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Red-backed Shrikes (*Lanius collurio*) adjust the mobbing intensity, but not mobbing frequency, by assessing the potential threat to themselves from different predators

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We studied the ability of Red-backed Shrikes to adjust their nest defence to the potential threat posed to defending adults and their nests. We presented mounts of two raptor species which prey on adult birds (Eurasian Sparrowhawk, Common Kestrel; differing in the proportion of adult passerines in their diets), and two species of nest predators (Common Magpie, Eurasian Jay; differing in the proportion of bird eggs and nestlings in their diets). A mounted Feral Pigeon was used as a control. Shrikes regularly mobbed the Sparrowhawk, Kestrel and Jay, but not Magpie or Pigeon. The mobbing frequency, in terms of the number of mobbing events per 20 min, did not differ among the three regularly-mobbed predators. If shrikes tried to chase the predator away, they did not adjust the mobbing frequency to the level of potential threat to the nest. The proportion of mobbing events resulting in physical contact (mobbing intensity) declined from the most mobbed species, Jay to the Kestrel, to the Sparrowhawk, which was considered most dangerous to adult shirkes. The Red-backed Shrikes appeared to adjusted their mobbing intensity by assessing the potential threat to themselves. Our results show the importance of a differentiation between mobbing intensity and mobbing frequency in the study of nest-defence behaviour.

1. Introduction

Predator mobbing is an important form of avian antipredator defence (Caro 2005). It can occur year round (Shedd 1982, 1983), although it is usually more intense during the breeding season (Shedd 1982, Pavel 2006) when this behaviour is used to avoid nest predation (Biermann & Robertson 1981). Predator mobbing is also connected to various trade offs. Mobbing may force the predator to leave the nest (Pettifor 1990; Flasskamp 1994). If the predator discovers a nest, mobbing may be the only chance to save the nest (Caro 2005). On the other hand, mobbing is conspicuous, and if the predator is not aware of the presence of the nest, the defence behaviour may draw attention to it, or even attract other predators (Krama & Krams 2005; Krams *et al.* 2007).

Like other forms of parental investment, predator mobbing is both time and energy consuming (Collias & Collias 1978, Dale *et al*. 1996, Scheuerlein *et al*. 2001); thus, the defending birds should adjust their mobbing behaviour according to the existing cost/benefit trade-off (Andersson *et al*. 1980). The importance of some factors involved in this trade-off (i.e., age and number of offspring, sex or life span) has been extensively studied in birds, demonstrating that the investment in mobbing behaviour is positively correlated with the value of the offspring (see Lima 2009 for a review). Nevertheless, this trade-off is not the only one: different predators represent different perils. The predator represents a threat not only to the nest content but also to the defending parents (Brunton 1986, Sordahl 1990, King 1999). These two threats may not be equal at the same time. Corvids, for example, represent a higher threat to the nest, while raptors often threaten the defending parents.

The responses of defending birds toward different predator guilds have been studied in several contexts, such as nest vs. adult predators (Knight & Temple 1986a, Sordahl 1990, Duckworth 1991, Jacobsen & Ugelvik 1992, Dale *et al.* 1996, Arroyo *et al*. 2001, Amat & Masero 2004, Hogstad 2005), owls vs. birds of prey (Arroyo *et al*. 2001), terrestrial vs. aerial predators (Bures & Pavel 2003, Hogstad 2005, Kleindorfer *et al*. 2005, Sordahl 1990) and predators vs. parasites (Duckworth 1991; Welbergen & Davies 2011; Trnka & Prokop 2012). Nevertheless, the danger presented by predators may differ significantly even within a specific guild: for example, a bird-capturing raptor is expected to represent a bigger threat for defending birds (and potentially for fledglings) than does a small mammal-catching raptor. In order for the defending birds to respond adequately to these predators, they should have the ability to discriminate between particular predator species and not only groups of predators. This ability has not been tested in the above-mentioned studies. Comparisons of more than one species within one predator group are scarce (Curio *et al*. 1983).

In our study, we focused on defence responses to different predator guilds. The tested predators (both within and between guilds) differ in their degree of threat to defending birds and/or their nestlings, so that the ability of a defending bird to discriminate between particular predator species could be tested. We examined the nest-defence behaviour in a 30-g passerine, the Red-backed Shrike (*Lanius collurio*) as a good experimental model species with which to study defence behaviour, as it vigorously defends its nest, even against humans (Gotzman 1967, Tryjanowski & Golawski 2004).

