Predation Risk of Tawny Owl Strix aluco Nests in Relation to Altitude, Breeding Experience, Breeding Density and Weather Conditions

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Predation risk of Tawny Owl *Strix aluco* nests in relation to altitude, breeding experience, breeding density and weather conditions

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Nest predation was studied in a population of Tawny Owls *Strix aluco* in the Duna-Ipoly National Park, Hungary during the period 1992–2009, and related to the choice of nesting sites at different altitudes, the breeding experience of males, and weather conditions. The use of nesting sites at high elevations reduced the risk of nest predation in comparison to lower elevations, where breeding territories occur at a higher density. Also, the risk of nest predation decreased as the local breeding experience of males increased. Adverse weather conditions, i.e. long-lasting snow cover, increasing breeding density, and later laying dates enhanced the probability of breeding failure by nest predation. Broods were depredated in the nestling period rather than during incubation.

Key words: breeding experience, nest predation, nest-site choice, *Strix aluco*, Tawny Owl

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Nest predation risk is an essential component of breeding habitat quality and often is the most important cause of complete breeding failure in birds (Ricklefs 1969, Martin 1992). Nest predation risk may be related to differences in individual skill and experience (e.g. Haskell 1994). Consequently, nest predation risk is probably associated with the age of breeding individuals (Forslund & Pärt 1995, Pärt 2001). Additionally, it may be expected that along an altitudinal range with different weather conditions, the rate of predation will vary (Badyaev & Ghalambor 2001). At high altitudes birds often breed at lower densities because of adverse weather conditions, but may suffer less nest predation than at low elevations.

For owls and other raptors, nest predation can be an important factor affecting population processes (Petty et al. 2003, Sunde 2005, Sergio & Hiraldo 2008). For example, predation by Ural Owls *Strix uralensis* decreased the size of the breeding population of Tengmalm's Owls *Aegolius funereus* (Hakkarainen & Korpimäki 1996), while predation by Eagle Owls *Bubo bubo* affected the population density of Tawny Owls *Strix aluco* (Sergio *et al.* 2003). Experimentally increased nest predation risk enhanced breeding dispersal of Tengmalm's Owls (Hakkarainen *et al.* 2001). Studies on the antipredator behaviour of owls showed that nest defence is an important reproductive investment that increases successful breeding. Nest defence may be, however, costly in terms of energy and includes the risk of injury or even death (Wallin 1987, McKell Sproat 1993). Nevertheless, it is suggested that during the nestling period parents will spend more time engaging in intense defence activity, and take greater risks to defend their offspring (Galeotti *et al.* 2000).

We carried out a study on the reproductive performance of Tawny Owls, a sexually dimorphic, monogamous and single-brooded species which is resident in the Palearctic region. An earlier study showed that the breeding success of Tawny Owls varied with the quality of territories found at different altitudes (Sasvári *et al.* 2009). At low elevations, where food was in plentiful supply and owls bred at high densities, the parents produced more fledglings than at higher elevations. In addition, it was shown that adverse weather conditions, defined as ground snow cover during incubation and in the early nestling period, negatively influenced reproductive performance (Sasvári *et al.* 2004, Sasvári & Nishiumi 2005).

Tawny Owl males need to occupy and defend territories with sufficient resources to supply females during incubation and feed both the females and nestlings in the brooding period (Mikkola 1983). Hence, the breeding experience of males presumably plays a larger role in habitat choice than the experience of females. Also, in Tawny Owls older parents with more foraging experience had a greater ability than younger parents to choose alternative prey (mainly birds) in cases where the availability of the preferred prey (small mammals) was insufficient; older parents thereby achieved higher productivity (Sasvári *et al.* 2000). In breeding seasons with adverse weather, young parents started breeding later, which might be attributed to reduced availability of small mammal prey due to snow cover (Sasvári *et al.* 2000). It was hypothesized that older owls may have better knowledge of the breeding habitat and are expected to choose a territory that minimizes the risk of nest predation.

The aim of this study is to assess the predation risk on Tawny Owl nests in relation to altitude, the breeding experience of males, breeding density, weather conditions and laying date. We used data on nest predation recorded throughout an 18-year study period in Duna-Ipoly National Park in Hungary.

