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Indirect cues of nest predation risk and avian reproductive decisions

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Current life-history theory predicts that increased mortality at early stages of life leads to reduced initial investment (e.g. clutch size) but increased subsequent investment during the reproduction attempt. In a field experiment, migratory pied flycatchers *Ficedula hypoleuca* perceived differences in mammalian nest predation risk and altered their reproductive strategies in two respects. First, birds avoided nest sites manipulated to reflect the presence of a predator. Second, birds breeding in risky areas nested 4 days earlier and laid 10 per cent larger clutches than those in safe areas, a result that runs counter to the prevailing life-history paradigm. We suggest that the overwhelming importance of nest predation to individual fitness reduces the value of collecting other information on habitat features leading to expedited onset of nesting, and, consequently, to larger clutch size.

Keywords: life-history variation; nest predation; information value

1. INTRODUCTION

Local mortality risk is a crucial element of habitat quality, and thus adaptations to anticipate mortality risks in habitat choices are expected. However, we know little about how birds acquire information about mortality risk and what related cues they use when selecting breeding habitats (Caro 2005). Furthermore, it is unclear how information on spatial variation in mortality risk should affect breeding investment decisions.

According to life-history theory, increased nestling mortality should lead to reduced initial parental investments in their clutch in the current breeding attempt, because smaller broods will shorten the time the nests are exposed to predation (Roff *et al.* 2005), reduce the number of feeding visits that could attract the attention of predators (Martin *et al.* 2000) and allow more energy for re-nesting in the event of failure (Martin 1995). Additionally, life-history theory also implies that high nest mortality may select for increased parental investment in incubation and feeding, to accelerate offspring development and minimize exposure to predators (Lack 1968; Ricklefs 1969).

Flexible, adaptive investment in reproduction requires that parent birds, be well informed about the current risk of predation relative to other fitness-related factors such as food. However, information should only be acted upon if the benefits exceed the cost (Dall *et al.* 2005). If predation is the major determinant of fitness and breeders perceive a high risk of mortality, they may stop collecting information, a step that would hasten the decision-making process.

Here we experimentally tested how information on nest predation risk influences nest site selection and the subsequent reproductive strategies of pied fly-catchers (*Ficedula hypoleuca*). First, we tested whether individuals can perceive and use visual and/or olfactory cues indicating the presence of mammalian predators to select safer nest-boxes without direct encounters with predators. Second, at a larger spatial scale of risky versus safe habitat, we tested how birds respond to experimentally increased perceived nest predation risk.

2. MATERIAL AND METHODS

The study was conducted in April to June of 2006 and 2007 in central Finland (62°30' N, 26°20' E). The landscape is characterized by a patchy mosaic of managed coniferous forests, small fields, peatlands and watercourses. Owing to intensive forest management in the region, the density of natural nesting cavities is very low. The pied flycatcher is a migratory passerine bird that arrives in its breeding grounds in the north in May, nests once per year, moults and migrates back to sub-Saharan Africa in August. Annual adult mortality is approximately 40–50% (Lundberg & Alatalo 1992). The majority of individuals breed only once or twice during their life, and thus each breeding attempt is very valuable for individual fitness. Female flycatchers make decisions in which territory and with which male to settle, and subsequently which nest cavity to select (Lundberg & Alatalo 1992).

(a) *Experiment 1: nest-site selection*

This experiment consisted of triplets of nest-boxes, such that a female could select among three treatments: least weasel (*Mustela nivalis nivalis*; risky), vinegar (smelly) and control (safe) treatment. Least weasel treatment boxes were kept in the cage of a captive weasel for 5 days, during which weasels urinated and defecated on the boxes. We also glued a small tuft of weasel hair under the nest-box entrance. Nest-boxes for the other treatments were also kept indoors for 5 days and a drop of glue was placed at the entrance to control for handling effects. As a novel odour control, we treated one nest-box with vinegar (50 ml of 10% acetic acid dissolved to 1 l of water). All nest-box replicates were distributed along a small dirt road. Triplets were separated by more than 150 m but nest-boxes within a replicate were within 20 m of each other. In this set-up, all boxes of a triplet are defended by a single male, and the female has to make a choice between the three boxes. Nest-boxes were checked and received additional treatments of distilled water (control box), vinegar or weasel urine sprayed on the boxes every 2 days until the first egg was laid in one of the nest-boxes within a triplet. For all nests we recorded the onset of egg laying as well as clutch size.

