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ORIGINAL ARTICLE

Nest predation decreases with increasing nest height in forest songbirds: a comparative study

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Abstract

Nest predation is the most important factor responsible for nest failure in birds. Nest height may be a factor that affects the rate of nest depredation in different species. In this comparative study, we tested a relationship between nest height and nest depredation in open nesting songbirds. We analyzed data from 357 populations of 252 species and found that nests built high in trees were safer than those closer to the ground. Nest depredation rates strongly decreased with increasing nest height above 5 m. This could be because there are fewer nest predator species foraging in the canopy or because there is a lower density of nesting birds making it less profitable for predators to search for nests there. We also found that ground nests in open habitats were more likely to be depredated than those in shrublands and forests. This may be because open habitats are less complex and thus more easily searched by nest predators, or because most nests in open habitats are ground nests and predators can focus on them without having to search other vegetation layers.

Keywords Comparative study · Habitats · Nest failure · Passeriformes · Vegetation layers

Zusammenfassung

Mit zunehmender Nisthöhe nimmt die Nesträuberei bei Waldsingvögeln ab: eine vergleichende Studie.

Nesträuberei ist der wichtigste Faktor, der für das Scheitern von Nestern bei Vögeln verantwortlich ist. Die Nisthöhe könnte ein Faktor sein, der die Häufigkeit der Nestplünderung bei verschiedenen Arten beeinflusst. In dieser vergleichenden Studie haben wir den Zusammenhang zwischen Nisthöhe und Nestplünderung bei offen nistenden Singvögeln untersucht. Wir analysierten Daten aus 357 Populationen von 252 Arten und stellten fest, dass Nester, die hoch in Bäumen gebaut wurden, sicherer waren als solche, die näher am Boden lagen. Mit zunehmender Nisthöhe über 5 m nahm die Zahl der Nesträuber stark ab. Dies könnte darauf zurückzuführen sein, dass in den Baumkronen weniger Arten von Nesträubern auf Nahrungssuche sind oder dass die Dichte der nistenden Vögel geringer ist, so dass es sich für Räuber weniger lohnt, dort nach Nestern zu suchen. Wir haben auch festgestellt, dass Bodennester in offenen Lebensräumen eher geplündert werden als solche in Gebüschen und Wäldern. Dies könnte daran liegen, dass offene Lebensräume weniger komplex sind und daher von Nesträubern leichter durchsucht werden können, oder daran, dass die meisten Nester in offenen Lebensräumen Bodennester sind und die Räuber sich auf sie konzentrieren können, ohne andere Vegetationsschichten durchsuchen zu müssen.

Introduction

Nest predation is the most important factor responsible for nest failure in birds (Ricklefs 1969; Martin 1993; Remeš et al. 2012b; Matysioková and Remeš 2022). The rate of nest depredation varies highly between species and populations, and there is a large number of factors which could be responsible for this variation. They can be connected to predators themselves (e.g. predator density; Remeš et al. 2012a), properties of nesting species or individuals (e.g. body mass, parental behavior; Matysioková and Remeš 2018; Unzeta

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et al. 2020), characteristics of the nest (e.g. nest type; Matysioková and Remeš 2022) or nest site (e.g. nest concealment; Martin 1988a, Kelly 1993, Remeš 2005b, but see Borgmann and Conway 2015).

Nest height is easily measured and thus among the most often studied nest characteristics. Traditionally it was believed that the lowest rate of nest survival should be associated with ground nests and nest survival should increase with increasing nests height as nests are getting out of the reach of predators active on the ground (Ricklefs 1969). However, results of previous studies were equivocal. While some supported this view (Holcomb 1969; Wilson and Cooper 1998; Balakrishnan 2010, Ó hUallacháin 2014), others did not (Eguchi et al. 2002; van Dongen and Yocom 2005; Hammond et al. 2016) or even found an opposite relationship (Goddard and Board 1967; Longcore and Jones 1969; Beckmann and McDonald 2016). A possible explanation could be a nonlinear relationship between nest height and the probability of nest depredation. While mammalian predators may mostly focus on nests built on the ground, those built high in the canopy can be more often depredated by avian predators (Remeš 2005a; Kleindorfer et al. 2021). Nests situated in the middle part of vegetation thus can suffer lower nest predation than those built closer to the ground or in the canopy (Filliater et al. 1994; Sockman 1997; Kleindorfer et al. 2021).

In this study, we tested a relationship between nest height and the rate of nest depredation in open nesting songbirds. Using a large number of studies, we analyzed (a) whether ground nests had higher probability of depredation than above-ground nests, (b) whether ground nests were affected by nest predation differently in different habitats, and (c) whether and how nest predation changed with nest height in different habitats.

