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Mammalian nest predation induces small-scale nest site switching in territorial tawny owl (*Strix aluco*) females

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Nest predation is a major factor affecting fitness in birds. Individuals are expected to respond to nest predation by selecting safe nesting sites and by moving away from risky sites. Thereby, perceived risk or experience of predation should lead to shifts in nest site selection. Experimental studies on behavioural and life-history consequences of nest predation have traditionally manipulated the risk of predation and studied the immediate consequences thereof. Fewer studies have however analysed the behavioural consequences of perceived predation risk to future breeding events and we know little about how sedentary territorial species respond to nest predation. We experimentally manipulated tawny owl (*Strix aluco*) breeding nest site choice by providing an additional alternative nest box within the territory, nearby the original nesting sites. The new nest box was provided either after a successful reproductive event (control group), or following a failed reproductive event caused by a nest predator (i.e. pine marten *Martes martes,* predated group). We show that tawny owls generally switched to the alternative nest site in the current breeding season when the nest was predated in the previous year, whereas they used the same nest after a successful breeding. We found no effects of previous predation experience on the probability to breed nor on clutch size. We conclude that small scale movement within the territory are used by tawny owls to minimize predation risk and that the owls use information on past predation events and nest failure to optimize their breeding decision in the following season.

1. Introduction

One of the most important causes of reproductive failure in birds is nest predation (Ricklefs 1969, Martin 1993, Lima 2009). For this reason, life histories are expected to evolve in response to the risk of nest predation (Martin 1995). Nest site choice is a crucial antipredator response for animals, a decision that can strongly affect both parents and offspring fitness and survival. Birds are known to occupy more often sites with low predation risk and to invest more in reproduction in safer sites (Fontaine and Martin 2006a, b, Morosinotto *et al*. 2010, Zanette *et al*. 2011). Following a nest predation event, a bird can renest in a different site within the same territory or it can move to a different territory (Caro 2005, Lima 2009, Chalfoun & Martin 2010, Ibáñez-Álamo *et al*. 2015) in an attempt to reduce the risk of predation (Caro 2005). This is because predators may remember the spatial location of cavities and nest sites where they found prey in previous years and may return to the same area in subsequent breeding seasons (Sonerud 1985). Furthermore, in long-lived species individuals may skip breeding in one breeding season if the perceived risk of predation is high (Quakenbush *et al*. 2004, Goutte *et al*. 2011, Öst *et al*. 2018).

A common response to nest predation risk is to engage in breeding dispersal by changing territory to a safer breeding site for future attempts (Lima 2009). For example, Tengmalm's owls (*Aegolius funereus*) are both more likely to disperse and to disperse longer distances after they have been experimentally exposed to a simulated mammalian nest predation attempt (Hakkarainen *et al*. 2001). Such long-distance breeding dispersal may nevertheless involve costs, especially in territorial species, since nest sites may be limited, they may need to claim a new territory involving competition with conspecifics, and they need to learn to use the foraging grounds in the new territory.

On the other hand, some species, such as pinyon jays (*Gymnorhinus cyanocephalus*) may move only within the territory and choose a less exposed nest site to renest in after its nest has been predated (Marzluff 1988). Such small scale movements may improve reproductive success, since also sparrow hawks (*Accipiter nisus*) reusing their nest sites suffer higher predation risk than those individuals who build new ones, even within rather small distances of 10–40 meters away from the original sites (Otterbeck *et al*. 2019). In Tengmalm's owls, females prefer to nest in new nest-boxes over older ones to reduce the risk that a nest predator would locate them (Sonerud 1985). Furthermore, in Tengmalm's owls predation risk decreased considerably in nest-boxes that were relocated within the same territory after a predation event compared to nest-boxes that remained in the same original position (Sonerud 1989). However, experimental studies of small scale movements after nest predation are scarce, although such responses to nest predation are likely to be commonplace in birds (Caro 2005, Lima 2009).

