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Proximity of shrub nests to ground nests increases the chance of ground nest predation

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In nature, ground-nesting birds rarely nest under an active shrub nest of another species. In the case of the proximity of the two nest types, we assumed that if a nest predator finds one nest, it will most likely rob the other nest as well. To test this, we exposed artificial nests with one quail and one plasticine egg on shrubs and underneath on the ground, in oleaster shrub rows and forest edges. We found a higher predation on ground nests than on shrub nests in both habitats. More importantly, predation events in shrub nests resulted in a higher predation of more concealed ground nests too. Our results suggest that proximity of two nest types can be detrimental to predation pressure, especially in forest edges.

1. Introduction

Nest predation is the primary cause of bird mortality (Ricklefs 1969), thus selection of suitable nesting habitats for birds may be more critical than food resources (Martin 1988). The survival of nests on the ground or in shrubs can be significantly influenced by the type of vegetation and also by the edge effect (*e.g.* Bayne *et al.* 1997, Batáry *et al.* 2014). Fontaine *et al.* (2007) suggested that the risk of predation varies with nest types and predator abundance independently of parental care. Survival chances of different nest types (*e.g.* open cup shrub or ground nest) are affected by features of the nesting habitat and the predator community occurring surrounding the nest (*e.g.* Hoi & Winkler 1994, Söderström *et al.* 1998). The higher density of nests either in shrubs or on the ground increased overall predation on both types (Schmidt & Whelan 1999). Moreover, an increase in the density of one nest type increased the predation rate on the other nest type (Hoi & Winkler 1994). Nevertheless, most bird species are characterized by territorial behaviour (Nice 1941). For this reason, different solitary species rarely build their nests close to each other, but if they do, such associative nesting serves to reduce predation pressure for at least one species

(Quinn & Ueta 2008). Such associative nesting in nature is not frequent, but it is confirmed between the Woodchat Shrike (*Lanius senator*) and the Western Orphean Warbler (*Sylvia hortensis*), as well as the Red-backed Shrike (*Lanius collurio*) and the Barred Warbler (*Sylvia nisoria*). It suggests a mutualistic relationship in the fight against nest predators (Isenmann & Fradet 1995, Polak 2014). However, little is known about the effect of different co-occurring bird species with different nest types on their nesting success (Elmberg & Pöysä 2011). The survival chance of shrub and ground nests close to each other can be investigated by using artificial nests and eggs (Moore & Robinson 2004). This method is applicable to estimate the daily survival rate of nests in different habitats as well as to the identification of predators (Major & Kendal 1996, Bateman *et al.* 2017). A great advantage of this method is that during the experiment with artificial nests and eggs the real nests or the breeding birds are not disturbed (Major & Kendal 1996, Kurucz *et al.* 2015), and this contributed greatly to the spread of this method (Bateman *et al.* 2017).

The aim of our study was to estimate the survival rate of shrub and ground nests in two different habitats (forest edge and oleaster rows) and to provide answers to the questions: 1) what proportion of predation events are due to bird or mammal predator?; 2) what is the difference in the daily survival rate of the two nest types?; and 3) is the predation risk related to the type of nest location – ground or shrub?

2. Materials and methods

2.1. Study area

The study area was situated on the southern slope of the Mecsek Mountains, close to the north-eastern outskirts of the city of Pécs, in South Hungary. Intensive opencast coal mining in Mecsek Mountains lasted from 1968 to 1996, after that the northern part of the area extending over 15 ha was recultivated (latitude: 46.115710° N, longitude: 18.230088° E, a.s.l. 366 m). The covering soil layer has been planted with saplings of various tree species since 1996. In the time of our study (2003), the ground was overgrown by herbaceous vegetation of the initial stage of primary succession. Oleaster (*Elaeagnus angustifolia*) shrubs were successfully planted on the hillsides in rows (1.5–2.5 m high and 2 m wide) 15–25 m apart, and the spontaneously colonizing black locust (*Robinia pseudoacacia*) reached a height of 2–3 m. The recultivated area was bordered from the east, north and west by turkey oak forests (Purger *et al.* 2004a,b, Kurucz *et al.* 2015). We performed the artificial nest experiment in oleaster rows and along edges of these native forests with diverse canopy and shrub layers, while the herbaceous layer was very weak, and the ground was mainly covered by litter. Ornithofauna of the Mecsek Mountains is relatively rich (Bankovics 2006), though during our previous study in the shrubs on the forest edge were found only nests of Eurasian Blackbird (*Turdus merula*) and Turtle Dove (*Streptopelia turtur*), but in the oleaster rows several nests of the Red-backed Shrike were located (Purger *et al.* 2014a). There were only three ground nesting species, Common Pheasant (*Phasianus colchicus*), European Nightjar (*Caprimulgus europaeus*), and Yellowhammer (*Emberiza citrinella*) found in clearings, forest edge and inside forest (Purger *et al.* 2014b).