We investigated variation in nest defence by using mounted individuals of four avian predators that differ in the degree of their potential threat either to the nest content or to the defending parents. We used the Eurasian Sparrowhawk (*Accipiter nisus*) and the Common Kestrel (*Falco tinnunculus*), both of which have the ability to prey upon both adults and fledglings, and which usually do not prey upon nestlings (see below). Note, however, that some raptors at least occasionally prey on the nest contents of Red-backed Shrikes (Lefranc 1993).

The Sparrowhawk is specialized on small birds (Opdam 1978, Simeonov 1984, Frimer 1989, Kropil & Sladek 1990, Varga & Rekasi 1993, Zawadzka & Zawadzki 2001, Bujoczek & Ciach 2009), including the Red-backed Shrike (Glutz von Blotzheim *et al*. 1971), while the Kestrel primarily feeds on small mammals and is less likely to prey on birds (Korpimäki 1986, Vanzyl 1994, Salata-Pilacinska & Tryjanowski 1998). We further tested two specialized nest-content (eggs, nestlings) predators: the Common Magpie (*Pica pica*) and the Eurasian Jay (*Garrulus glandarius*). The Magpie was identified as more of a nest predator than Jay by Groom (1993) and Chiron and Julliard (2007), including the Red-backed shrike (Roos & Part 2004). However, the true relative levels of predation by these two species on nests is unknown. Finally, as a control, we presented a non-threatening Feral Pigeon (*Columba livia* f. *domestica*).

We tested the following predictions: (1) The frequency of mobbing behaviour is adjusted according to the apparent threat to the nest content. Mobbing frequency should be lower towards the two raptors than towards the two corvids, and within corvids, Jay should be mobbed less often than Magpie. (2) The intensity of mobbing behaviour is adjusted according to the threat perceived by the defending birds to themselves. Mobbing intensity should therefore occur as Jay > Magpie > Kestrel > Sparrowhawk.

2. Material and methods

2.1 Study site, and the focal species

The experiments were conducted around the village of Slapy, Central Bohemia (49°48' N, 14°23' E) during the breeding period, i.e., from June to late July, in 2002 through 2004, and near the town of Karlovy Vary, Western Bohemia (50°14' N, 12°53' E) during the same months in 2004.

The Red-backed Shrike is found in open habitats with scattered shrubs (including spiny species such as wild rose *Rosa* spp., blackthorn *Prunus spinosa* and hawthorn *Crataegus* spp.) where it builds an open-cup nest. Only the female incubates, and lays 3–7 eggs during 14 days, while the male feeds her. Nestlings are subsequently provisioned by both parents for approximately 14 days after hatching (Lefranc & Worfolk 1997). The Red-backed Shrike is mainly insectivorous, catching larger insects in the air and on the ground using a sit-and-wait strategy; however, it also preys upon small vertebrates (Golawski 2007).

In South Bohemia, Czech Republic, the breeding success in the Red-backed Shrike is 51% (Simek 2001), and the major causes of nest failure are predation and weather. The spectrum of nest and adult predators at our localities has not been studied, but Magpie and Jay are considered the main nest predators and Sparrowhawk is presumably the main predator of adults (Lefranc & Worfolk 1997). All of the tested predator species are roughly equally abundant at our experimental localities (Stastny *et al*. 2010). Between 2002 and 2004, we conducted 90 single trials on 18 nests (36 individuals).