Nest predation risk may also affect reproductive output, because reproductive effort is expected to be smaller when the value of the brood decreases due to the risk of predation (Martin 1995, Doligez & Clobert 2003). For example, in Siberian Jays (*Perisoreus infaustus*) those females, which were exposed to predator calls laid smaller clutches than those exposed to non-predator calls or no calls at all (Eggers *et al*. 2006). Similarly, Morosinotto *et al*. (2010) found that pied flycatchers (*Ficedula hypoleuca*) breeding close to active pygmy owl (*Glaucidium passerinum*) nests laid smaller clutches than those breeding in the absence of a pygmy owl nest.

Our study species, the tawny owl (*Strix aluco*), is a sedentary highly territorial forest-dwelling owl (Sunde 2011) with 80–90% site fidelity and 80–85% mate fidelity between years (Saurola 1987). Females lay 2–6 eggs and incubate them, brood the young and guard the nest, whereas males are the main food providers for the offspring (Mikkola 1983). The number of breeding events mainly determines the fitness of tawny owls and it is commonplace that they skip breeding, but still remain territorial, under unfavourable food conditions (Brommer *et al*. 2005, Karell *et al*. 2009, Hoy *et al*. 2016).

In this paper we investigated the behavioural response of nest box breeding territorial female tawny owls in response to nest predation events which occurred in the previous year. Nest failure is an important determinant of fitness in tawny owls since it also reduces the probability of a female to breed in the following year (Hoy *et al*. 2016). Nest failure is common in tawny owls: in a long-term study of our study population between 13–45% of the breeding owl pairs were found to fail to fledge young and this failure is often caused by pine marten (*Martes martes*) predation at an early stage of breeding (Ericsson *et al*. 2014). Also in the post-fledging period mammalian predation is the major cause of mortality (Sunde 2005). To study the consequences of predation-induced nest failure we provided alternative nest boxes in territories, which had experienced predation (hereafter "predated") and in territories which bred successfully

Table 1. Experimental set up per year. The “number of territories” refers to the experimental territories in which an alternative nest box was provided in the autumn of the “year of experiment”, divided respectively in “predated nests” and “control (successful) nests”. Females recaptured in the following breeding season (in the “year of response”) are shown as “N total (N predated, N controls)”.

Year of experiment	N territories	Predated nests	Control nests	Recaptured
2005	10	5	5	7 (4, 3)
2006	5	3	2	0
2007	6	4	2	4 (2, 2)
2008	7	5	2	5 (4, 1)

(hereafter “controls”) to observe the tawny owls’ breeding decisions in the following season. Based on these notions we predicted that 1) predation decreases the probability of the female breeding in the territory in the following year, and 2) predation increases the probability that the female will switch nest box, but not switch territory because of high mate- and site fidelity.

2. Material and methods

The study was conducted in an approximately 1,000 km^2 sized area consisting of mixed boreal forests, agricultural areas and lakes located west of Lake Vättern in Sweden (58°37’47.6”N, 14°18’41.9”E). In the early 1990s the area was equipped with tawny owl sized nest boxes (size height: 500mm, width: 300mm, depth: 320mm, opening diameter 135mm) in suitable deciduous forests, mixed coniferous forests, larger parks and semi-open pastures in the area. This nest box breeding tawny owl population has been monitored, and nearly all breeding females and their offspring have been ringed, from 1996 onwards by authors PE, DE,KH, L-ON (see Ericsson *et al*. 2014 for details).

Within this long-term monitoring project, we experimentally manipulated the nest site options in 28 territories. These experimental manipulations of nest site options were spread over 4 years, 2005–2008 (Table 1). In each of the territories in the experiment an alternative nest box was placed in the close vicinity of the existing nest box (between 25 and 100m) in autumn after breeding, both in territories that were predated during breeding (17 nest sites, hereafter “predated”) or from which offspring successfully fledged (11 nest sites; hereafter “control”). The year in which a territory was either a “predated nest” or a “control nest” and subsequently equipped with an alternative nest box is defined as “year of experiment”, whereas the following year is defined as “year of response” (see table 1). All boxes were cleaned each year and a fresh sawdust layer was added on the bottom. Each of the 28 territories was included only once in the nest site option experiment, *i.e.* the effect of an alternative nest box from the “year of experiment” to the “year of response” on female breeding site choice was monitored only one time in each territory.