Methods

Twenty two artificial 'colonies' for breeding Tawny Owls were situated in a mixed oak/hornbeam/beech Quercus-Carpinus-Fagus forest with 40–60 year old trees in the Duna-Ipoly National Park, 30 km northwest of Budapest, Hungary (47°35'N, 19°02'E) from 1992–2009. The nest-box colonies were separated by 2–5 km, and each colony consisted of eight nestboxes, spaced 300–600 m. The 22 nestbox colonies, totalling 176 nestboxes, covered a total area of 18 × 23 km. The altitudinal range of the study area was 560 m (120–680 m) and was divided into low (<400 m) and high elevations (≥400 m), each containing 11 nestbox colonies, each with 8 nestboxes.

Nestboxes were checked between the end of January and the middle of June. When a nest with a clutch was detected, the nestbox was checked at 4–8 day intervals. Laying date was defined as the day the first egg was laid. If first egg-laying, or any other event regarding the clutch or the brood, occurred between two visits, the day half-way between visits was recorded. Each year, the interval between the first egg of the first clutch and the first egg of the last clutch was equally divided into three periods: early, mid and late laying date. Males, captured by placing a net over the entrance of the box while the birds were inside, were marked with different combinations of coloured rings to enable individual identification throughout subsequent breeding years. Male age was determined by the pattern of the primaries and secondaries (Petty 1992). Breeding density was calculated as the occupation rate of the nestboxes (maximum 8) in the nestbox colony.

A nest was recorded as predated when all eggs or nestlings had disappeared, and remnants of egg shells or feathers or corpses were found in the nestbox. Remains of fur and faeces in or near the nestboxes showed that the most frequent predators were Polecats *Mustella putorius* and Beech Martens *Martes foina*.

We evaluated the risk of mortality by predation on individual nests, ignoring the possibility that the offspring in some nests might be reared by males that had already been included in the study in previous years. Nevertheless, we considered that prior breeding experience of males might influence the likelihood of nest survival. Hence the nests were separated into three groups: males in their first, second, or third or more breeding season. We identified 110 males which bred in their first breeding year in the study area, 94 males which bred in their first and second years, and 82 males who had bred three or more times (within the study area). The rate of predation was thus recorded on 286 nests with males in their first breeding year, 176 with males in their second breeding year, and 82 where males had three or more years breeding experience. The rate of nest predation was evaluated separately for nests in the low and the high altitude range.

Weather conditions in the breeding season were quantified by recording the number of snow days. A snow day was defined as a day with ground snow covering the whole study area. Each year the recording of snow days started on the day the first egg was found. The number of snowy days could be stated with a confidence of ±1 day deviance, depending on the contribution of rangers working in the National Park. The number of snow days was averaged for the 18 study years (mean 15.6 ± 7.9; range 4–26), and years were classified as mild and adverse breeding years depending on whether they contained a lower than average or larger than average number of snow days (mild years were 1993, 1995, 1997, 2000, 2003, 2007–2009; adverse years were 1992, 1994, 1996, 1998, 1999, 2001, 2002, 2004–2006). In adverse breeding years snow covered the ground not only during the incubation period but also in the early nestling period.

The relationship between predation risk and male breeding experience, altitude of the nest site, breeding density, weather conditions and laying date was analysed with Generalized Linear Mixed Models (GLMMs) with Gaussian error distribution (Pinheiro & Bates 2000). Chi-square tests were applied for goodness of fit to a null model of constant frequency. The breeding experience of males, nest altitude, breeding density, weather condition and laying date were modelled as fixed effects. Significance of fixed effects was based on *F*-tests. We pooled data from eighteen years, hence we modelled year as a random effect. Nest identity and male identity were also modelled as random effects in order to avoid pseudo replication. The significance of the random effect variable was assessed by a likelihood ratio test between models with and without the random effect (Pinheiro & Bates 2000). The likelihood ratios test was calculated as –2× the difference in log-likelihood between two hierarchical models, and tested as a chi-square value with one degree of freedom (the difference in degrees of freedom between the two models tested). Analyses were carried out in SPSS v. 12.0 (SPSS Inc.)

Table 1. Summary of GLMMs examining which factors influence nest predation in Tawny Owls. Fixed effects: breeding experience, altitude range, breeding density, weather condition, and laying date. Random effects: year, male identity, and nest identity.