2.2. Experimental design

All experiments were conducted at nests containing nestlings from 5 to 10 days old, so we expected both parents to show nest defence because their probability to obtain successful offspring and existing investment to the nest was significantly higher than in previous stages of development (McLean & Rhodes 1992, Halupka 1999, Rytkönen 2002). We presented mounted individuals of two predators of adult birds (Sparrowhawk and Kestrel), two predators of nest content (Jay and Magpie) and one non-threatening control species (Feral Pigeon), all of which were in the upright posture with their wings folded. In the Sparrowhawk, the presented dummies were females because in this species a significant sexual size dimorphism occurs, suggesting a distinct foraging niche (Overskaug *et al*. 2000). Together, we used three mounted specimens of Kestrel, two Sparrowhawks, two Magpies, five Jays and two Pigeons. All used dummies were without aberrance and were new-made by the same taxidermist. The mounts were placed on a 1.5 m high pole, 1 m away from the nest, and facing toward the nest. During installation, the tested mounts were covered by a cloth to prevent early reactions of the shrikes. Each pair of shrikes was presented with all five mounts exposed individually in a randomized order during one day. Each mount trial lasted 20 minutes from the appearance of at least one parent. If the parents showed no inclination to mob a mount within 20 minutes, the trial was terminated and recorded as a reaction value of zero. The minimum time interval until the presentation of the next dummy was one hour. To check for habituation or positive reinforcement, which may affect the defence behaviour significantly (Knight & Temple 1986a, 1986b), the order of presentation was used as an explanatory variable in model. The behaviour of the defending birds was taped on a VHS-C video camera on a tripod at a distance at least 30 m from the nest, so as not to disturb the parents. All experiments were conducted between 07:00 and 19:00 in conditions free of precipitation and no or only light wind.

Two types of behaviour were included in the statistical analyses: (1) Mobbing frequency, i.e., the total number of mobbing events (where the bird flies over the mount, decreases its flight altitude and sometimes strikes the mount) accomplished by a tested bird during a 20-min trial; and (2) Mobbing intensity, i.e., the occurrence of mobbing events with physical contact (the bird hits the mount during the mobbing event, usually with its bill), contrary to non-physical mobbing.

2.3. Statistical analyses

A positive correlation in the mobbing frequency was found between males and females of the same

Table 1. Pair-wise test results for the total number of mobbing events performed by Red-backed Shrikes to particular mounts. Test (*t*) values are shown down and left, and respective *p* values are shown up and right. Probabilities are Bonferroni adjusted.

	Kestrel	Jay	Sparrowhawk	Magpie	Pigeon
Kestrel	–	0.52	0.16	>0.01	>0.01
Jay	–0.65	–	0.45	>0.01	>0.01
Sparrowhawk	1.40	0.75	–	>0.01	>0.01
Magpie	–6.40	–5.75	–5.00	–	0.65
Pigeon	5.95	5.30	4.55	–0.45	–

pair (Spearman's rank correlation: $N = 36$, $r = 0.716$, $p < 0.001$), so the pair was counted as a unit of repeated measures. To filter out the individual variability in the mobbing behaviour, pairs were added to the models as a hierarchical random factor.

The mobbing frequency was tested first. The number of mobbing events towards all dummies did not meet the assumption of normality so we transformed data by ln (number of mobbing events + 0.01) to improve the data normality. Generalized linear mixed models (GLMM) with Gaussian distribution and logit link function were used to evaluate variation in mobbing frequency between the five test species. Explanatory variables were predator type, sex (within the tested pair), age of nestlings, and the order of presentation of dummies (within the tested pair and within the particular experimental day). Other explanatory variables, such as year, experimental location or dummy individual, could not be added as the model would have run out of degrees of freedom. Nevertheless, as all tested predator (and control) species were used in all years and on both localities with the same proportion, the effect of these factors should be negligible.

We then tested the mobbing intensity. Here, the unit of repeated measures was mobbing event (presence of a physical contact = 1, absence of a physical contact = 0). GLMMs with binomial distribution and logit link function were used to evaluate the differences in the mobbing strength. The explanatory variables were predator type, sex, age of nestlings and the order of presentation. Pair was added as a random factor. Only regularly-mobbed mounts were included (Sparrowhawk, Kestrel and Jay), as the total number of all mobbing events upon Magpie and Pigeon were 6 and 15, respectively, which does not allow for a balanced design.

GLMMs were used in order to include the random effect of the pair, by applying glmmPQL in R 2.12.1 (www.r-project.org). As the analysis output did not provide general effects of particular categorical explanatory variables with more than two values on the variability of tested data, these effects were assessed according to pair-wise comparisons of these variables. Therefore, results of pair-wise comparisons within a multiple-value explanatory variable (dummy type) are summarized in tables (using *t* tests as a criterion) and for possible interactions between tested variables, both interacting variables are listed. As pair-wise comparisons within a given model has specific vector orientations, the values of the test criterion (*t*) may acquire positive and negative values, depending on