2.2. Fieldwork

We prepared a total of 50 artificial shrub nests and 50 ground nests and exposed them on oleaster shrubs in the recultivated area on June 14, 2003. On the same day, we also exposed 50 artificial shrub nests and 50 ground nests in the forest edge. For shrub nests, we used wire mesh, attached them to branches at a height of about 1.5 m and lined them with dry grass (Purger *et al.* 2004a). Directly below the shrub nests, we established ground nests by making a shallow hole lining with dry grass. We placed one quail and one plasticine egg of similar size in each nest. Pairs of nests were located at least 20 m apart from each other (Bayne *et al.* 1997, Bayne & Hobson 1999). We controlled the nests on the first (15 June), second (16 June), fourth (18 June) and seventh (21 June) day after placement, between 13.00–19.00 hours each time. A nest was considered depredated if natural quail or plasticine eggs were damaged in some way or missing from the nest (Bayne

& Hobson 1999, Purger *et al.* 2004b). Based on the beak and tooth impressions on the plasticine eggs, it can be determined with certainty that the predator was a small or large bird or mammal (Ludwig *et al.* 2012, Bravo *et al.* 2020). Large mammal predators were identified by the help of our collection of mammal skulls. The most useful measures in the tooth imprints are the size and curvature of the incisors and the distance between the canines. Using imprints left in plasticine eggs a birds and small-bodied mammals (mice, voles, shrews) cannot be determined at the species level. This investigation was based on indirect sampling, therefore this article does not contain any studies with animals performed by any of the authors.

2.3. Statistical analysis

All statistical analyses were performed in R statistical environment using 4.0.3 program version (R Core Team 2020). First, we analysed the effects of nest type and habitat type and their interaction on the daily probability of nest survival using a generalized linear mixed-effects model (GLMM) with binomial error distribution, logit link function, and involving nest days as the denominator. This method is known as Mayfield logistic regression (Hazler 2004), and for this, we used the ‘glmer’ function and the maximum likelihood method from the ‘lme4’ package (Bates *et al.* 2015). Nest days were rounded up to the nearest day before analyses (Hazler 2004). In the model, we used the following random structure for accounting for spatial autocorrelation originating from our study design: nests were grouped in pairs, which were nested in transects, and transects were nested in East or West side of the recultivated area (in R language: Side / Transect / Pair). Furthermore, we made a pairwise post hoc (least square difference) comparison with the emmeans package in order to compare all possible combinations of nest and habitat types (Lenth 2021). Second, we also performed a GLMM model with ground nest survival (again predation event as numerator and nest day as denominator) and nest days of shrub nests as explanatory variable for directly testing the dependence of ground nest predation on shrub nest predation. In this case, the random structure was as follows: Habitat type/Side/Transect.

3. Results

During the week-long study, all nests were depredated except for the shrub nests in oleaster rows (34% of which remained intact). The plasticine eggs in the nests in the oleaster rows and in the forest edge were damaged in 75% and 94%, respectively. Most of the imprints preserved on plasticine eggs were left by small mammals and small-bodied birds (Fig. 1). Based on the tooth prints, the nest predators of the ground nests were red foxes (*Vulpes vulpes*) (in 2 cases), martens (in 6 cases), while the shrub nests were depredated by martens (in 5 cases), which are also able to remove quail eggs. Bill imprints of larger-bodied birds were found only on two plasticine eggs in shrub nests at the edge of the forest. From a total number (n=169) of depredated plasticine eggs, 31% (n=53) were missing. From the total number (n=182) of depredated quail eggs, 88% (n=161) were removed from nests, and remains of only