Fixed effects	*df*	*F*	*P*
Breeding experience	2,541	6.31	< 0.001
Altitude range	1,542	5.50	0.021
Breeding density	7,536	2.49	0.019
Weather condition	1,542	6.47	0.012
Laying date	2,541	3.42	0.033
Random effects	*df*	χ^2	*P*
Year	1	5.3	< 0.023
Male identity	1	8.2	< 0.004
Nest identity	1	6.4	< 0.011

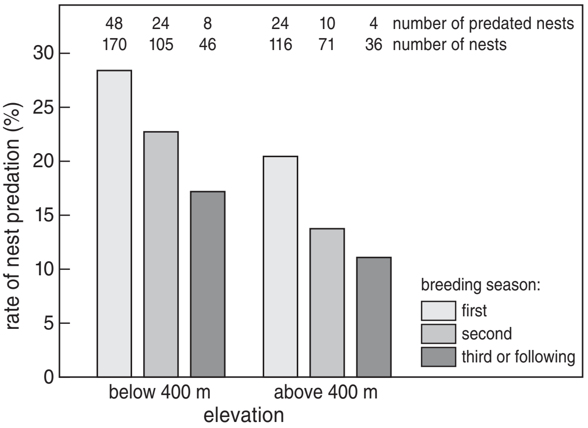

Figure 1. Rate of nest predation (%) experienced by males in their first, second, or third or following breeding seasons, at low or high altitudes. Numbers above the columns denote number of predated nests; numbers below the columns in parentheses denote the number of nests.

Results

At low altitudes, 65 (38.2%) males attempted to breed only once during the study period, 59 (34.7%) twice, and 46 (27.1%) more than twice ($\chi^2_2 = 6.4$ $P < 0.05$). At higher altitudes 45 (38.8%) males attempted to breed only once during the study period, 35 (30.2%) twice and 36 (21.0%) more than twice ($\chi^2_2 = 6.1$, $P < 0.05$). Pooled data showed that males attempted breeding more often at lower altitudes than at high altitudes. During the 18 study years, the mean number of occupied nestboxes per nestbox colony (averaged per breeding year) was higher at low altitudes than at high altitudes (mean ± SD: 1.54 ± 1.07 and 0.94 ± 0.78, $t_{17} = 3.61$, $P < 0.01$). More males occupied nestboxes in the lower altitude range regardless of whether they were in their first, second, or greater than second breeding year ($\chi^2_1 = 8.2$, $P < 0.05$, Fig. 1)

In total we recorded 118 fatal nest predations during 544 breeding attempts by Tawny Owl males during the 18 years. This means that overall 21.7% of the broods were depredated. Of the 286 males in their first breeding season, 72 (25.2%) suffered nest predation; 34 (47.2%) attempted a second breeding year in the study area. Of these 34 males, 19 males (55.9%) changed nest site after having suffered predation, but only four (11.8%) changed from nest sites at high altitudes to the low altitude range. Of the 176 males in their second breeding year 36 (20.5%) males lost their nests to predators and 12 males (33.3%) attempted to breed the following year in the study area, six of these 12 males (50.0%) changed nest sites, but only two (16.7%) changed from nest sites at high altitudes to the low altitude range. Of the 82 males with more than two years breeding experience, 12 males (14.6%) failed to breed due to predation and three (25.0%) changed nest sites, but none changed their altitude range.

Nests of males who were breeding in the study area for the first time were more likely to be depredated; the rate of predation declined with breeding experience in the study area (Table 1, Fig. 1). Males nesting at high altitude were less likely to suffer predation than those nesting at low elevations. Year, male identity and nest identity significantly influenced the predation rate (Table 1).

Ground snow cover during the incubation and nestling stage, and later laying date significantly increased the risk of nest predation (Table 1). In years with extended periods of snow cover more nests were predated in the nestling phase than during incubation (46 and 28%, $\chi^2_1 = 8.6$, $P < 0.01$), but no significant difference in nest predation between the nestling phase and incubation phase was detected in mild breeding seasons (25 and 19%, $\chi^2_1 = 1.7$, ns).

Discussion

In Tawny Owls, nest predation risk was found to be density-dependent. We also detected an age-related reduction in predation rate. Furthermore, adverse weather conditions, i.e. extended periods of ground snow cover, and later laying dates increased the chance of nest predation.