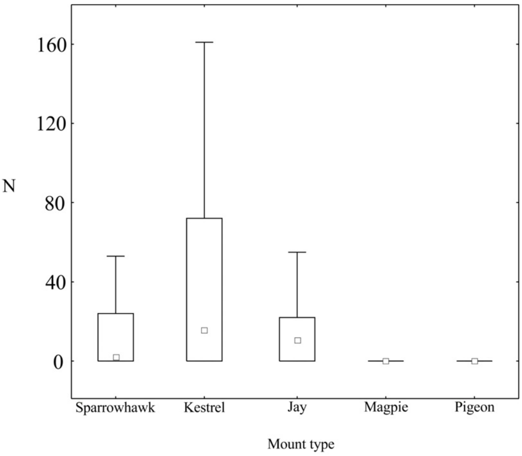

Fig. 1. Numbers of all mobbing events performed by particular shrike pairs towards particular mount types during 20-min study trials.

Table 2. The dependence of mobbing frequency in the Red-backed Shrike on mount type and shrike sex. Mobbing events with and without physical contact, performed by males and females to particular mount pairs, are tested. Probabilities are Bonferroni adjusted.

Comparison	*t*	df	*p*
Male/Female × Sparrowhawk/Kestrel	0.59	153	0.56
Male/Female × Sparrowhawk/Jay	0.74	153	0.46
Male/Female × Sparrowhawk/Magpie	0.89	153	0.37
Male/Female × Sparrowhawk/Pigeon	–1.02	153	0.31
Male/Female × Kestrel/Jay	0.16	153	0.88
Male/Female × Kestrel/Magpie	0.31	153	0.76
Male/Female × Kestrel/Pigeon	–0.44	153	0.66
Male/Female × Jay/Magpie	0.15	153	0.88
Male/Female × Jay/Pigeon	–0.28	153	0.78
Male/Female × Magpie/Pigeon	–0.13	153	0.90

Table 3. Pair-wise comparisons of the proportion of mobbing events with physical contact over all mobbing events (mobbing intensity), performed towards particular mounts. Test (*t*) values are shown down and left, *p* values are shown up and right. Probabilities are Bonferroni adjusted.

	Jay	Kestrel	Sparrowhawk
Jay	–	>0.01	>0.01
Kestrel	6.02	–	>0.01
Sparrowhawk	8.77	4.68	–

the position of the basal value in the comparison. As the GLMMs had to be run repeatedly, having various basal values in pair-wise comparisons, the Bonferroni adjustment was used to adjust for multiple probabilities. For more details of GLMM, see Zuur *et al*. (2009).

3. Results

3.1. Mobbing frequency

The age of nestlings ($t = 1.18$, df = 16, $p = 0.2554$) and the order of presentation of particular dummies ($t = 1.10$, df = 156, $p = 0.2726$) had no significant effect on the mobbing frequency; therefore, they were removed from the model. Only the dummy type, sex of the shrike individual, and their interaction was included in the newly-created model.

Only the mount type significantly influenced the number of mobbing events performed by shrikes by dividing the mounts into two groups (Fig. 1, Table 1). The first group contained Sparrowhawk, Kestrel and Jay, all of which obtained large numbers of mobbing events, while Magpie and Pigeon were only occasionally, if at all, mobbed (Fig. 1). This difference was statistically significant (Table 1). Male and female shrikes mobbed the mounts with an almost equal rate ($t = –0.45$, df = 153, $p = 0.65$). Interaction of both tested explanatory variables showed no significant effect (Table 2).

3.2. Mobbing strength

The age of nestlings and the order of presentations did not significantly affect the mobbing strength ($t = 1.17$, df = 16, $p = 0.2574$ and $t = 0.43$, df = 156, $p = 0.6707$, respectively), so they were removed from the model. Hence only sex, dummy type and their interaction was included in the newly-created model.

Both the mount type and sex of shrike significantly influenced the proportion of mobbing events with physical contact, and these factors also showed a significant interaction (Tables 3–4, Figs. 2–4). The Jay was physically mobbed more often than Kestrel or Sparrowhawk, and Kestrel more often than Sparrowhawk (Table 3, Fig. 3). Male shrikes generally made contact more often during the mobbing behaviour than did females ($t = –3.08$, df = 2292, $p > 0.01$; Fig. 2) but this difference was significant only for Sparrowhawk and Kestrel (Table 4, Fig. 4).

