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IS THE LONG-TERM DECLINE OF BOREAL OWLS IN SWEDEN CAUSED BY AVOIDANCE OF OLD BOXES?

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Abstract.—Numbers of Boreal Owls (*Aegolius funereus*) breeding in nest boxes in northern Sweden have declined since the 1980s. The main cause of this decline is thought to be a similar decline in voles, the owls' main prey. However, an alternative reason for the decline might be the aging of nest boxes and the owls' avoidance of old nest boxes to reduce the risk of predation. In this study we tested this alternative hypothesis in an experiment during the first two years of a 3-yr vole cycle by comparing predation and the number of breeding owls in old and new nest boxes at their original location, and old and new nest boxes placed at new locations. Predation was lower at relocated nest boxes, but Boreal Owls showed no preference for any of the four nest-box treatments, and breeding parameters did not vary between treatments. We conclude that the decline in the number of Boreal Owls breeding in nest boxes is real, and not caused by aging of nest boxes.

Key Words: *Boreal Owl*; *Tengmalm's Owl*; Aegolius funereus; *laying date*; Martes martes; *nest cavity*; *predation risk*; *vole cycle*.

¿ESTÁ LA DISMINUCIÓN POBLACIONAL DE *AEGOLIUS FUNEREUS* EN SUECIA CAUSADA POR EL RECHAZO A USAR CAJAS VIEJAS?

Resumen.—Los números poblacionales de *Aegolius funereus* reproduciéndose en cajas nido en el norte de Suecia han disminuido desde la década de 1980. Se piensa que la principal causa de esta disminución ha sido un declive similar en la población de ratones de campo, la principal presa de estos búhos. Sin embargo, una razón alternativa de esta disminución puede ser el envejecimiento de las cajas nido y el rechazo por parte de los búhos de las cajas nido viejas para reducir el riesgo de depredación. En este estudio, probamos esta hipótesis alternativa en un experimento durante los dos primeros años de un ciclo de tres años de ratones de campo, al comparar la depredación y el número de búhos reproduciéndose en cajas nido nuevas y viejas en su ubicación original, y en cajas nido viejas y nuevas colocadas en ubicaciones nuevas. La depredación fue menor en las cajas nidos reubicadas, pero los individuos de *A. funereus* no demostraron preferencia por ninguno de los cuatro tratamientos de cajas nido, y los parámetros reproductivos no variaron entre los tratamientos. Concluimos que la disminución en el número de individuos de *A. funereus* reproduciéndose en cajas nido es real y no está causado por el envejecimiento de las cajas nido.

[Traducción del equipo editorial]

In northern Scandinavia, there has been a gradual decline in cyclic vole population densities and dampening of the cycles since the 1970s, characterized by an increased frequency of overwinter declines leading to decreased spring densities (Hörnfeldt 1994, 2004, Hanski and Henttonen 1996, Hansen et al. 1999, Solonen 2004, Hörnfeldt et al. 2005, 2006, Ims et al. 2008). Voles are the main prey of several highly specialized predators in the region, including the Boreal Owl (Tengmalm's Owl; *Aegolius funereus*), a small, cavity-nesting owl found throughout Europe's boreal region. The decline in vole densities in spring led to the general prediction that reproductive output and population size are likely to have declined in such a specialized predator species. Indeed, a thirty-year study of Boreal Owls breeding in nest boxes in northern Sweden has revealed a gradual decline in numbers of breeding owls (Fig. 1), and this trend has been attributed to the decline in voles (Hörnfeldt et al. 2005).

