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Experimental increase of predation risk induces breeding dispersal of Tengmalm's owl

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Abstract Nest predation and its avoidance are critical components of an individual's fitness and play an important role in life history evolution. Almost all studies on this topic have been observational, and thus have not been able to separate the effects of individual quality, habitat selection and predation risk of given nest sites from each other. More experimental studies on nest predation and breeding dispersal, therefore, are needed to avoid confusing interpretations of the results. In western Finland, pine marten (*Martes martes*) predation risk was experimentally simulated at the nests of Tengmalm's owls (*Aegolius funereus*) by using a caged American mink (*Mustela vison*) as a predator. Nests without exposure to a mink served as controls. In accordance with our predictions and earlier observational studies, males exposed to simulated predation risk increased nest-hole shift and breeding dispersal distances compared to control males. Nest-hole shift and long breeding dispersal distances probably decrease the risk of nest predation, because pine martens are known to revisit nest-holes they have found.

Keywords Bird of prey · Habitat selection · Mammalian predator · Nest predation · Predator avoidance

Introduction

Nest predation and its avoidance are critical components of an individual's fitness and play an important role in life history evolution (e.g. Martin 1995; Saether 1996). Despite a large body of published literature, more experimental evidence on nest predation avoidance by dispersal is needed, because there is increasing evidence that lifetime reproductive success and survival rates among bird populations are largely related to nest predation (Martin 1995; Wiklund 1996a). Therefore, in addition to intensive nest

defence behaviour, selection for safe nest sites should be favoured to minimize nest predation. So far, most studies on the avoidance of nest predation have been observational (but see e.g. Haas 1998), in which it is often difficult to separate the effects of habitat selection and predation risk of given nest sites from each other. For example, nest site shift due to predation risk may be difficult to distinguish from nest site shift caused by food depletion (Korpimäki 1993). Nest predation may also be correlated with other factors, confusing causal interpretations such as individual and habitat quality (for a review, see Andren 1995). One problem in dealing with observational data on the presence or absence of predators is that their numbers and influences may be difficult to estimate in the field.

In this study, we simulated a nest predation attempt on the nests of Tengmalm's owls (*Aegolius funereus*) by setting a caged American mink (*Mustela vison*) on the roof of the nest-box. Our prediction was that if male owls try to minimize nest predation risk in the following breeding season, the probability for nest-hole shift should be higher and breeding dispersal distances longer in the treatment group than in males of the control nests. To exclude the effects of other possible factors which could obscure the interpretation of our results, all the known important background variables (such as age of individuals, territory quality, food abundance, nest-box quality, breeding success, laying date and nest-box density) were similar between treatment and control groups. Male Tengmalm's owls are suitable for this study, because the choice of nest site is mostly dependent on the male's decision. In the beginning of the breeding season, a male occupies a certain nest-hole and tries to attract a female to breed in it by hooting and delivering courtship prey to a suitable nest-hole (e.g. Hakkarainen and Korpimäki 1998).

Materials and methods

Study species and study population

Tengmalm's owl is a small hole-nesting bird of prey, which is one of the most numerous bird of prey species in boreal forests

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(Mikkola 1983). In this study we examined only male Tengmalm's owls, because they are resident after the first breeding attempt (annual median breeding dispersal distances vary from 0.8 to 1.5 km; Korpimäki 1993), while females disperse widely between successive breeding seasons (up to 500 km; Korpimäki et al. 1987). During their life span (on average 3.5 years) males use approximately one to three nest holes for breeding in an area of 2–5 km² (Korpimäki 1992). Among hundreds of males ringed and recaptured in our study area, only one male has ever moved more than 5 km inside our large study area, and only one breeding male has been later reported to have bred outside our study area, although in the vicinity of our study population there are about 1,000 nest-boxes suitable for Tengmalm's owls. These nest-boxes are annually checked and parent birds trapped by bird ringers (see e.g. Hakkarainen et al. 1996). In Tengmalm's owl mate switching occurs between seasons (Korpimäki et al. 1987). The male provides the family with food during the breeding season, including the courtship period (e.g. Hakkarainen and Korpimäki 1998).