Table 4. The dependence of mobbing intensity in the Red-backed Shrike on mount type and shrike sex. Mobbing events with and without physical contact, performed by males and females to particular mount pairs, is tested. Probabilities are Bonferroni adjusted.

Comparison	*t*	df	*p*
Male/Female × Jay/Kestrel	2.79	2,292	0.01
Male/Female × Jay/Sparrowhawk	2.46	2,292	0.01
Male/Female × Kestrel/Sparowhawk	0.36	2,292	0.72

4. Discussion

We did not find clear evidence for the hypothesis that the frequency of mobbing behaviour would be adjusted according to the apparent threat to the nest contents. While the Jay was mobbed equally as often as both raptors, the Magpie was mobbed at a rate equal to the control pigeon. Thus, nest predators (Jay and Magpie as a category) were not mobbed more often than predators of adult birds (Sparrowhawk and Kestrel). Red-backed Shrikes primarily have to decide whether to use mobbing in nest defence or not. The main criterion affecting this decision may not be the threat to nest contents, given the quite different responses to Magpie and Jay. When shrikes mobbed the predator, the frequency of this behaviour appeared more or less equal towards each species. This may reflect the fact that a common objective of mobbing is to chase any predator away, which demands comparable costs and brings about equal benefits (see Dale *et al*. 1996).

Our second hypothesis – that mobbing intensity would be adjusted to the threat to the defending birds – received some support. Mobbing intensity, in terms of occurrence of mobbing events

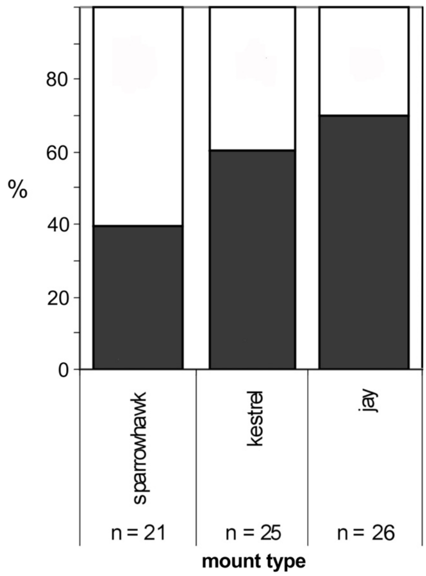

Fig. 2. Proportion of attacks with (black parts of columns) and without (white parts) physical contact, performed by Red-backed Shrikes towards particular mount types. Sample size is shown under each column (total *n* = 36). Only regularly-attacked dummies were included, i.e., Magpie and pigeon were excluded from this comparison. Total numbers of attacks were 419 for Sparrowhawk, 1,316 for Kestrel and 643 for Jay.

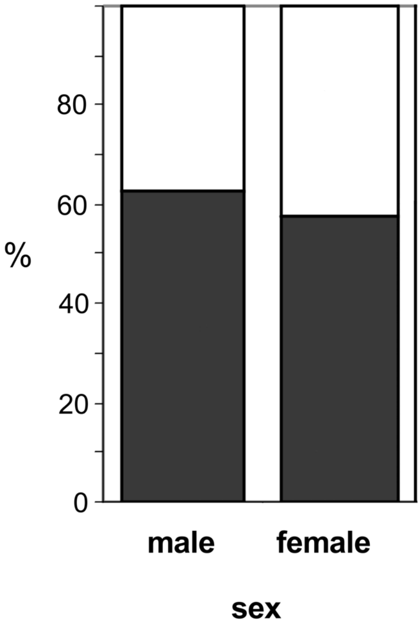

Fig. 3. Proportion of attacks with (black parts of columns) and without (white parts) physical contact performed by Red-backed Shrikes towards all mount types pooled. Sample sizes were 1,411 for males and 872 for females.