However, an alternative hypothesis, that can be derived from Sonerud (1985a, 1989, 1993) is that the decline in Boreal Owls is an artifact of aging

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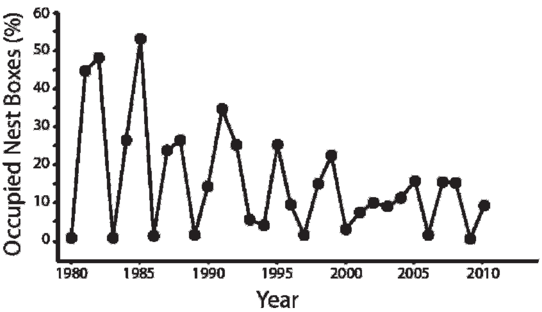

Figure 1. Percentage of nest boxes occupied by breeding Boreal Owls (≥1 egg laid) in Västerbotten, northern Sweden, 1980–2010. Some data previously published in Hörnfeldt et al. 1990 and Hörnfeldt et al. 2005.

nest boxes, because the owls avoid old nest boxes to reduce the risk of predation. The European pine marten (*Martes martes*) is a relatively common generalist predator in Scandinavia's boreal forest (MacDonald and Barrett 1993). It is the main predator of Boreal Owl nests (Sonerud 1985a, Korpimäki 1987), and is thought to memorize and revisit places where it has previously found food (Sonerud 1985a, 1989, 1993, Nilsson et al. 1991, Sorace et al. 2004). There is indeed an increased risk of predation in older boxes and in boxes where Boreal Owl nests have been depredated previously (Sonerud 1985a, 1989, 1993; but see Korpimäki 1987), and Boreal Owls have been shown to use new nest boxes more frequently than old ones (Sonerud 1985a). To ascertain whether the decline in Boreal Owls breeding in nest boxes is a genuine issue of conservation concern, it is important to investigate whether or not it is an inherent methodological artifact of the thirty-year nest-box study. As far as we know, however, methodological tests are rarely undertaken to validate whether observed long-term population trends are real and trustworthy.

In this study, we examine whether the decline in Boreal Owls breeding in nest boxes is due to avoidance of old boxes by comparing recent use of old and new nest boxes at their original location, and old and new nest boxes placed at new locations. If the decline of owls was caused solely by aging nest boxes leading to increased predation risk and box avoidance by the owls, we predicted that the breeding frequency of owls would be higher in relocated nest boxes than in boxes at their original sites, and as high as in the early 1980s. Alternatively, if the decline in owls was caused solely by aging nest boxes through increased wear, we predicted that the breeding frequency of owls would be higher in new nest boxes than in older ones irrespective of location, and as high as in the early 1980s.

METHODS

We studied Boreal Owls near Umeå in Västerbotten, northern Sweden (approx. 64°N, 20°E). This area is within the middle boreal vegetation zone (Ahti et al. 1968) and is dominated by managed coniferous woodland with patches of wetland and low-intensity agriculture. Boreal Owls have been monitored in this area since 1980 using a nest-box program (see Löfgren et al. 1986, Hörnfeldt et al. 1990, 2005 for details), which in later years has comprised approx. 275 nest boxes. The nest boxes (made of untreated wood, 20 × 20 cm base, 8.5-cm diameter entrance hole) were placed in trees at heights of 3–4 m, at approx. 1-km intervals along 50-km roadside routes. If required, nest boxes have been repaired, replaced, and occasionally slightly relocated due to logging, etc. All boxes were kept fresh by replacing old wood shavings and removing old nesting material and other debris.

Our experiment was based on the nest-box monitoring program, after some of the original nest boxes were replaced or moved. One-fourth of the nest boxes were each (1) left as controls, i.e., old nest boxes at their original location, (2) replaced by new ones but left at their original location, (3) relocated 100–200 m away, or (4) replaced by new ones and relocated 100–200 m. Treatment was allocated sequentially, i.e., the first box along a route was designated treatment 1, the second box treatment 2 and so on. In this study, nest boxes were defined as new or relocated up to 2 yr after they were erected. As far as possible, relocated nest boxes were erected within the same forest stand to minimize effects of habitat quality. Relocated nest boxes also were erected in a tree of the same species and of approximately the same size and age class as before. The relocation distance of 100–200 m (a similar distance to that used in Sonerud's [1985a, 1989 and 1993] box relocation experiment) assured that the nest boxes were not visible from their original locations, while making it likely that they remained within the same Boreal Owl territory.

