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Indirect cues of nest predation risk and avian reproductive decisions

Mikko Mönkkönen[1,*], Jukka T. Forsman[2],
Tiina Kananoja[1] and Hannu Ylönen[3]

[1]*Department of Biological and Environmental Science,
University of Jyväskylä, PO Box 35, Jyväskylä 40014, Finland*
[2]*Department of Biology, University of Oulu, PO Box 3000, Oulu
90014, Finland*
[3]*Konnevesi Research Station, University of Jyväskylä, PO Box 35,
Jyväskylä 40014, Finland*
Author for correspondence (mikko.monkkonen@jyu.fi).

**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 manipu-
lated 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 determi-
nant 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 olfac-
tory 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 charac-
terized 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 treat-
ments 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;
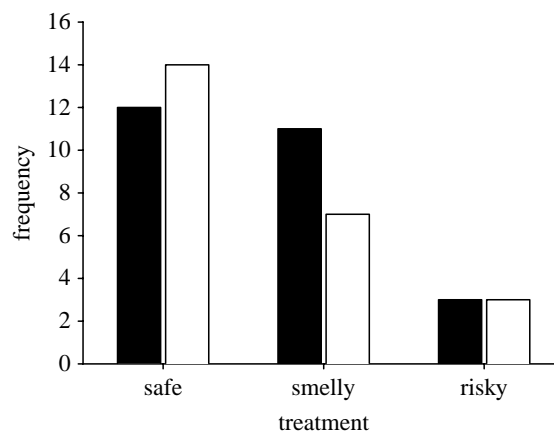
Figure 1. Frequency of nest-box selections by pied flycatchers among the three treatments.
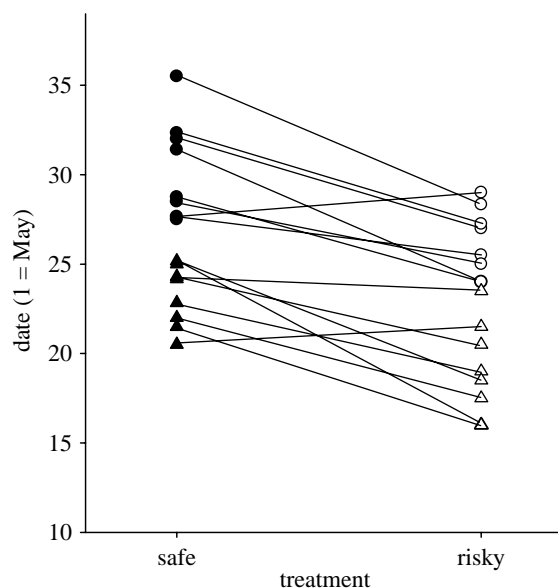

Figure 2. Onset of nesting during the two treatments. The mean date of onset of nest building (triangles; grand mean (s.d.) for risky patches 19.2 (3.9) and for safe patches 23.1 (4.0); $p = 0.001$) and egg laying (circles; grand mean (s.d.) for risky patches 26.8 (2.9) and for safe patches 30.7 (4.7); $p = 0.001$) 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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