All breeding females in these 28 territories were caught during breeding with a net in front of the nest box opening, ringed, measured and the clutch size was determined. The territories were visited around hatching to estimate the number of hatchlings and age of nestlings. The brood was considered predated when eggs were clearly eaten by a pine marten. Pine martens leave marks in the egg shells as they open them with their teeth and eat the contents. The marten often leaves also other signs of its presence in the nest box (hair tufts in the entrance, excrements on the nest box roof). The chicks in the successful broods were ringed prior to fledging when they were between 16–26 days old.

In the following breeding season (year of response) both the original and the alternative nest boxes were checked in the same way. We recorded whether either the original or the alternative nest box in each territory was occupied or not (”probability to breed in the territory”) and if the nesting attempt was in the original nest box or in the alternative nest box (i.e. moved or stayed, “movement”). All breeding females were captured, their identities were confirmed and their reproductive output was measured. One of the females that bred in the following season (year of response), did not stay in the original box nor chose the alternative box we provided, but moved to a different territory after the predation event (2.4 km away from the original nest box). We consider this a "movement" to an alternative nest box in the results. Discarding this observation (i.e. considering it as "not breeding") does not change the interpretation of the results.

We used a binomial GLM to analyse the "probability to breed in the territory" (in either of the two nest boxes available per site) as a function of predation ("predated" / "control") and year. Similarly, we used a binomial GLM to model the "probability of movement" ("moved to the new nest box" / "stayed in the original one") as a function of whether the nest was predated or not ("predated" / "control"), while accounting for annual differences. Significance of the effects were tested with z-tests of the slopes, and the beta values ± SE of the slopes are presented in those cases where they are significant. We used a linear model LM to inspect the effect of nest predation on clutch size. We modelled the change in clutch size from one year to another by calculating the proportional change in clutch size between years

$$\Delta\text{clutch size} = (\text{clutch size}_{\text{year2}} - \text{clutch size}_{\text{year1}}) / \text{clutch size}_{\text{year2}}$$

The model included the explanatory variables "Predation" and "Year" and significance was tested with an F-test. In this model we did not consider the effect of "Movement" because of the observed strong correlation between "Predation" and "Movement".

In addition to the GLMs we used Fisher's exact test to confirm the GLM results by analysing the contingency table data between predated and control territories on number of females which skipped breeding in the "year of response" and the number of females which moved to the replacement box in the "year of response". All statistical models were run in R3.4.2 (R Development Core Team 2016).

3. Results

Of the 17 predated and the 11 control territories involved in the experiment 6 females made a breeding attempt in the same nest box in the following year ("year of response"), 10 females switched to the alternative box, 4 females were replaced by new breeders and 8 territories were not occupied. Predation occurred before hatching in all 17 predated nest cases.

3.1. Probability to breed in the territory

Among the 12 territories where the female was replaced or there was no breeding attempt in the "year of response" 58% (7/12) had their nest predated in the previous year and 42% (5/12) were successful (controls) in the previous year. Thus, females were as likely to skip breeding independently if they reared a predated or a successful nest (Fisher's exact test: 1.18, $P > 0.99$). Since the nests included in the experiment were from different years we used a binomial GLM to test the effect of predation on the probability to return while accounting for yearly variation. There was no effect of predation on the probability to return to breed in the following year ($z = 0.25$, $N = 28$, $P = 0.80$). The probability to return did not vary between years ($z < 0.17$, $N = 28$, $P > 0.86$).