Territorial species, such as the Tawny Owl, are predicted to display an ideal despotic distribution in habitat choice in which high quality individuals monopolize high quality sites (Fretwell & Lucas 1969, Zimmerman *et al.* 2003). Territorial behaviour regulates access to high quality sites, and lower quality individuals are relegated to progressively inferior territories. Since superior habitats are the most desirable, territory quality may be measured by the occupancy rate of the specific breeding area (see review in Sergio & Newton 2003). This would mean that the detected high and low settlement densities of Tawny Owls colonies at low and high altitudes respectively indicate that territory quality differs between altitudes. The presumed high quality of occupied territories at lower elevations is indeed reflected in the prey supplied to the broods (Sasvári *et al.* 2009). A previous study comparing the reproductive performance of different bird species over a large altitudinal range (0–4000 m) found no differences in the risk of nest predation between low and high elevations (Badyaev & Ghalambor 2001). Our study however, detected different rates of nest predation over a much smaller altitudinal range. This might be related to a strong correlation between altitude and breeding density. Nest predation is indeed often density dependent (Martin 1988). Predators increase their search intensity with increasing density of prey and, as a consequence, increasing nesting density results in a larger proportion of the nests suffering predation. Several authors have shown density-dependent predation primarily on open nests (Hill 1984, Sugden & Beyersbergen 1986, Martin 1988), however, density-dependent predation has also been documented for hole-nesting birds (Krebs 1971, Dunn 1977). Our studies suggest that Tawny Owls, as a hole nesting species, may also suffer density-dependent predation in the breeding area.

In owls, breeding performance improves with the age of the parent (Saurola 1989, Brommer *et al.* 1998, Pärt 2001, Linkhart & Reynolds 2006). The reduction in nest predation with age detected in this study suggest that in the Duna-Ipoly National Park population breeding performance improves with age. The age-related reduction in nest predation rate might be explained by an increased intensity and effectiveness of antipredator activity in older parents. Nevertheless, a possible consequence of nest defence against predation is that, to avoid predators, males may change nest sites in subsequent breeding years. Several studies suggest that animals gather information about the quality of the habitat prior to making a decision about their breeding territory (e.g. Danchin *et al.* 2004). This might include information on the location or behaviour of predators (Thomson *et al.* 2006, Lima 2009, Morosinotto *et al.* 2010). Future studies are needed to clarify which factors are responsible for the reduced nest predation rate in owls with more breeding experience.

In Tawny Owls, nest predation risk also increased with laying date. Several studies have shown that breeding success decreases over the course of the breeding season (Verhulst & Tinbergen 1991, Daunt *et al.* 1999) and it may be that nest predation plays an important role in declining reproductive performance late in the breeding season.

We showed that the risk of nest predation increased in adverse weather conditions. Remains of fur found in the nests indicated that the main predators on Tawny Owl nests are mustelids, who favour preying on small mammals. When snow cover prevents both Tawny Owls and mustelids from hunting small mammals, they both choose alternative prey. Tawny Owls hunt mainly songbirds, and mustelids change their foraging habitats and search for food in trees, where they find Tawny Owl nests.

In summary, we found that the higher settlement densities of Tawny Owls at low rather than higher elevations reflected the higher quality breeding habitat of these lower territories. Although parents nesting at high densities suffered higher nest predation, the predation risk declined with increasing breeding experience and older birds were more likely to nest at lower altitudes. Adverse weather, with long-lasting snow cover, enhanced the risk of nest predation, and the main predation threat to the young was in the nestling period rather than during incubation.

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Samenvatting

De auteurs bestudeerden de kans op nestpredatie in een populatie van Bosuilen *Strix aluco* in de bergen van het Duna-Ipoly Nationale Park in Hongarije tussen 1992 en 2009. Ze relateerden de keuze voor nestlocatie met hoogte, de ervaring van mannen en de weersomstandigheden. Hoger in de bergen was het risico van nestpredatie beperkter dan lager in de bergen, waar de uilen in hogere dichtheden nestelden. Het risico van nestpredatie nam met de lokale broedervaring van de mannen af. Slecht weer, zoals sneeuwbedekking die tot laat in het seizoen aanhield, hogere broeddichtheid en latere legdatum deden de kans op het mislukken van het nest door predatie toenemen. De meeste legsels werden gepredeerd tijdens de jongenfase en niet zozeer tijdens het broeden. (YIV)

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