Methods

For this study we used data presented in Matysioková and Remeš (2022). From this dataset we selected only open nesting species, and used data on daily predation rates (DPR) and study site. From original articles, we extracted data on habitat type. We excluded all studies conducted in wetlands or habitats highly affected by human presence such as town center, university campuses, parks or orchards since those habitats might be avoided by predators (Morton et al. 1993; Vincze et al. 2017), which could bias our analyses. We also excluded studies conducted in more than one type of habitat. Remaining habitats were categorized based on authors' description as open, shrubland and forest. From the same primary studies we also extracted data on nest height (in meters). We decided not to convert nest heights into vegetation layers sensu Martin (1993), because we believed that with the exception of well-defined ground nests, this delimitation was artificial. Hence, we only categorized nests 0–30 cm high as ground nests and used them as such in subsequent analyses. All other nests were categorized as above-ground nests. Finally, we excluded all studies missing information either on habitat type or nest height.

To perform statistical tests, we used linear mixed models with study site and species identity as random effects. Daily nest predation rates and nest height were square root transformed to bring them closer to a normal distribution. All continuous variables were scaled (their mean was subtracted, and they were divided by their standard deviation) to allow for proper testing of both linear and quadratic effects (Schielzeth 2010). We did not test differences in predation rate among habitats for above-ground nests, because there were too few nests in open habitats. Since the range of nest heights in open habitats was very small (0–1.16 m, $N = 90$), we analyzed the relationship between the nest height and nest predation rate in shrublands and forests only. We fitted all models in the phyr package for the R language (Li et al. 2020). Body mass has been shown previously to predict nest predation rates (Unzeta et al. 2020). We thus checked that it did not differ among habitats (F-value = 0.63, $P = 0.531$) or along nest height (estimate (SE) = 0.01 (0.01), Z-score = 1.05, $P = 0.293$). Accordingly, our results were not biased by a potential confounding effect of body mass.

Results

Altogether, 357 populations of 252 songbird species were included in our final dataset. Most data came from populations breeding in forests ($N = 199$), followed by those from open habitats ($N = 90$), and shrublands ($N = 68$). Average nest height across the habitats was 2.44 m (range 0-18m, $N = 357$) and differed significantly among the three habitats ($F = 122.9$, $P < 0.001$). One hundred and fourteen populations had ground nests, while the remaining 243 populations had above-ground nests.

Ground nests had similar nest predation rate as above-ground nests in all three habitats (estimate (SE) = 0.05 (0.13), Z-score = 0.40, $P = 0.688$, Fig. 1). However, when we compared nest predation of ground nests between the three habitats, they were significantly less often depredated in shrublands (estimate (SE) = − 0.55 (0.28), Z-score = − 1.98, $P = 0.048$) and forests (estimate (SE) = − 0.58 (0.28), Z-score = -2.08, $P = 0.038$, Fig. 1) than in open habitats. Considering the relationship between nest height and nest predation, there was a significant quadratic relationship in forests (estimate (SE) = − 0.16 (0.05), Z-score = − 3.07, $P = 0.002$), while the linear term was not significant (estimate (SE) = − 0.11 (0.07), Z-score = − 1.60, $P = 0.110$, Fig. 2). However,

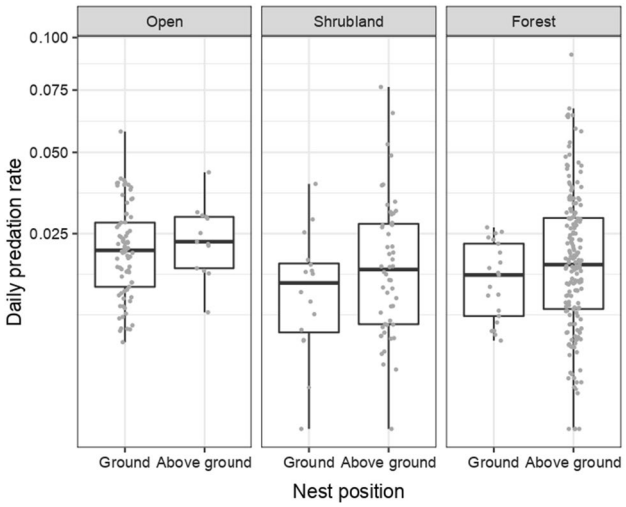

Fig. 1 Daily nest predation rates of ground and above-ground nesting populations of songbirds in open habitats ($N = 90$), shrublands ($N = 68$) and forests ($N = 199$)