3.2. Probability of moving

Among the 16 females that bred in the "year of response" 10 had their brood predated and 6 were successful in the previous year. The females whose broods were predated in the previous year had a higher probability to move to the alternative nest box than expected (9/10 switched nest boxes), whereas the majority of the females with successful nests in the "year of experiment" (5/6) did not change nest box (Fisher's exact test: 29.19, $P = 0.008$). A binomial GLM confirmed this pattern (Fig. 1): predation had a strong effect on the probability to move ($b = 3.71 \pm 1.53$, $z = 2.422$, $N = 16$, $P = 0.015$), whereas there were no differences in this response between years (year 2007: $z = -0.091$, $P = 0.928$; year 2008: $z = 0.343$, $P = 0.732$). Repeated predation in both the "year of experi-

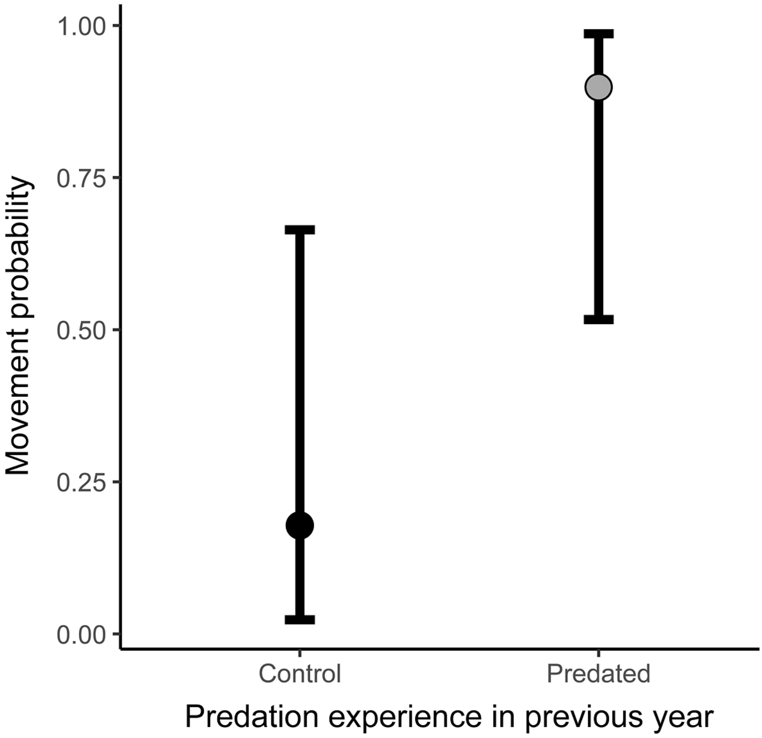

Fig 1. Least square means (± upper and lower asymptotic confidence limits) of the probability of tawny owl female nest site switching as a response to predation (control vs predated) in the previous breeding attempt. The estimates are averaged over the level of year. See text for statistical test.

ment" and in the "year of response" occurred in 1 out of the 16 nests. This female experiencing predation in both years moved to the alternative nest box in the "year of response".

3.3. Effect of predation on clutch size next year

The mean clutch size in the year after predation was 3.81 ± 0.98 (SD). The effect of predation on reproductive output in the following year was modelled with a Gaussian linear model. Predation in the year of response did not affect clutch size ($F_{1,12} = 0.003$, $P = 0.96$), but clutch size varied between years ($F_{2,12} = 6.67$, $P = 0.01$).

4. Discussion

Our results show that a nest predation event occurring in the previous year clearly affected nest-site choice of tawny owls in the current breeding season. Adult tawny owls rarely change territories, but little is known how nest predators impact the within-territory movement decisions of the tawny owls. We found that nearly all tawny owl females that failed to raise a brood because of nest predation decided to use the alternative nest box within the territory, whereas the females that successfully fledged young almost never switched nest box. Only one of the females in the study was recaptured away from its original territory after a predation event while none of the control females did, as expected since breeding dispersal away from the territory is rare in the tawny owl (Saurola 1987).

Our results clearly suggest that nest predation induced female tawny owls to switch to a presumed safer (new) nesting site in the following breeding event. We acknowledge that our sample size in this experiment is fairly limited, but the results are convincingly robust regardless, and clearly points out that a female tawny owl avoids laying her clutch in a cavity where she has experienced predation of her eggs in the previous season. This is in agreement with previous results on Tengmalm's owls where nest predation rate was lower in nest boxes that were relocated within the territory after a predation event compared to nest boxes that remained in the exact same location in several years (Sonerud 1989). In Tengmalm's owls the probability of nest predation in a breeding attempt was higher if the nest box was predated upon by pine marten also in the previous year (Sonerud 1985) and this was interpreted as a memorized search image in pine martens.