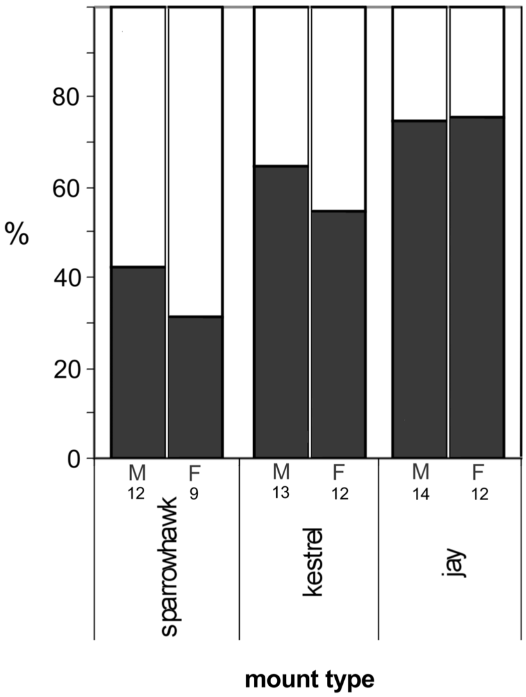

Fig. 4. Proportion of attacks (black parts of columns) and without (white parts) physical contact performed by Red-backed Shrikes towards particular mount types. Numbers under sex (M = male, F = female) show the number of included birds out of a total of 18. Only regularly-attacked dummies were included, i.e., Magpie and pigeon were excluded from this comparison. Numbers of all attacks were 428 for Sparrowhawk (M = 297, F = 131), 1,323 for Kestrel (M = 828, F = 495) and 551 for Jay (M = 287, F = 264).

with physical contact, upon the three regularly-mobbed predators steeply decreased from Jay through Kestrel to Sparrowhawk. This suggests that the shrikes have an ability to discriminate not only corvids from raptors, but also particular species within raptors, and to assess their potential risk.

Studies on the responses of breeding birds to avian predators posing different levels of risk have shown lower mobbing rates towards predators of adult birds than to nest predators (Jacobsen & Ugelvik 1992, Amat & Masero 2004, Hogstad 2005, Dale *et al*. 1996). The weaker mobbing of predators of adult birds has been interpreted as being both the result of a lower threat to eggs or nestlings (Dale *et al*. 1996) and of a greater threat to adults (Hogstad 2005). Our results agree with the above-listed studies in terms of intensity of mobbing. In most of these studies, the measured behavioural response of birds usually comprises alert postures, predator following and approaching, whereas in our study, the responses were fly-overs of the mount, decreases of the flight altitude and even physical attacks. Such behaviour reflects a willingness to take risks in the presence of a predator rather than an effort to chase it away. Our results thus do not contradict with the other works, but this comparison shows the importance of a differentiation between mobbing intensity and mobbing frequency.

Only a few studies have tested several predators of adult birds with varying levels of threat. Curio *et al*. (1983) presented three species of raptors to Great Tits (*Parus major*) and found that their responses changed according to the potential threat of the raptor against themselves. Conversely, Kleindorfer *et al*. (2005) showed that *Acrocephalus* warblers responded to predators according to the threat to the nest. This contradiction can be explained by our results in that, besides the level of the risk to adults or nest content, the mobbing behaviour is affected also by its target. Curio *et al*. (1983) measured the willingness to approach the presented mount, i.e., the willingness to risk. This parameter was affected by the potential risk to defending birds, as in our shrikes. Kleindorfer *et al*. (2005) measured a complex reaction score of response comprising the distance from the mount, latency of response and alarm calls. Alarm calls were usually addressed to nestlings (Serra & Fernandez 2011), which is why this behaviour was affected mainly by the potential threat of a presented predator to the nest.

We are puzzled by the apparent lack of response by Red-backed Shrikes towards the Magpie, in contrast to the frequent mobbing events upon the Jay. The former apparently represents a similar if not bigger threat to the nest, compared to the Jay (Chiron & Julliard 2007). The Magpie is larger and apparently more frequently preys upon adult birds than the Jay (Tatner 1983, Cramp 2000), so it may represent a greater threat to the adults. Some studies have shown that Blackbirds (*Turdus merula*) have higher nesting success at sites where Magpies do not occur but where Jays are common, compared to sites with abundant Magpies (Polakova & Fuchs 2006). Nevertheless, the reaction of the shrikes to the extremely dangerous Sparrowhawk was considerably stronger than to the Magpie.