The study area is located in the Kauhava region, western Finland (approximately 63°N, 23°E). It covers 1,300 km² and contains some 500 nest boxes and 30 natural cavities suitable for Tengmalm's owls. The density of nest boxes (approximately 0.5/1 km²) does not differ from that in old forests of southern Finland where the density of natural cavities suitable for Tengmalm's owls is 0.5–1.5 km² (Pouutu 1985). The breeding frequency of Tengmalm's owls varies in synchrony with changes in vole abundance: in good vole years 20–33% of the nest-boxes were occupied, while in poor vole years only 1–3% were occupied (Korpimäki 1994).

Nearly all breeding males were trapped, aged and ringed (e.g. Hakkarainen et al. 1996 and references therein). Males were divided into three age groups (1, 2 and ≥3 years old) according to the moult pattern of primary feathers (Glutz von Blotzheim and Bauer 1980; Hörnfeldt et al. 1988). Nests were visited as many times as necessary to trap the males, to determine the laying date, final clutch size and number of fledglings produced. All nest-boxes and known natural cavities in the study area were checked at least twice per breeding season to determine the breeding occupancy.

Territory quality was ranked from 1 (one breeding attempt per last 10-year period) to 5 (at least five breeding attempts per last 10 years). On the basis of intensive snap-trapping on individual territories, the abundance of voles of the genera *Microtus* and *Clethrionomys* (staple prey of Tengmalm's owls; e.g. Koivunen et al. 1996) in good vole years is lower than in high-quality territories (Hakkarainen et al. 1997). In the peak vole year, males in highly ranked territories delivered more prey items to the nest and produced more fledglings than did males in low-quality territories (Hakkarainen et al. 1997). To get also direct estimates on food abundance within a territory, we counted the number of *Microtus* and *Clethrionomys* voles cached in the nest-boxes during the incubation stage, when there are generally many more prey items than females can consume (for further details, see e.g. Koivunen et al. 1996).

Our study area includes two types of nest-boxes for Tengmalm's owls classified as high and low quality. Most nest-boxes were optimal for Tengmalm's owls (bottom area 20×20 cm, height ca. 50 cm, entrance diameter ca. 9 cm; see Korpimäki

1985). Other nest-boxes were of lower quality as they were relatively large for Tengmalm's owls (bottom area ca. 30×40 cm, height ca. 50 cm, entrance diameter 13–18 cm). The latter ones are accessible for the larger birds of prey, such as the Ural owl (*Strix uralensis*), which is one of the main competitors and predators of Tengmalm's owls (Hakkarainen and Korpimäki 1996).

The dispersal distances between the previous year's and present year's nest-sites of males were measured from a landscape map (scale 1:50,000) to the nearest 50 m.

Predator simulations

A live brown American mink was used to simulate a nest predation attempt in 106 randomly chosen nests of Tengmalm's owls in 6 years (1990–1992, 1994–1996; annual sample sizes 13–25). We used a live mink, because owls responded to a live mink more actively than to a stuffed pine marten (H. Hakkarainen, unpublished data). An American mink resembles the pine marten *Martes martes* in size, colour and movements, the main nest predator of Tengmalm's owls in our study area. Approximately 5% of nests are destroyed by pine martens (Korpimäki 1987; for other areas see e.g. Sonerud 1985). On light nights (10 p.m.–2 a.m.) in May and early June, a mink in a wire net cage (1×0.5×0.5 m) was placed on the roof of the nest-box, when nestlings were about 2 weeks old. After a male had returned from his hunting trip, his response to the mink was observed from a hiding place at a distance of 30 m to the nest. Defensive behaviour of males was recorded for 10 min. In most cases owls responded to the mink by several warning calls, beak-snaps and pseudo-attacks. Some males showed extremely high activity in the defence of the nest by direct strikes in which a male touched the cage of the mink (for further details, see Hakkarainen and Korpimäki 1994). Therefore, we were able to simulate a "true-to-life" predation danger at the nests of Tengmalm's owls, because all males responded to the mink.