The designated nest boxes were moved in November–December 2005, in preparation for the owl breeding seasons of 2006 and 2007. In our experience, these dates were early enough to allow the owls to find the nest boxes in time for the ensuing breeding season, which starts at the end of February at the earliest. In our study area, small mammals are

Table 1. Number of nests (≥1 egg laid) of Boreal Owls in four nest-box treatments in 2006 and 2007. Number of nest boxes in parentheses.

Treatment	2006	2007
Old boxes at original locations	1 (69)	9 (68)
New boxes at original locations	3 (69)	10 (68)
Old and relocated boxes	0 (69)	13 (69)
New and relocated boxes	1 (68)	10 (68)
Total	**5 (275)**	**42 (273)**

Table 2. Number of depredated Boreal Owl nests in four nest-box treatments in 2006 and 2007. Total number of nests (≥1 egg laid) is given in parentheses. Note that no nests were depredated in 2006.

Treatment	2006	2007
Old boxes at original locations	0 (1)	1 (9)
New boxes at original locations	0 (3)	4 (10)
Old and relocated boxes	0 (0)	0 (13)
New and relocated boxes	0 (1)	0 (10)
Total	**0 (5)**	**5 (42)**

trapped in spring and fall as part of the Swedish Environmental Protection Agency's National Environmental Monitoring Program (Hörnfeldt 1978, 1994, 2004, 2012). Here 2006 represented the first year (increase phase) of a 3-yr vole cycle, with low vole abundance in spring and previous fall, and 2007 the second year (peak phase) with a much higher vole abundance in spring and previous fall (Hörnfeldt 2012).

All nest boxes were checked at least three times in 2006 and four times in 2007 at intervals of approximately 4 wk. Nest boxes with breeding Boreal Owls were visited more often to obtain data on clutch size and laying date. We banded brooding females and nestlings, and estimated the laying date of most detected clutches by backdating. If the clutch was discovered during laying, a laying interval of 2 d per egg was used, and if the clutch was discovered later, the wing-length of the oldest nestling was measured to determine its age, and an incubation period of 29 d was assumed (Carlsson and Hörnfeldt 1994). We assumed that nest predation had occurred when broken eggs were found. However, because pine martens sometimes plunder nests and remove all eggs without trace, some occurrences of predation may have been unrecorded, and we may have underestimated the frequency of nest predation (cf. Sonerud 1985b). We recorded nestling mortality, and thus the number of fledged young, by X-raying nest-box remains to detect aluminum bands from dead nestlings.

We tested preference by Boreal Owls for the four nest-box treatments using a chi-square test on the number of breeding attempts (≥1 egg laid) for both years pooled (owing to the small sample size in 2006; Table 1). However, we also tested for the two years separately using Fisher exact tests (valid for low sample sizes; Siegel and Castellan 1988). We analyzed the occurrence of predation using Fisher exact tests for 2007 only (no predation was observed in 2006; Table 2). For this analysis, nest-box treatments were pooled into two groups; either old vs. new or relocated vs. unmoved nest boxes. We analyzed effect of nest-box treatment on three important breeding parameters (laying date, clutch size, and number of fledglings) using least squares linear regression, controlling for the effect of year. We checked the validity of the regression models by visually examining the raw residuals.

Results

The number of breeding Boreal Owls in 2006 was very low, with only 1.8% ($n = 5$) of the nest boxes occupied. In 2007 occupancy increased considerably, with 15.4% ($n = 42$) of the nest boxes occupied by Boreal Owls. The owls showed no preference for any particular nest-box treatment, either for both years pooled ($\chi^2 = 0.57$, df = 3, $P = 0.90$), or for the two years separately (Fisher exact test: 2006, $P = 0.84$; 2007, $P = 0.76$; Table 1).