We hypothesize that the decision by shrikes to actively defend the nest is affected not only by the actual threat to the nest and/or the adults, but also by the likelihood of success in chasing the predator away, which may differ between the Sparrowhawk and the Magpie. If the former appears in the vicinity of a shrike's nest by chance and is suddenly attacked by aggressive parents, it flies away. The Magpie, – which is known to prey on birds' nests (Chiron & Julliard 2007), may well have *a priori* experience of mobbing, and use this information to search the area after a mobbing event for the nest's proximity. The effort not to disclose the location of the nest might represent an optimal antipredatory behaviour in such cases. Experimental studies have shown high conspicuousness of the mobbing behaviour and its effect on the probability of nest survival (Krama & Krams 2005, Krams *et al.* 2007), so the zero activity in the presence of a Magpie, demonstrated here, may reflect optimal behaviour as regards the parents' fitness. This trade-off was understood also by Hogstad (2005) who found that Fieldfares (*Turdus pilaris*) ended chasing stoats (*Mustela erminea*) from their nests which might have returned to prey on the nests. Nevertheless, such an explanation assumes that the Magpie is a more skilled and/or specialized nest predator than the Jay,, yet no studies have truly compared the relative effects of the share of Jays and Magpies on nest predation.

Our experiment suggests small differences in the sex-related difference in mobbing frequency for the Red-backed Shrike, which partly contradicts other studies showing higher male activity in nest defence (see Lima 2009 for a review). This pattern is common in species where the male provides food not only for nestlings but also for the incubating female, which is the case in the Red-backed Shrike (Lefranc & Worfolk 1997). However, in our study, we observed a sex-specific response difference when the nestlings were 5–10 days old. At this stage, the investment of the male should be greater, as it feeds an incubating female and subsequently feeds the nestlings with the same frequency as the female (Lefranc & Worfolk 1997). The observed, strong correlation in the mobbing frequency between male and female has been shown rarely and only in birds with vigorous nest defence (Hogstad 2005), though nest defence may be more easily achieved if both partners participate.

Mobbing intensity (strikes on the model 'predator') differed between males and females. Male attacks were more acute than female ones, but only in case of predators of adult birds (Sparrowhawk and Kestrel), suggesting an important difference between mobbing intensity and mobbing frequency. Higher risk-taking by males may also be explained by the generally higher aggression of males, possibly caused by higher levels of testosterone (Wacker *et al.* 2010). However, Montgomerie and Weatherhead (1988) proposed there were different allocations of energy in sexes with different abilities to raise the offspring unaided, as in the Red-backed Shrike (Lefranc & Worfolk 1997). Alternatively, females may be less active or more reluctant to take risks during the defence than males because of their different vulnerability. Female Red-backed Shrikes are more cryptically coloured than males (Lefranc & Worfolk 1997) which may more often cause furtive behaviour and therefore lower their activity during the nest defence.

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Pikkulepinkäinen säätelee saalistajaan kohdistamaansa häirinnän voimakkuutta muttei panostamaansa aikaa arvioimalla saalistajan itseensä kohdistamaa uhkaa

Tutkimme pikkulepinkäisen (*Lanius collurio*) kykyä säädellä aikuisten ja pesän puolustustaan. Käytimme pesien vierelle tuotuja, täytettyjä, aikuisia lintuja saalistavia petolintu- (varpus- ja tuulihaukka) sekä pesiä ryöstäviä varislintulajeja (harakka ja närhi) sekä kontrollilajia (kesykyyhky). Pikkulepinkäiset hätistivät säännöllisesti varpus- ja tuulihaukkaa sekä närheä, mutteivät harakkaa

tai kesykyyhkyä. Hätistelyyn käytetty aika (hätistelykertoja/20 min) ei vaihdellut mainittujen hätisteltyjen lajien välillä.

Jos taas lepinkäiset yrittivät hätistää saalistajan pois, voimakkuuteen ei vaikuttanut itse pesään kohdistuva potentiaalinen uhka (oletetusti suurempi varis- kuin petolinnuilla). Päinvastoin fyysisen kontaktin sisältävien hätistely-yrityksien osuus väheni närhestä ja tuulihaukasta varpushaukkaan, vaikka viime mainittua pidettiin tässä vaarallisimpana. Pikkulepinkäiset saattoivat säädellä hätistelyn voimakkuutta arvioimalla itseensä kohdistunutta uhkaa. Tuloksemme kertovat hätistelyn voimakkuuden ja ajallisen panostuksen erottamisen merkityksestä pesäpuolustuksen tutkimuksessa.

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