However, we did not see a pattern with predation in consecutive years as only one nest was predated in the following year ("year of response"). On the other hand our findings suggest that female tawny owls are able to distinguish between a risky nest site and a potential safer one even one year after the nest predation has occurred. These notions suggest that the tawny owls can memorize predation events, which occurred in previous breeding attempts and use this information in future breeding decisions. This finding is in line with the results of Fontaine & Martin (2006b) who demonstrated by experimentally manipulating predation risk that birds can assess increase or decrease in nest predation risk and alter their reproductive strategies accordingly.

Breeding dispersal, here defined as moving to a new breeding territory, is one way of avoiding repeated nest predation by mammalian predators. This strategy was found to be adopted by Tengmalm's owl where experimentally induced predation risk by pine marten led the male owls to disperse to new territories in the following year (Hakkarainen *et al*. 2001). In Tengmalm's owl males are territorial, whereas the females are more dispersive (Korpimäki & Hakkarainen 2012), and as comparison, in tawny owls both females and males are highly territorial (Southern & Lowe 1968, Southern 1970, Hirons 1985, Sunde 2011) and site-tenacious with high mate-fidelity throughout life (Saurola 1987).

In our data on tawny owls we found that only 1/10 tawny owl females dispersed to a new territory after a predation event and none of the control females moved. Predation seems not to affect the probability to skip breeding or to move out of the study area as there was no difference in the probability to breed between those females who had their nest predated and those that were successful in the previous year. Skipping a breeding event seems therefore not to be a major response to nest predation risk / experience in tawny owls, but mainly driven by food availability as previously acknowledged (Southern 1970, Roulin *et al*. 2003, Karell *et al*. 2009, Millon *et al*. 2014, Hoy *et al*. 2016, Saurola & Francis 2018).

Altogether, these findings suggest that, in terms of fitness, knowledge of the hunting grounds and resting sites in the territory of the long-lived tawny owl is more beneficial than changing territory due to nest predation, and thus the benefits of remaining in the territory outweighs the risk of a repeated predator attack. However, a predation event clearly induces a shift in nesting site within the territory and pinpoints that the owls do memorize and react to a predation event. Future studies should aim at comparing these nest site choice dynamics with areas where nest predators are absent and where the predator community differs from ours, where pine martens is the major nest predator.

For forest dwelling owls, which require large cavities for breeding, nesting sites are rare in managed forests (Lohmus 2003). Therefore, since tawny owls readily breed in nest boxes, the provision of replacement nest boxes in their territories may be a good approach to ensure long-term maintenance of successful tawny owl reproduction, especially in areas with high abundance of mammalian predators such as pine marten.

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Bopredation av mård (*Martes martes*) föranleder byte av bohål hos territoriella kattugglehonor (*Strix aluco*)

Bopredation är en viktig faktor som påverkar förökningsframgången. Individer förväntas reagera till följd av bopredation genom att sträva efter att välja en säker boplats och genom att flytta bort om boplatsen blir osäker. Av den orsaken förväntas individers erfarenhet av bopredation att påverka valet av boplats. Experimentella studier av konsekvenser av bopredation har vanligtvis manipulerat predationsrisken och studerat följderna av denna. Färre studier har analyserat beteendekonsekven-

serna av erfarna händelser av bopredation inför kommande förökningsförsök, och det är allmänt taget dåligt känt hur stationära revirtrogna arter reagerar på bopredation.

Vi manipulerade experimentellt kattugglehonors val av boplats genom att förse dem med en ny alternativ holk inom reviret i närheten av den gamla holken. Den alternativa holken sattes upp efter en framgångsrik häckning (kontrollgrupp) eller efter en misslyckad häckning som förorsakats av skogsmård (predationsgrupp).