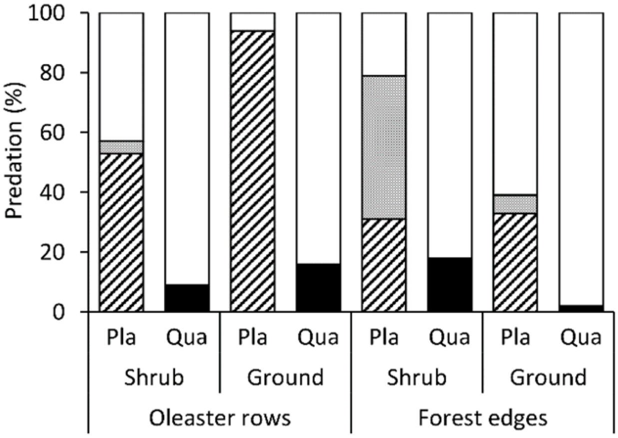

Fig. 1. Predation of plasticine (Pla) and quail eggs (Qua) in the shrub and ground nests at the two habitats: eggs taken away (white bars), eggs marked by birds (grey bars), eggs marked by mammals (hatched bars), broken and consumed quail eggs (black bars).

1.5% (n=21) were found in the nests (Fig. 1).

Daily survival rates of nests varied significantly by habitat and nest type (Table 1, Fig. 2). The interaction of nest type and habitat type was non-significant and was discarded from the final model (Table 1). The daily survival rate of nests in oleaster tree rows was higher than at the forest edges with higher predation on ground nests in both habitats. Our direct model testing nest predation dependence showed that if shrub nests are depredated, it increases the chance that ground nests was also destroyed (estimate ± SEM = –0.16 ± 0.06, z = –2.85, P = 0.004).

Table 1. The effect of habitat type (Or – Oleaster rows) and nest types (Gn – Ground nests) on the daily probability of nest survival.

	Estimate	SEM	I value	*P*
(Intercept)	1.28	0.14	8.89	<0.001
Habitat type (Or)	0.84	0.17	5.03	<0.001
Nest type (Gn)	–0.54	0.17	–3.24	<0.001

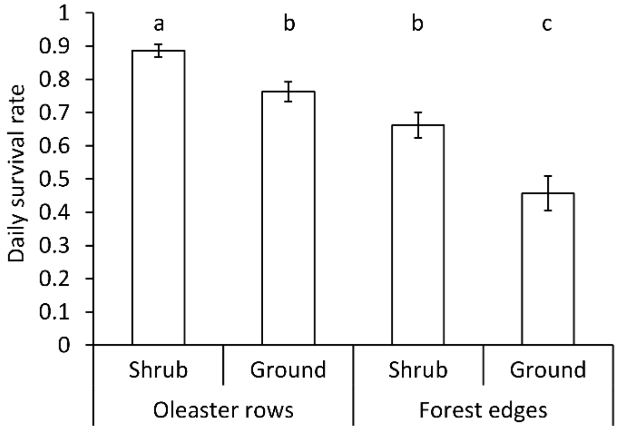

Fig. 2. Daily survival rates (± SEM) of shrub and ground nests in oleaster rows and forest edges.

4. Discussion

In our experiment based on the imprints preserved on plasticine eggs, most predators were mammals, however, a significant proportion of plasticine eggs and most quail eggs disappeared from shrub and ground nests at both habitats suggesting that birds played a more important role in predation. Larger-bodied mammals with good olfactory cues and nocturnal activity, such as red fox, European badger (*Meles meles*), and wild boar (*Sus scrofa*), which also occur in the study area, can only damage ground nests. However, martens and rodents can also damage nests on shrubs or trees. Some of the mammalian predators and birds can damage both types of nests. Small mammals and small-bodied birds can rarely break shells of quail eggs or take away from the nests, but their traces are preserved in plasticine eggs (Bayne *et al.* 1997). For predators with good eyesight, such as the corvids, both the shrub and the ground nests are available (Olsen & Schmidt 2004, Madden *et al.* 2015). Beak imprints of large-bodied birds were most likely left by Eurasian Jay (*Garrulus glandarius*) similarly as in our previous study which is performed in the same area (Purger *et al.* 2004a).

