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Does Reed Bunting (*Emberiza schoeniclus*) predict the risk of nest predation when choosing a breeding territory? An experimental study

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Increasing evidence suggests that birds minimize the risk of nest predation by preferentially settling in territories with low predator encounter rate. However, little is known about whether they are also able to assess the actual risk of nest predation at the time of habitat occupancy and choose their breeding territories accordingly. Here, we tested this prediction experimentally, using artificial nests placed in 29 Reed Bunting territories and 29 in randomly-selected non-territories located in the same habitat. Simultaneously, we estimated the spatial distribution of the main Reed Bunting nest predator in the study area, viz. the Marsh Harrier. Nests located in Reed Bunting territories were predated less frequently (14%) than were nests placed in non-territories (41%), and this was also associated with the relative abundance of Marsh Harriers in territories (average 3.7) and in non-territories (average 5.8). These findings support the hypothesis that Reed Buntings may be capable of choosing their territories according to the actual predation risk.

1. Introduction

Nest predation is an important factor influencing habitat- and territory-settlement decisions in passerine birds (Söderström 2001, Roos & Part 2004). Although passerines apparently avoid settling close to the nests of bird predators (Meese & Fuller 1989, Suhonen *et al.* 1994, Forsman *et al.* 2001, Thomson *et al.* 2006) or dens of mammalian predators (Tryjanowski *et al.* 2002), little is known about whether they are also able to assess the abundance and distribution of main nest predators at the time of habitat occupancy and choose their breeding territories accordingly. Some studies support this hypothesis. For example, Forstmeier *et al.* (2001) showed in the Russian Far East that female Dusky Warblers *Phylloscopus fuscatus* preferentially settle in territories with low abundance of the Siberian Chipmunk *Tamias sibiricus.* Similarly, in Bialowieza Forest, Wood Warblers *Phylloscopus sibilatrix* settled in numbers inversely proportional to the spring numbers of the Yellow-necked Mouse *Apodemus flavicollis* and the Bank Vole *Clethrionomys glareolus* (Jedrzejewska & Jedrzejewski ex Forstmeier & Weiss 2004). Finally, Morosinotto *et al.* (2010) found that Pied Flycatchers *Ficedula hypoleuca* are even able to distinguish between potential predators during territory selection. However, some bird species are apparently not able to accurately assess the risk of nest predation (Bollmann *et al.* 1997, Misenhelter & Rotenberry 2000), possibly because of low predation-pressure predictability and/or lack of reliable cues for predator assessment. On the other hand, breeding near predators may be beneficial to some bird species because the presence of a specific predator may discourage other perpetrators from depredating their nests (Norrdahl *et al.* 1995, Duncan & Bednekoff 2008).

In this study, we tested the nest-predation risk assessment hypothesis in the Reed Bunting *Emberiza schoeniclus*, a small ground-nesting passerine inhabiting reed beds, wet meadows and other wetland habitats; the species suffers relatively high rates of nest predation (Cramp & Perrins 1994, Glutz von Blotzheim & Bauer 1997). As large birds, particularly the Marsh Harrier *Circus aeruginosus*, are considered the main predators of Reed Bunting nests in our study area (Trnka *et al.* 2009, A. Trnka unpubl. data), we predicted that if Reed Buntings are capable of directly assessing the risk of nest predation when choosing a breeding territory, then (i) they should preferentially settle in territories with lower abundance of Marsh Harriers and (ii) artificial nests located within recently active Reed Bunting territories should be less frequently predated than artificial nests located in randomly-selected non-territories.

To investigate these hypotheses, we carried out an experiment with artificial nests resembling the nests of Reed Buntings in size and appearance, and baited these artificial nests with one fresh Quail *Coturnix coturnix* egg and one plasticine egg. After the Reed Bunting fledging period, we placed additional nests within the Reed Bunting territories and within randomly-selected non-territories located in the same habitat. We estimated the relative frequency of the Marsh Harrier by direct observations. To control for possible effects of nest concealment and nest location on predation of artificial nests, we also measured other components of territory quality in both territories and non-territories (see Material and methods).

