpublished data). In boreal forests, a large array of mesopredator species coexist and share similar prey, including passerine nests (Weidinger and Kočvara 2010). Therefore, passerine nest predation risk depends on the distribution of the entire mesopredator community in the area and on the interspecific interactions occurring among mesopredators. Moreover, mesopredator distribution and hunting behaviour might also depend on other environmental factors such as cone crop availability for woodpeckers and squirrels, and vole cycle phase for mustelid mesopredators.

A higher density of mesopredators in top predator nest sites, suggested by higher predation rates on pied flycatcher nests, could be explained by similar habitat preference between top and mesopredators. However, all control patches were previously occupied by Ural owls and the habitat did not change visibly between years. Ural owl

breeding success is strongly affected by vole abundance (Lundberg 1981; Pietiäinen 1989); however, it is not clear which factors affect its habitat choice. Admittedly, Ural owls and mustelid mesopredators share food resources and may spatially select territories with high local vole densities. Shared resources cannot, however, explain attraction for the full range of mesopredators (woodpeckers, squirrels and jay) that do not eat voles, but respond to spruce cone availability. Mustelids were the majority of nest predators identified; however, our nest predator identification might be biased towards mustelids due to the conspicuous scent left by these predators, suggesting that unidentified nest predators were not mustelids. In the same study area, predation from woodpeckers and squirrels was observed frequently (C. Morosinotto, unpublished data). Nevertheless, additional data on abundances of voles among sites and information on mesopredators distribution and their possible attraction to top predators are needed to further test the mesopredator attraction hypothesis.

Our study further suggests that the outcome of interspecific associations is not consistent across years (Häkkilä et al. 2011). In 2008 and 2010, nest predation rates were high in Ural owl nest sites (71 and 50 %), but completely absent in control sites. In contrast, 2009 showed an overall high nest predation rate with no obvious differences between control and Ural nest sites (83 and 55 %, respectively). This difference in the relative predation rate between sites may be explained by the vole population cycle, since *Microtus* voles are the main prey of both Ural owls (Korpimäki and Sulkava 1987) and small mustelids (Korpimäki et al. 1991). Therefore, although voles and passerines do not interact directly, their interactions with mesopredators may result in indirect impacts on their predation risk. Such indirect interactions between rodents and birds have been suggested by Larsen (2000) who observed how fluctuation in lemming populations seems to change the predation risk of bar-tailed godwit (*Limosa lapponica*) due to shift in the diet of their protector species, the long-tailed skua (*Stercorarius longicaudus*). However, the exact mechanism determining this variation in predation risk across years remains unclear and requires further study.

Our results suggest that pied flycatchers do not avoid Ural owl sites but do not actively seek an association either. Using laying date as a proxy, flycatcher arrival times did not differ between sites. Mönkkönen et al. (2007) documented a similar flycatcher response relative to goshawk nests. Previous studies have also shown that pied flycatchers modify their habitat selection according to perceived predation risk from predators of adults birds (Thomson et al. 2006; Morosinotto et al. 2010); however, assessing densities of inconspicuous mammalian predators might be more difficult, especially when the community of predators species is complex (Chalfoun and Martin 2010). Moreover,

laying date might be influenced by several other factors than predation risk.

Clutch size of pied flycatchers in Ural owl sites was smaller than in control sites. This was despite the quality of birds in these sites being similar, as suggested by similar arrival dates. Birds lay smaller clutches when under high perceived predation risk (Doligez and Clobert 2003; Eggers et al. 2006; Morosinotto et al. 2010). Smaller clutches in Ural owl nest sites suggest that pied flycatchers perceive them as sites of lower habitat quality compared to controls. This result supports the idea that nest predating mesopredators were more abundant in Ural owl sites, and flycatchers were responding to this threat by reducing reproductive investment.

High nest predation rates and reduction of flycatcher reproductive investment suggest that the neighbourhood of an Ural owl nest is characterised by a relatively high risk of nest predation, at least over the gradient of distances from the owl nest that we examined. Our experimental nest box approach allowed us to study nest predation using real nests with parental activity at the nest. Although it might be argued that nest boxes also create bias in studies, our experimental design partially controlled for this possible bias. Indeed, nest boxes are conspicuous nesting sites and may increase prey densities compared to natural nests, which might attract predators in the area. However, our results show a complete absence of nest predation in 2 years at control sites, which strongly suggest few predators in the landscape except those aggregated around top predators nest sites. Therefore, our experimental design suggests that the predation rate we observed is a real estimation of the predation pressure in Ural owl nests sites.

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