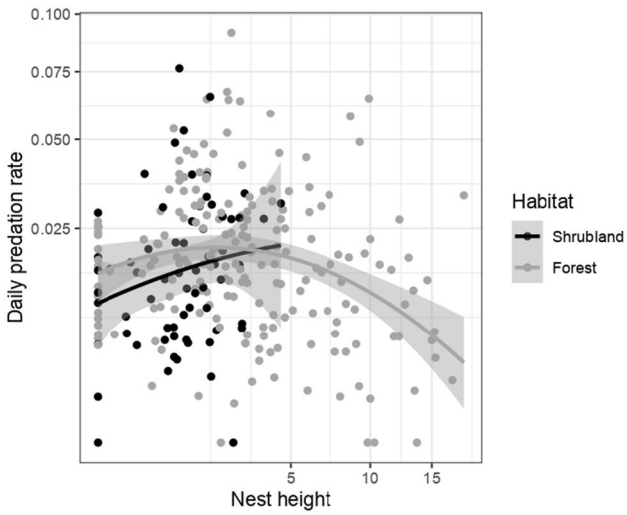

Fig. 2 Quadratic relationships of daily nest predation rates to nest height in songbird populations nesting in shrublands ($N = 68$) and forests ($N = 199$)

when the quadratic term was removed, the linear term was statistically significant (estimate (SE) = − 0.15 (0.07), Z-score = − 2.08, $P = 0.038$). These results together show that there was a negative trend in nest predation rate with nest height that was particularly apparent above ca. 5 m. On the other hand, nest predation did not change with nest height in shrublands (estimate (SE) = 0.12 (0.12), Z-score = 0.99, $P = 0.324$, Fig. 2).

Discussion

Ground nests are often thought to be more vulnerable to nest predation than above-ground nests, since they are easily accessible to a wide range of ground predators including mammals, snakes, ants, and birds (Best 1978; Weidinger 2009; Conkling 2010; Chen et al. 2015). This was indeed observed in some studies (Craighead and Stockstad 1961; Lloyd 2004), domed nests in Marini (2017). However, other studies found ground nests being more successful (Knapton 1978; Pietz and Granfors 2000; Marzluff et al. 2007; Chen et al. 2015; Pierce et al. 2020) or not different at all from above-ground nests in nest predation rate (Morton et al. 1993), open nests in Marini (2017), which was also true for our data. This equivocality in results suggests that if present, the relationship might be confounded by locality-dependent variables such as dominant type of nest predators or habitat.

While we did not find any difference in nest predation between ground and above-ground nests in any habitat, nest predation in ground nests was higher in open habitats compared to both shrublands and forests. It is possible that the lack of above-ground cover of shrubs and trees in open habitats makes finding nests easier for visually oriented predators. These include birds and snakes (Weatherhead and Blouin-Demers 2004; DeGregorio et al. 2014), and are important nest predators in grasslands, agricultural landscape, and other open habitats (Andrén et al. 1985; Klug et al. 2010; Samsonov et al. 2018). Alternatively, since nests in open habitats are built on the ground or close to the ground, nest predators can focus exclusively on this type of nests. Consequently, their nest searching can be more effective than searching for nests in shrublands and forests, where nests are placed in various vegetation layers (Martin 1988b).

We expected to find nest predation to decrease with increasing height, because higher nests are less accessible to terrestrial nest predators (Mullin and Cooper 2002; Natusch et al. 2017; Kleindorfer et al. 2021). However, the nest predation rate did not change until the nest height reached around 5 m. Above this height it started to significantly decrease and the highest nests experienced the lowest predation rate altogether. Since the really high nests are missing in shrublands, this negative relationship between nest predation rate and nest height could only be observed in forests. This would agree with Martin (1993) who found nest predation in forest habitats being lower in canopy layer compared to mid-height (shrub layer).

One possible explanation could be that nests built lower in the vegetation can be reached by a wide range of nest predators. On the other hand, some predators do not climb (for example European badger *Meles meles* or terrestrial

species of snakes such as European viper *Vipera berus*) or it might be impossible or difficult for them to get to canopy due to weaker support of thin branches and twigs. Accordingly, empirical evidence shows that only some types of predators such as raptorial birds or some species of snakes depredate nests high in the trees, while other groups such as fire ants or larger mammals are nearly or completely missing there (Reidy and Thompson III 2013; Chiavacci et al. 2014; DeGregorio et al. 2016; Kirby et al. 2018; Morozov 2021). Absence of whole predator guilds in the canopy thus could lead to a lower overall predation rate. Alternatively, the density of nesting birds might decrease with increasing height and it might be more profitable for nest predators to search for nests in lower heights (Martin 1988b; Martin and Martin 2001; Shitikov et al. 2018).

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