Because many males in our experiment were recaptured after years of increasing vole density, data only from 1991 and 1994 which showed increasing numbers of voles were included in the analyses. In addition, the number of nests not exposed to an American mink (control nests) was low during the other years. We selected as controls ($n=8$) all males in our study population that matched the males in the experimental group with respect to laying date (± 3.6 days). First, the control nest with the same laying date to the experimental nest was searched for by using the "find" option of the SYSTAT statistical program. If such a nest was not found, searches were repeated using ± 1 , ± 2 , ± 3 ...day's difference, respectively, in laying dates as criteria between the control and the experimental nest. As a result, the laying dates between control and experimental nests did not differ (Table 1). The sample sizes between the treatment and control groups differ, because most males were not met as breeders in the following breeding season, although some of them bred some years later within our study area. They were excluded from this study because of possible annual variation in breeding dispersal distances and long intervals between observations. All nests used in this study were located at least 2 km away from the edge of our study area, which suggests that the probability of recapture within our study area was about the same for all males.

Table 1 Laying date (1=1 April), clutch size, fledgling production, territory quality, nest-box quality (percentage of poor-quality nest-boxes), the number of voles cached in the nest-box, male age (year) and the distance to the nearest unoccupied nest-box between the treatment and control groups. Statistical tests were performed using Mann-Whitney *U* and *t*-tests and nest-box quality by the Fisher exact test

| | Treatment | | Control | | Test | <i>P</i> |
|---------------------------------|-----------|----------|------------|----------|-----------------|----------|
| | Mean±SD | <i>n</i> | Mean±SD | <i>n</i> | | |
| Laying date | 5.40±8.86 | 15 | 6.50±17.41 | 8 | <i>U</i> =57.0 | 0.85 |
| Clutch size | 5.27±1.22 | 15 | 5.57±0.98 | 7 | <i>t</i> =0.58 | 0.57 |
| No. of fledglings | 1.67±1.35 | 15 | 2.25±1.98 | 8 | <i>t</i> =0.84 | 0.41 |
| Territory grade | 2.93±1.49 | 15 | 2.50±1.31 | 8 | <i>U</i> =49.0 | 0.47 |
| Nest-box quality (%) | 27 | 15 | 25 | 8 | | 1.00 |
| Cache size | 2.50±2.28 | 14 | 3.00±3.37 | 7 | <i>U</i> =51.0 | 0.88 |
| Male age (years) | 2.67±0.62 | 15 | 2.38±0.74 | 8 | <i>U</i> =46.00 | 0.28 |
| Nearest unoccupied nest-box (m) | 560±291 | 15 | 600±278 | 8 | <i>t</i> =0.32 | 0.75 |

Results

As annual sample sizes for male owls that were recaptured in the following breeding season were small (for 1991, $n=14$ and for 1994, $n=9$), we pooled data from both years in our analyses. Territory quality, the number of voles cached in the nest-box, male age, breeding dispersal distances and breeding characteristics did not differ between 1991 and 1994, which suggests that dispersal behaviour and breeding performance of male owls were not affected by annual variation (Table 2).

Breeding success, individual quality and territory quality

By including only males that bred at about the same time within a breeding season (Table 1), we were able to control for the most important factors that could affect breeding dispersal distances of males. For example, breeding success and site fidelity are higher in good-quality territories than in poor ones (e.g. Korpimäki 1988a; Hakkarainen et al. 1997), old individuals breed earlier and more successfully than young individuals (Korpimäki 1988b) and food abundance in the field, varying largely in the course of the breeding season (Korpimäki and Hakkarainen 1991), affects the breeding dispersal distance of male Tengmalm's owls (Korpimäki 1993). This could obscure our interpretation of to what extent predation risk per se influenced breeding dispersal compared to other inter-correlated factors.

As a result of similar laying dates between the control and treatment males (Table 1), territory quality, nest-box quality, the number of voles cached in the nest-box, breeding performance and male age did not differ between these groups (Table 1). Moreover, the distance to the nearest unoccupied nest-box did not differ (Table 1). In conclusion, treatment and control males had similar possibilities for nest-hole shift within their territories.