Both quail and plasticine eggs are mostly taken away from the nests by crows (Söderström *et al.* 1998), mostly broken up on hard substrates and consumed there. For this reason, usually these eggs are not found near the nests (Kurucz *et al.* 2015). Plasticine eggs are likely to be recognized by birds after a negative experience and left in the nest. The smell of plasticine can be attractive to mammals with good olfactory cues, and their visits leave more traces at the nests which can increase the predation rate (Bateman *et al.* 2017). For this reason, the predation rates of artificial nests are somewhat higher than those of real nests (Major & Kendal 1996). Using dummy birds in similar experiments increased the survival chance of artificial nests (Trnka *et al.* 2008), demonstrating the important role of the parent birds in hiding and protecting nests. Nonetheless, artificial nests and dummy eggs can be useful tools for comparative studies (*e.g.* Pärt & Wretenberg 2002, Batáry & Báldi 2005, Kurucz *et al.* 2012), however, it must be noted that artificial nests are suitable for measuring predation rates only but will not adequately measure breeding success.

In our experiment, the survival chances of both nest types were higher in the rows of oleaster trees in the recultivated area than at the forest edges, which is consistent with the finding that nest predation is often elevated at forest edges even compared to hedgerows (Batáry & Báldi 2004, Ludwig *et al.* 2012). Similar results were obtained a year earlier in the study area, even if there were exclusively plasticine eggs or only quail eggs in the shrub nests (Purger *et al.* 2004a). The results of previous study showed that predation pressure on the ground nests in the open recultivated area between forest edge and oleaster rows was also lower than on ground nests at the forest edges (Purger *et al.* 2004b). Our previous results suggested that for Black-headed Shrike and Yellowhammer, the oleaster rows in the recultivated area were more attractive to nesting in than the forest edge (Purger *et al.* 2004a). Both of these bird species prefer newly established shrubberies (such as in our study area) and, therefore, considered to be indicators of successional stages of abandoned agricultural areas with different woody vegetation cover (Mikulić *et al.* 2014).

In our study, the daily survival rates of shrub nests in both habitats were significantly higher than those of ground nests. Previous experiments with artificial nests have shown that ground nests are more often damaged by predators than shrub nests, but this may be mainly true for the species that breed in shrub and grassland habitats (Martin 1993). In contrast, ground-nesting species in forests are subject to lower predation pressure than shrub-nesting species. This can be explained by the fact that larger clutch size and longer nesting period of ground-nesting species in forests are indirect evidence that ground-nesting species have suffered lower nest predation over evolutionary time (Martin 1993). Consequently the habitat type and its condition (*e.g.* vegetation composition or level of disturbance) also influence which nest type has a higher survival chance (*e.g.* Batáry & Báldi 2004, Batáry *et al.* 2014, Wozna *et al.* 2017). The results of experiments with artificial shrub and ground nests in the temperate zone suggest that in open habitats close to the forest edge shrub nests suffered higher rates of depredation, predominantly robbed by avian predators (Söderström *et al.* 1998, Batáry & Báldi 2004). In shrub nests eggs can be discovered primarily by birds thanks to their good vision or possibly by tree-climbing mammals. When this happens, the predator can easily notice the eggs in the ground nests under the shrub nest so that they can also be depredated. Most mammals are more active at night and do not climb trees, so only ground nests can be depredated by them, while the shrub nests above them remain hidden in most cases.

5. Conclusion

In our study, we demonstrated that the features of the habitat (shrub rows, forest edge) and the type of nests (shrub, ground) had a significant effect on the daily survival rates of nests. Despite the increased presence of small mammals in both habitats, larger-bodied birds played a greater role in nest predation. The proximity of the shrub and ground nests adversely affected their survival chances.

Pensaspesien läheisyys maapesiin lisää maapesien saalistuksen todennäköisyyttä

Maassa pesivät linnut harvoin pesivät toisen pensaassa pesivän lintulajin alapuolella. Oletuksemme on, että jos pesäsaalistaja löytää yhden pesistä, se todennäköisesti löytää ja ryöstää myös toisen lähellä olevan pesän. Testataksemme tätä oletusta sijoitimme pensaisiin ja niiden alapuolelle maahan keinotekoisia pesiä, joissa oli yksi viiriäisen muna ja yksi muovailuvahamuna. Tutkimus toteutettiin kahdessa eri elinympäristössä, hopeapensasistutuksilla ja metsän reunoilla. Havaitsimme, että maassa oleviin pesiin kohdistui enemmän saalistusta kuin pensaspesiin molemmissa elinympäristöissä. Jos saalistus kohdistui pensaspesiin, se johti myös lisääntyneeseen saalistukseen vaikeammin havaittavissa maapesissä. Tuloksemme viittaavat siihen, että kahden pesätyypin läheisyys voi lisätä saalistuspaineen haitallisuutta, erityisesti metsän reunoilla.

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