2. Material and methods

We conducted the study during the breeding season in 2006 at two localities in the Podunajská nížina lowland, SW Slovakia, around fish-pond systems near Trnava (48°22’ N, 17°32’ E, 144 m a.s.l.) and Pusté Úľany (48°13’ N, 17°34’ E, 114 m a.s.l.). The distance between these localities was ca. 15 km. Both fish-pond systems are surrounded by large areas of terrestrial reed beds and wet meadows, where Reed Buntings occupy reeds mixed with other vegetation at the landward side edge of reed beds. The species is strongly territorial. Males in our study area establish territories during April and early May, shortly after their arrival from the wintering grounds. Territories are used primarily for mating and nesting and may range in size from 96 to 7,500 m^2 (Glutz von Blotzheim & Bauer 1997). Females build their nests on or just above the ground in thick vegetation.

In our study area, Reed Buntings usually nest twice per breeding season, between late April and early July. Nest predation is the main cause of nesting failure in this species (Cramp & Perrins 1994, Glutz von Blotzheim & Bauer 1997). Contrary to experiences from other localities (Pasinelli & Schiegg 2006, Schiegg *et al.* 2007), Marsh Harriers are the predominant Reed Bunting nest predators in our study area, responsible for more than 70% of all nest losses (authors’ unpubl. data).

We applied the territory-mapping method to identify Reed Bunting territories. The study areas were visited weekly from April to July 2006, and all positions of singing males were recorded on maps to define territory borders. To minimize the influence of weather and time of day, we conducted all observations between 6 and 10 AM and only on days with no rain and/or no strong wind. We marked the borders of each territory with red ribbons, and detected nest locations within territories by following the behavior of the parent birds. To avoid nest disturbance we did not check nests during breeding period. Non-territories were selected randomly in similar habitats at a distance of 100 m of the boundary of each active territory.

The spatial distribution of Marsh Harriers in the study localities was recorded during the territory-mapping period. The total observation time was 48 h. All observations were made by the first author using 7–15 power magnitude binocular.

The position and flight height of each bird observed in the study area were recorded on a map. The flight height was estimated using items with known height, such as trees and powerline pylons, located in the study area. Subsequently, after territory identification, the spatial distribution of Marsh Harriers was transformed into the map of Reed Bunting territories. The actual occurrence of raptors within territories and randomly-selected non-territories was defined as either concerning a bird that was observed soaring low over marked territory or non territory, or a bird flying over a marked territory or non-territory at a height of less than 10 m. Observations concerning Marsh Harriers flying at a height of more than 10 meters were excluded from the analysis. The frequency of Marsh Harrier occurrence in each territory or non-territory was then used as a rough measure of the relative abundance of this raptor.

We conducted the artificial-nest experiment between 15 and 26 July, when adult and young birds had just left their territories, to avoid influencing the survival of artificial nests by the behavior of parents from potential active nests. We used handmade artificial nests closely resembling the size and appearance of Reed Bunting nests. To standardize our experimental design with other artificial nest experiments in marsh habitats (Batáry *et al.* 2004, Schiegg *et al.* 2007, Trnka *et al.* 2009), each nest received one Quail *Coturnix coturnix* egg and one plasticine egg, the latter similar in size and shape to a Reed Bunting egg. In each territory, an artificial nest was placed within 1–5 m from the nearest real Reed Bunting nest, and likewise an artificial nest was placed in the centre of each non-territory. The nests were exposed for 12 days, which corresponds to the minimum incubation time in this species (Cramp & Perrins 1994, Glutz von Blotzheim & Bauer 1997), and checked at four days intervals. A nest was considered predated if any of the eggs was missing or appeared damaged. The predators were identified on the basis of peck marks left on plasticine eggs in accordance with Hansson *et al.* (1997) and Batáry *et al.* (2004) and distinguished into one of the following three categories: large birds, small birds and mammals. For each artificial nest, we measured the following nest-site characteristics after finishing the experiment: number of all plant stems within a square of 0.5 × 0.5 m with the nest in the centre, and height and diameter of ten randomly-chosen stems in each square (see also Trnka *et al.* 2010).