Nesting failure seemed to be more common among some males than others, suggesting that individual or territory quality may differ in the breeding population. Among six males which failed in their nesting attempts, four (67%) were unsuccessful also in the following breeding season, whereas only three (18%) nesting failures were observed among the males that bred success-

fully in the previous year ($n=17$; Fisher exact test, $P=0.05$). This probably reflects variation in territory quality or differences in feeding efficiency of males, which are mostly responsible for feeding the whole family during the breeding season (e.g. Koivunen et al. 1996). The proportion of males producing no fledglings, however, was the same between the control and treatment groups (two out of eight in the control group and four out of 15 in the treatment group), suggesting that either male or territory quality did not differ between the control and treatment groups. In addition, territory quality was not related to the probability of nesting failure at nestling stage (deserted nests, mean \pm SD, 2.50 ± 1.76 , $n=6$; successful nests, 2.88 ± 1.32 , $n=17$; $U=42.5$, $P=0.54$).

Simulated predation risk, nest hole shift and breeding dispersal distance

In the treatment group, fidelity to the nest-box in the following year was low (20%) compared to control males (75%; Fisher exact test, $P=0.02$). Likewise, breeding dispersal was longer in the treatment than control group (square-root-transformed breeding dispersal distance; t -test, $t=2.18$, $df=21$, $P=0.04$; Fig. 1). Despite the high efficiency of owl trapping around the study area

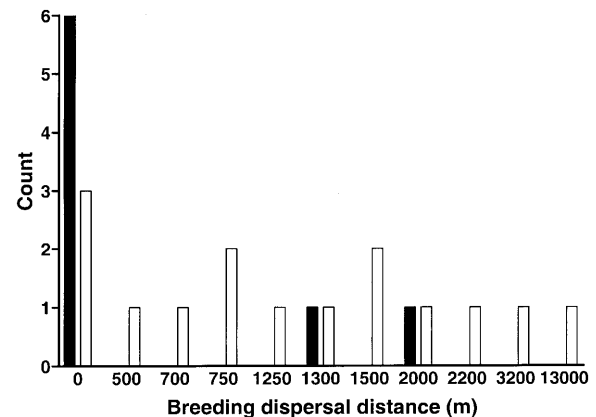


Fig. 1 The frequency distribution of breeding dispersal distances of control (filled bars) and treatment (open bars) male Tengmalm's owls. Medians 0.0 m and 1250 m, respectively

Table 2 Laying date (1=1 April), clutch size, fledgling production, the number of voles cached in the nest-box, territory and nest-box quality, parental age and breeding dispersal distances of male Tengmalm's owls in 1991 and 1994. Statistical tests were performed by Mann-Whitney U and t -tests. Nest-box quality (percentage of poor quality nest-boxes) was tested by the Fisher exact test

| | 1991 | | 1994 | | Test | P |
|------------------------|------------------|-----|-------------------|-----|----------|------|
| | Mean \pm SD | n | Mean \pm SD | n | | |
| Laying date | 2.93 \pm 12.79 | 14 | 10.22 \pm 10.07 | 9 | $t=1.44$ | 0.16 |
| Clutch size | 5.50 \pm 1.23 | 14 | 5.13 \pm 0.99 | 8 | $t=0.74$ | 0.47 |
| No. of fledglings | 2.21 \pm 1.25 | 14 | 1.33 \pm 1.94 | 9 | $t=1.33$ | 0.20 |
| Territory grade | 2.64 \pm 1.15 | 14 | 3.00 \pm 1.80 | 9 | $U=55.0$ | 0.61 |
| Nest-box quality (%) | 29 | 14 | 22 | 9 | | 1.00 |
| Cache size | 3.08 \pm 3.12 | 13 | 2.00 \pm 1.41 | 8 | $U=57.5$ | 0.69 |
| Male age (years) | 2.50 \pm 0.76 | 14 | 2.67 \pm 0.50 | 9 | $U=58.5$ | 0.74 |
| Breeding dispersal (m) | 789 \pm 999 | 14 | 2322 \pm 4080 | 9 | $U=44.0$ | 0.22 |

(Hakkarainen et al. 1996), no males belonging to the experimental or control groups were later found outside our study area.