Våra resultat visar att kattugglan i regel bytte till den alternativa holken inför den kommande häckningen om dess kull hade blivit prederad av skogsmård under förra häckningen, medan de använde den gamla holken om häckningen var framgångsrik. Sannolikheten att kattugglehonan häckade i reviret påverkades inte av bopredation föregående år och kullstorleken var lika i båda experimentella grupperna. Vår slutsats är att småskalig flyttning inom reviret utövas av kattugglan i mån av möjlighet för att minimera predationsrisken och att kattugglan använder information från tidigare erfarenheter av bopredation och misslyckade häckningar för att optimera kommande häckningar.

References

Brommer, J.E., Ahola, K. & Karstinen, T. 2005: The colour of fitness: plumage coloration and lifetime reproductive success in the tawny owl. — Proceedings of the Royal Society of London, series B 272: 935–940.

Caro, T. 2005: Antipredator defenses in birds and mammals. — The University of Chicago Press, Chicago, USA.

Chalfoun, A.D. & Martin, T.E. 2010: Parental investment decisions in response to ambient nest predation risk versus actual predation on the prior nest. — Condor 112: 701–710.

Doligez, B. & Clobert, J. 2003: Clutch size as a response to increased nest predation rate in the Collared Flycatcher. — Ecology 84: 2582–2588.

Eggers, S., Griesser, M., Nystrand, M. & Ekman, J. 2006: Predation risk induces changes in nest-site selection and clutch size in the Siberian jay. — Proceedings of the Royal Society of London, series B 273: 701–706.

Ericsson, P., Nilsson, L.-O., Haglund, K. & Ericsson, D. 2014: Breeding biology of a Tawny Owl *Strix aluco* population in southwestern Sweden – a 15 year survey. — Ornis Svecica 24: 41–50.

Fontaine, J.J. & Martin, T.E. 2006a: Habitat selection responses of parents to offspring predation risk: an experimental test. — American Naturalist 168: 811–818

Fontaine, J.J. & Martin, T.E. 2006b: Parent birds assess nest predation risk and adjust their reproductive strategies. — Ecology Letters 9: 428–434

Goutte, A., Kriloff, M., Weimerskirch, H. & Chastel, O. 2011: Why do some adult birds skip breeding? A hormonal investigation in a long-lived bird. — Biology Letters 7: 790–792.

Hakkarainen, H., Ilmonen, P., Koivunen, V. & Korpimäki, E. 2001: Experimental increase of predation risk induces breeding dispersal of Tengmalm's owl. — Oecologia 126: 355–359.

Hirons, G.J.M. 1985: The effects of territorial behavior on the stability and dispersion of tawny owl (*Strix aluco*) populations.— Journal of Zoology 1: 21–48.

Hoy, S.R., Millon, A., Petty, S.J., Whitfield, D.P. & Lambin, X. 2016: Food availability and predation risk, rather than intrinsic attributes, are the main factors shaping the reproductive decisions of a long-lived predator. — Journal of Animal Ecology 85: 892–902.

Ibáñez-Álamo, J.D., Magrath, R.D., Oteyza, J.C., Chalfoun, A.D., Haff, T.M., Schmidt, K.A., Thomson, R.L. & Martin, T.E. 2015: Nest predation research: recent findings and future perspectives. — Journal of Ornithology 156:247–262.

Karell, P., Ahola, K., Karstinen, T., Zolei, A. & Brommer, J.E. 2009: Population dynamics in a cyclic environment. Consequences of cyclic food abundance on tawny owl reproduction and survival. — Journal of Animal Ecology 78: 1050–1062.

Korpimäki, E. & Hakkarainen, H. 2012: The Boreal Owl: ecology, behaviour, and conservation of a forest-dwelling predator. — Cambridge University Press, Cambridge, UK.

Lima, S.L. 2009: Predators and the breeding bird: behavioral and reproductive flexibility under the risk of predation. — Biological Reviews 84: 485–513.

Lohmus, A. 2003. Do Ural owls (*Strix uralensis*) suffer from the lack of nest sites in managed forests? — Biological Conservation 110: 1–9.

Martin, T.E. 1993: Nest predation and nest sites: new perspectives and old patterns. — Bioscience 43: 523–532.