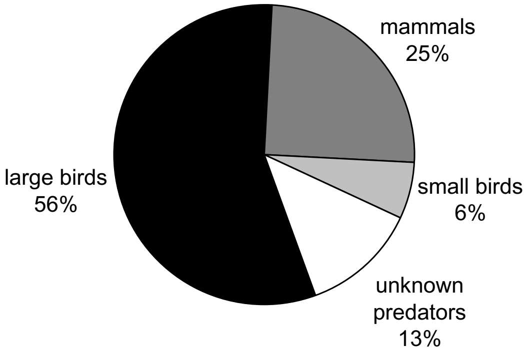

Fig. 1. Nest predators identified from peck marks left on plasticine eggs placed in artificial nests located in Reed Bunting territories and randomly selected non-territories (n = 14).

Vegetation measures were submitted to a principal component analysis (PCA) with Varimax rotation, which resulted in one factor that explained 47.6% of variance. We used territory occupancy (territory or non-territory) as a categorical predictor, and the rate of nest predation as a dependent variable in multiple logistic regression. To control for the potential effect of sampling locality (the two areas), the factor score obtained from vegetation measures was adjusted for the effect of locality. Residuals were then defined as a continuous predictor in multiple logistic regression. The frequencies of Marsh Harriers in Reed Bunting territories and random non-territories were compared using two-tailed *t* test. All statistical analyses were conducted using Statistica 7.0. Mean values are presented with standard errors (SE).

3. Results

We studied 29 Reed Bunting territories and 29 randomly-selected non-territories. Overall, 16 of 58 artificial nests (27.6%) had been predated. Based on pecking marks on 14 predated plasticine eggs, 9 (56%) of the identified predators had been large birds, and the others had been mammals and small birds (Fig. 1). The only large avian predator regularly observed in the experimental area was the Marsh Harrier.

Artificial nests placed in territories were predated less frequently than the nests located in non-territories: 4 (14%) and 12 (41%), respectively (Fisher's exact test; $P = 0.038$). More importantly, multiple logistic regression revealed that the only categorical predictor, territory/non-territory, significantly affected predation rate (Wald's $\chi^2 = 5.18$, df = 1, $P = 0.02$), while vegetation measures, controlling for the effect of locality, were not significant (Wald's $\chi^2 = 0.19$, df = 1, $P = 0.66$).

Out of the total of 266 Marsh Harrier occurrences, 103 were recorded within Reed Bunting territories and 163 within randomly selected non-territories. The relative abundance of the Marsh Harrier was significantly lower in the territories than in the non-territories (3.7 ± 0.45 and 5.8 ± 0.56, respectively; $t = -3.025$, df = 27, $P = 0.005$; Fig. 2).

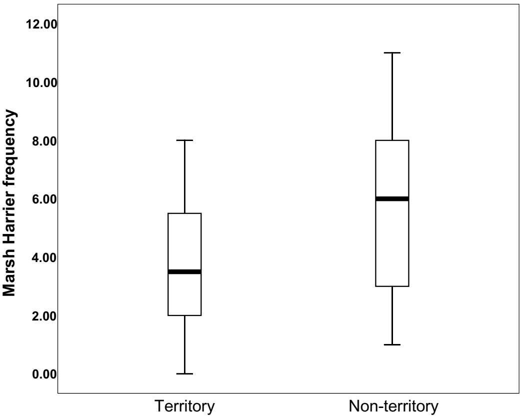

Fig. 2. Medians (horizontal bold lines), quartiles (boxes) and minimum and maximum abundances of Marsh Harriers observed on Reed Bunting territories and on randomly selected non-territories.