In 2007 five Boreal Owl nests (12%) were lost to predation (Table 2). None of the nests in 2006 were depredated, giving an overall predation rate of nearly 11% for both years combined. We identified European pine marten as the likely predator in one case, but usually the predator could not be identified. Predation rate did not differ significantly between old and new nest boxes (unmoved and relocated boxes pooled; Fisher exact test, $P = 0.17$), but predation rate was significantly lower in relocated nest boxes than in boxes that were left at their original location (new and old boxes pooled; Fisher exact test, $P = 0.01$). Mean number of fledged young tended to be higher for relocated nest boxes (new and old boxes pooled) than for unmoved nest boxes (3.9 and 2.6 respectively for both years pooled). However, least squares regression analysis on this sample (controlling for year) showed no significant difference ($n = 47$, F-ratio = 2.17, $P = 0.15$).

Table 3. Mean laying date (day of year), clutch size and number of fledgling Boreal Owls in four nest-box treatments in 2006 and 2007. Number of nests (≥1 egg laid) in parentheses.

Treatment	Laying Date		Clutch Size		No. of Fledglings	
	2006	2007	2006	2007	2006	2007
Old boxes at original locations	126 (1)	107 (9)	5.0 (1)	5.3 (9)	3.0 (1)	2.4 (9)
New boxes at original locations	132 (3)	89 (10)	3.7 (3)	6.3 (10)	1.0 (3)	3.2 (10)
Old and relocated boxes	— (0)	93 (13)	— (0)	6.8 (13)	— (0)	4.0 (13)
New and relocated boxes	140 (1)	95 (10)	4.0 (1)	5.8 (10)	3.0 (1)	3.9 (10)

Least squares regression analysis revealed no effect of nest-box treatment on laying date, number of eggs laid, and number of fledged young after the effect of year had been removed (Tables 3, 4). Thus, owls were not selecting a certain nest-box treatment earlier than the others, and productivity did not appear to differ between treatments.

Discussion

Boreal Owls did not show a preference for new or relocated nest boxes during two consecutive breeding seasons during the increase and peak phases of a 3-yr vole cycle (Table 1). Furthermore, the number of breeding owls occupying nest boxes was much lower during the peak breeding year than at peak densities in the early 1980s. Therefore, we found little evidence to support the hypothesis that the long-term decline in nesting Boreal Owls (Fig. 1) is an artifact of owls avoiding old nest boxes. We assume that the observed decline reflects a general decline in the Boreal Owl population that can be explained by the decline in vole populations (Hörnfeldt 2004, Hörnfeldt et al. 2005). Owls nesting in natural cavities (usually old Black Woodpecker [*Dryocopus martius*] nest holes) could have a different population trend than those in nest boxes. Although we do not have data on these owls, we do not suspect this and are not aware of any such indications in our study area or elsewhere. Furthermore, natural cavities are considered a rare resource for nesting owls (Lundberg 1979), and as old trees and stands are becoming more rare in Swedish forests (Esseen et al. 1997), natural cavities are more likely a decreasing resource.

Table 4. Least squares regression results for the effect of the four nest-box treatments on Boreal Owl breeding parameters, controlling for year.

Breeding Parameter	Model r^2	n	F-ratio	P
Laying date	0.23	36	0.60	0.62
Clutch size	0.20	47	1.16	0.34
No. of fledglings	0.08	47	0.73	0.54

Our results contrast those of Sonerud (1985a), who found that Boreal Owls in southern Norway used new nest boxes more frequently than older ones. This pattern of use was attributed to a reduction in pine marten predation risk in new nest boxes (Sonerud 1985a, cf. Sonerud 1989, 1993). In our study, predation rate was significantly lower in boxes that had been relocated, which agreed with the hypothesis that pine martens remember and revisit places where they have previously found food (Sonerud 1985a, 1989, 1993, Nilsson et al. 1991, Sorace et al. 2004). Nevertheless, the owls did not appear to prefer relocated nest boxes. Interestingly, the incidence of predation on Boreal Owl nests in southern Norway was more than four times higher than that we report here (48%; Sonerud 1985a, vs. 11% in our study); predation rates by pine marten reported from western Finland were even lower, at 5% (Korpimäki 1987). If predation risk is truly so much lower in northern Sweden (with a caveat that the predation rate may have been underestimated: see Methods), then owls should be under less selective pressure to avoid it. Indeed, the overall productivity (measured as number of fledged young) was not significantly higher in relocated nest boxes, despite the prevalence of predation in unmoved boxes. Consequently, other factors such as local food supply or other habitat features might be more important for the owls when selecting a nest site. Also, female Boreal Owls in southern Norway may be less nomadic than their counterparts in Sweden (Sonerud et al. 1988). If turnover rates of breeding owls were indeed higher in the current Swedish study, fewer individuals would have experienced local predation and may be less prone to select new or relocated nest boxes.