(b) *Experiment 2: reproductive strategies in risky versus safe habitat*

We selected eight study patches (approx. 6 ha) and assigned all six nest-boxes within a patch as either control or least weasel treatment. The patches were located more than 500 m apart. Nest-boxes were treated following the same methods (see above), with four patches as controls (safe) and four as predator (risky) treatments. Treatment on a patch was switched between 2006 and 2007. We retreated boxes every other day until mid-June. We monitored nests until chicks fledged. We also weighed the eggs within 2 days after the clutch was completed using a digital balance (accuracy 0.01 g). Nestling weight, wing length and tarsus length were measured at the age of 12 days. For each nest, we also calculated the time in days they contained eggs (egg laying + incubation period) or nestlings.

Nest-box choice in experiment 1 was analysed using the goodness-of-fit test against the null hypothesis of equal distribution of choices among treatments. We used re-sampling techniques to analyse all other treatment effects (Manly 1997). In experiment 1,

we first calculated observed mean date of the first egg and mean clutch size in each treatment, and then summed the absolute differences between the grand mean and experiment specific means. We repeated these calculations for 1000 randomized datasets where we shuffled the observations among treatments, and counted how often the sum of absolute differences is higher than or equal to the observed sum to yield two-tailed p-values that the observed differences are due to chance alone.

The reciprocal design in experiment 2 (i.e. each patch received both treatments in alternative years) controls for site and year effects. We first calculated for each patch the observed difference in the response variables between the two treatments, and summed the plot-specific differences. We then repeated these procedures for 1000 randomized datasets and counted how often the difference is equally or more extreme than the observed difference between the treatments (two-tailed test). To test if there is, for a constant laying date, a significant treatment effect on clutch size, we conducted a regression of the clutch size against date of first egg, saved the residual for each nest and subjected these residuals to randomization tests (see above). Similar analyses were carried out to test for a treatment effect on nesting duration for a constant clutch size.

3. RESULTS

In the nest site selection experiment, 50 nest-box choices were observed during the 2 years (24 in 2006 and 26 in 2007). Yearly results were consistent (year difference $\chi^2_2 = 0.964$, $p = 0.703$). Pied flycatchers avoided risky nest-boxes but tended not to differentiate between control and smelly nest-boxes (years combined; $\chi^2_2 = 12.2$, $p = 0.002$; figure 1). Egg-laying initiation date ($n = 50$, mean (s.d.) = May 26 (4.23), $p = 0.901$) and clutch size ($n = 47$, mean (s.d.) = 6.55 (0.75) eggs, $p = 0.886$) did not differ among treatments.

In the second experiment, 48 pied flycatcher pairs started nesting (21 in 2006 and 27 in 2007) of which 46 completed their clutch and 39 nests fledged young. Treatments did not differ in the number of flycatchers per patch ($p = 0.307$), but pied flycatchers nesting in risky patches initiated nest building and egg-laying approximately 4 days earlier than those nesting in safe patches (figure 2). In addition, clutches were 10 per cent larger in risky than in safe patches (mean (s.d.) clutch sizes 7.1 (0.92) versus 6.4 (0.81) eggs; $p = 0.010$). The difference in clutch size disappeared when adjusted for a constant laying date (mean (s.d.) 6.7 (0.85) versus 6.6 (0.56) eggs; $p = 0.672$). The time that pied flycatcher nests contained eggs (egg laying and incubation) was 1 day longer in the risky treatment (mean (s.d.) 21.0 (1.5) versus 20.0 (1.2) days; $p = 0.032$), but this difference also disappeared after controlling for clutch size effects ($p = 0.280$). There were no differences between treatments in mean egg mass (mean (s.d.) risky 1.65 (0.11) g versus safe 1.63 (0.14) g; $p = 0.551$), number of nestlings (6.19 (1.05) versus 5.91 (1.16); $p = 0.822$), nestling size (e.g. nestling weight 13.8 (1.7) versus 13.1 (1.1) g; $p = 0.122$) or in the length of nestling period (16.0 (1.0) versus 15.5 (1.1) days; $p = 0.330$).