Costs of nest hole shift and breeding dispersal

We did not find any costs of nest-hole shift, because laying date (t -test, $t=0.44$, $df=20$, $P=0.66$), clutch size ($t=0.26$, $df=20$, $P=0.25$) and fledgling production ($t=1.13$, $df=21$, $P=0.27$) did not differ between males that reoccupied the same nest-box, or changed nest-box in the consecutive breeding seasons. In addition, the distance that males dispersed between consecutive breeding seasons was not related to the next year's laying date (Spearman correlation, $r_s=0.06$, $n=22$, $P=0.78$), clutch size ($r_s=0.19$, $n=22$, $P=0.40$) or fledgling production ($r_s=-0.32$, $n=23$, $P=0.14$).

None of the 23 nests examined were destroyed by pine martens or other predators.

Discussion

Our experiment showed that even a short-term nest predation risk due to an American mink increased nest-hole shift and breeding dispersal distances of male Tengmalm's owls. The distance between nests in consecutive years was at least 3 times larger in the treatment than in the control group, although the distance to the nearest unoccupied nest-box did not differ between the two groups. After predator simulation, males in the following year apparently attracted females to breed in a nest-box where the nest predation risk was expected to be lower (see also Hakkarainen and Korpimäki 1996). Nest-hole shift and long breeding dispersal distances probably decrease the risk of nest predation, because pine martens seem to revisit nest-holes they have found (Dow and Fredga 1983; Sonerud 1985).

A principal objective in research design should be to maximize the power of experiments by decreasing experimental error and increasing the precision of parameter estimates. In this study, we could exclude the effects of several factors between the treatment and control groups, which could influence dispersal distances such as age of individuals, breeding performance, territory quality, prey availability, density and quality of nest-boxes. This is important, because there is evidence that breeding dispersal distances and the probability of territory shift can be associated with territory quality (e.g. Sonerud 1985; Bollinger and Gavin 1989; Korpimäki 1993; Newton 1993; Wiklund 1996b), earlier breeding success (e.g. Newton and Marquiss 1982; Sonerud 1985; Pärt and Gustafsson 1989; Bollinger and Gavin 1989; Beletsky and Orians 1991; Wiklund 1996b), age of individuals (e.g. Korpimäki et al. 1987; Newton and Marquiss 1983; Newton 1993; Wiklund 1996b) and food abundance (e.g. Korpimäki 1993).

Despite the large body of literature published on various consequences of dispersal, surprisingly, the question of why particular dispersal strategies evolve has received much less attention (Dieckmann et al. 1999). In this study, we were able to examine the causal relationship between nest predation risk and breeding dispersal. The results from our experiment agree with those of a few other experiments conducted with birds. For example, Haas (1998) showed that small passerine birds subjected to experimental nesting failure returned at a significantly lower rate to their breeding site than birds which bred successfully. As far as we know, in mammals no experiments have been done to test the effects of predation risk on breeding dispersal distances. In conclusion, experimental tests on the mechanisms of dispersal in many organisms remain scarce, which probably is due to the fact that such field studies are extremely difficult to conduct within an appropriate spatial and temporal scale.

Our results are consistent also with earlier observational studies. For example, 89% of female goldeneyes, *Bucephala clangula*, shifted nest-box after having a clutch preyed upon, whereas among successful nests only 45% of females changed nest-box between the consecutive breeding seasons (Dow and Fredga 1983). In merlins (*Falco columbarius*), Wiklund (1996b) showed that nest predation resulted in a lower return rate of females to the breeding population. Results of observational studies, however, may be affected by factors other than predation risk, like individual or territory quality. For example, in this study, individuals that failed in their nesting attempts, had a high probability of failure in the following breeding season, whereas among successful breeders the probability of nesting failure was low. Similarly, habitat quality may also be related to predation risk. For example, nest predation risk may be higher at the edges of forests (Andren 1995), and these sites may also be suboptimal habitats for our study objects and may be occupied by subdominant and poor-quality individuals. In this case, we cannot be sure whether predation risk, habitat characteristics, or individual quality drive breeding dispersal of individuals. More experimental studies on nest predation avoidance, therefore, are needed to avoid confusing interpretations of the results.

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