Our experiment encompassed two years (increase and peak phase) of a 3-yr vole cycle. Predation risk from pine marten and consequent nest-selection behavior of owls might differ during the last year of the vole cycle. However, predation on Boreal Owl nests during 2008 (i.e., the year after the end of the current study) was at a similar level, at 14%. However, we refrained from including this year in our study, because we felt that the nest boxes that had been replaced and/or relocated in late 2005 could no longer be regarded as either ''new'' or ''relocated'' after 3 years.

Cavity-nesting birds may prefer newly excavated holes or new nest boxes because old, previously used sites have a higher level of ectoparasite infestation (Møller 1989, 1994, Mazgajski 2007). Additionally, nests in old cavities and nest boxes might be more exposed to the weather due to decay and disrepair (Korpimäki 1984, 1987). However, our nest boxes were continually repaired and refilled with fresh wood shavings between each breeding season, so older boxes should function as well as new ones. Thus, it was not surprising that we observed no preference for new nest boxes in our study.

The long-term decline in numbers of breeding Boreal Owls in northern Sweden has been accompanied by a change in their population dynamics: from 3–4-yr high-amplitude cycles, through a period of low-amplitude cycles, toward nearly annual fluctuations in the early 2000s (Fig. 1; Hörnfeldt et al. 2005). It is the peak years of high owl breeding density that have undergone a marked decline, thus reducing the overall numbers of breeding Boreal Owls in the long term. Declining trends similar to that in the Boreal Owl have been observed in other vole-eating birds of prey in Sweden. Great Gray Owls (*Strix nebulosa*) in northern Sweden have shown a long-term decline in brood size during peak vole years, corresponding to the dampening amplitude of vole cycles in the region (Hipkiss et al. 2008). Although the data were not robust enough to reveal an overall decline in the Great Gray Owl population, the researchers predicted that decreasing peak brood sizes would eventually lead to a general population decline, analogous to that of the Boreal Owl population. Further evidence of downward trends in northern vole-eating birds of prey can be found in autumn counts at Falsterbo, a Scandinavian migration bottleneck in southern Sweden. Counts of Northern Harriers (*Circus cyaneus*) have declined since the late 1970s and those of Rough-legged Hawks (*Buteo lagopus*), have declined since the mid-1980s, and decreasing rodent abundance was suggested as the cause of these trends (Kjellén and Roos 2000).

The decline and changed dynamics of vole populations in northern Fennoscandia, which is the most likely cause of the decline in breeding owls (Hörnfeldt 2004, Hörnfeldt et al. 2005), is probably related to increasingly milder and wetter winters in the region (Hörnfeldt 2004, Solonen 2004, Hörnfeldt et al. 2005, Ims et al. 2008). During milder winters, when conditions fluctuate between freezing and thaw, and the snow period is shorter and a hard crust of ice forms on the ground, small mammals are unable to use the subniveal space as efficiently for foraging and as a refuge against predators and adverse weather. Consequently, their mortality increases which leads to more pronounced winter population declines (Aars and Ims 2002, Hörnfeldt 2004, Solonen 2004, Korslund and Steen 2006, Kausrud et al. 2008). Mild and wet winters are likely to persist and become more frequent in Fennoscandia due to global warming, and lead to further dampening of vole cycles and lower numbers of their specialist predators (Hörnfeldt 1998, 2004, Strann et al. 2002, Solonen 2004, Ims et al. 2008). The Boreal Owl is not currently classified as a species of conservation concern in Sweden or the rest of Fennoscandia (BirdLife International 2012). However, if the declining trend presented here persists, then the conservation status of the Boreal Owl will have to be reviewed.

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