4. DISCUSSION

Previous studies have shown that birds can assess spatial (Eggers *et al.* 2006; Fontaine & Martin 2006) and temporal (Doligez & Clobert 2003) variation in predation risk and adjust their behaviour accordingly. So far the underlying assessing mechanism is unknown but recent studies imply that birds are able to detect visual and olfactory cues (Amo *et al.* 2008;
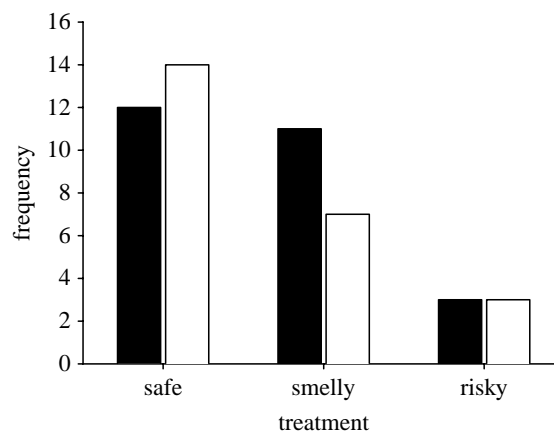
Figure 1. Frequency of nest-box selections by pied flycatchers among the three treatments.
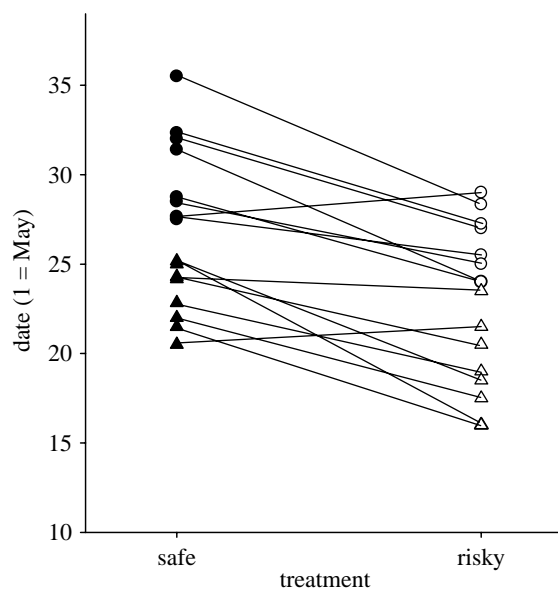

Figure 2. Onset of nesting during the two treatments. The mean date of onset of nest building (triangles; grand mean (s.d.) for risky patches 19.2 (3.9) and for safe patches 23.1 (4.0); $p = 0.001$) and egg laying (circles; grand mean (s.d.) for risky patches 26.8 (2.9) and for safe patches 30.7 (4.7); $p = 0.001$) in the study patches. Patch-specific values from the two experimental years are connected by a line.

Steiger *et al.* 2008). Our results demonstrate that pied flycatchers can use visual sense and/or olfaction to avoid risky nest sites without seeing predators themselves (experiment 1). At the scale of habitat patches (experiment 2), birds initiated nesting earlier in risky than in control patches suggesting that consistent, uniformly spread information on predation risk was used to adjust reproductive decisions.

Our result that birds advanced nesting in risky patches compared with control patches does not match the current life-history paradigm that increased risk of nestling mortality should lead to reduced initial investment in the current breeding attempt. There are alternative explanations for this result, which can be eliminated. First, earlier breeding in risky patches might allow more rapid re-nesting in case of predation. However, clutch sizes were larger in risky patches, indicating that energy was not saved for re-nesting. Second, nest-boxes in risky patches may appear less valuable to birds, because of higher nest

predation risk, and are thus less defended, leading to easier access for newcomers to settle and breed. Early nest initiation in risky patches, although, is inconsistent with this hypothesis. Third, a high rate of predation on incubating adults might increase investment in the current breeding attempt. It is hard to imagine that the incremental increase in risk of adult mortality during nesting could outweigh the already high mortality rate throughout the life history.

We suggest that clear signs of predation risk may lead to expedited and simplified decision-making because benefits of acquiring information on other habitat properties may not exceed the information value of predation risk. Gathering information can incur costs, such as a risk of losing a nest-cavity and reduced reproductive output with elapsed time, which has been documented in the pied flycatcher (Siikamäki 1998). By contrast, in safe patches it may pay to collect more information on the relative quality of alternative territories and nesting sites, even with the cost of reduced clutch size. Thus, females may have spent more time in assessment in safe patches, which resulted in smaller clutches. In line with this idea, Winnie *et al.* (2006) showed that elk (*Cervus elaphus*) used greatly simplified decision rules in selecting foraging habitats in the presence versus absence of wolves (*Canis lupus*). The relative value of information crucial to individual fitness and its effect on decision-making processes have remained conspicuously untested. Our findings represent an important step in this context, suggesting that the fear factor alone may exceed the information value of other variables.

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