Martin, T.E. 1995: Avian life history evolution in relation to nest sites, nest predation, and food. — Ecological Monographs 65: 101–127.

Marzluff, J.M. 1988: Do pinyon jays alter nest placement based on prior experience? — Animal Behaviour 36: 1–10.

Mikkola, H. 1983: Owls of Europe. — T & AD Poyser, Calton, UK

Millon, A., Petty, S.J., Little, B., Gimenez, O., Cornulier, T. & Lambin, X. 2014: Dampening prey cycle overrides the impact of climate change on predator population dynamics: a long-term demographic study on tawny owls. — Global Change Biology 20: 1770–1781.

Morosinotto, C., Thomson, R.L. & Korpimäki, E. 2010: Habitat selection as an antipredator behaviour in a multi-predator landscape: all enemies are not equal. — Journal of Animal Ecology 79: 327–333.

Otterbeck, A., Selås, V., Tøttrup Nielsen, J., Roualet, E. & Lindén, A. 2019: The paradox of nest reuse: early breeding benefts reproduction, but nest reuse increases nest predation risk. Oecologia 190: 559–568.

Quakenbush, L., Suydam, R., Obritschkewitsch, T. & Deering, M. 2004: Breeding biology of Steller's eiders (*Polysticta stelleri*). — Arctic 57: 166–182.

R Development Core Team 2016: R: a language and environment for statistical computing. —R Foundation for Statistical Computing. Available from: http://cran. r-project.org. Vienna, Austria.

Ricklefs, R.E. 1969: An analysis of nesting mortality in birds. — Smithsonian Contributions to Zoology 9: 1–48.

Roulin, A., Ducret, B., Ravussin, P.-A. & Altwegg, R. 2003: Female colour polymorphism covaries with reproductive strategies in the tawny owl *Strix aluco*. — Journal of Avian Biology 34: 393–401.

Saurola, P. 1987: Mate and nest-site fidelity in Ural and Tawny owls. — In Biology and conservation of northern forest owls (ed. Nero, R.W., Clark, R.J., Knapton, R.J. & Hamre, R.H.): 81–86. U.S. Forestry Services General Technical Report No. RM-142.

Saurola, P. & Francis, C. 2018: Towards integrated population monitoring based on the fieldwork of volunteer ringers: productivity, survival and population change of Tawny Owls *Strix aluco* and Ural Owls *Strix uralensis* in Finland. — Bird Study, DOI: 10.1080/00063657.2018.1481364

Sonerud, G.A. 1985: Nest hole shift in Tengmalm's owl *Aegolius funereus* as defence against nest predation involving long-term memory in the predator.— Journal of Animal Ecology 54: 179–192.

Sonerud, G.A. 1989: Reduced predation by pine martens on nests of Tengmalm's owl in relocated boxes. — Animal Behaviour 37: 332–343.

Southern, H.N. 1970: The natural control of a population of tawny owls (*Strix aluco*). — Journal of Zoology 162: 197–285.

Southern, H.N. & Lowe, V.P.W. 1968: The Pattern of Distribution of Prey and Predation in Tawny Owl Territories. — Journal of Animal Ecology 37: 75–97.

Sunde, P. 2011: What do we know about territorial behaviour and its consequences in tawny owls? — In Ecology and Conservation of European Forest Dwelling Raptors (ed. Zuberogoitia, I. & Martinéz, I.G.): 253–260. Diputación Foral de Bizkaia, Bilbao, Spain.

Sunde, P. 2005. Predators control post-fledging mortality in tawny owls, *Strix aluco*. — Oikos 110: 461–472.

Zanette, L.Y., White, A.F., Allen, M.C., Clinchy, M. 2011: Perceived predation risk reduces the number of offspring songbirds produce per year. — Science 334: 1398–1401.

Öst, M., Lindén, A., Karell, P., Ramula, S. & Kilpi, M. 2018: To breed or not to breed: drivers of intermittent breeding in a seabird under increasing predation risk and male bias. — Oecologia 188: 129–138.