4. Discussion

Nest predation is the most important factor determining reproductive success in Reed Buntings (Crick *et al.* 1994, Brickle & Peach 2004, Pasinelli & Schiegg 2006, Schiegg *et al.* 2007, Ejsmond 2008). Therefore, a Reed Bunting territory successfully producing fledglings should include a nest site with a low risk of nest predation (Bollmann *et al.* 1997, Hansson *et al.* 2000). Our experiment with artificial nests supported this hypothesis, showing that nests located in Reed Bunting territories were predated less frequently than nests placed in randomly-selected non-territories. This difference was associated with the distribution of the main nest predator, the Marsh Harrier, in the study area. These findings support our initial hypothesis that Reed Buntings may be capable of choosing territories according to the actual predation risk, and it appears to gain even fine-scaled information in this regard.

Birds, including the Reed Bunting, may be able to assess nest predation risk prior to making settlement decisions (for a review, see Forstmeier & Weiss 2004). Nest losses of many species are related to variation in rodent numbers, but small mammals were only responsible for less than a quarter of all nest losses in our study sites. This pattern agrees with other findings showing that birds are the main predators of Reed Bunting nests (Schiegg *et al.* 2007). Thus, our results imply that at the time of territory establishment, Reed Buntings may use the spatial distribution of Marsh Harriers as a cue to assess territory quality.

That Reed Buntings assess predator presence directly is further supported by the fact that at the time when Reed Buntings occupy their territories, other species are still scarce. For example, in our study area only two pairs of Common Stonechats *Saxicola torquata* were observed, and other common breeders, such as the Sedge Warbler *Acrocephalus schoenobaenus* and the Yellow Wagtail *Motacilla flava*, arrive 2–3 weeks later than Reed Buntings. Therefore, the use heterospecific social information of other species in settling decisions is unlikely (Thomson *et al.* 2003, Forsman & Thomson 2008, Hromada *et al.* 2008). Reed Bunting may select territories based on experience or information gathered in the previous breeding season, for example, based nest predation rates in previous years (see Ward 2005, Nocera *et al.* 2006, Seppänen *et al.* 2007). Low between-year site fidelity of this species in our study area (only 1.1–1.3% of individuals; A. Trnka, unpubl. data) suggests this mechanism may not be used. Furthermore, our study site has hosted research activity for the first time, so we are sure that this activity in earlier years did not impact current Reed Bunting decisions (Antczak *et al.* 2005).

A shortcoming of using artificial nests, from our perspective, is the absence of parent birds that may actively defend their nests by attacking and distracting predators or passively camouflage their brood by sitting on the nest (Montgomerie & Weatherhead 1988, Cresswell 1997, King *et al.* 1999, Weidinger 2002, Schmidt & Whelan 2005, Trnka *et al.* 2008). In the case of large predators such as the Marsh Harrier, the effect of active parent defense at or near the nest on the rate of Marsh Harrier nest predation seems to be negligible. However, the lack of nest camouflage during incubation may affect nest detectability of visually hunting harriers, although this increased risk would be constant across territories and non-territories and still suggests differences in harrier abundance between these sites.

We assume that seasonality in nest-predation rates only affected our results slightly. Temporal variation in the spatial nest-predation risk in marsh habitats relates mainly to nest density, horizontal distribution of nests (edge effect) and the type of vegetation (Batáry *et al.* 2004, Trnka *et al.* 2009). We conducted our experiment after the completion of second nesting of Reed Buntings, at a time when many other birds nesting in our study area had finished their breeding, and the nest density between experimental plots should thus be similar. Moreover, both Reed Bunting territories and non-territories were distributed randomly in the study area in terms of vegetation, as they had similar vegetation structure. Perhaps most crucially, predators might switch their hunting areas after prey species finish breeding, but additional experimental studies would be needed to test this hypothesis.

To conclude, the occurrence and spatial distribution of potential nest predators may be an important factor for the territory selection of breeding Reed Buntings. The birds may use various external cues, such as the spatial distribution of avian predators, in assessing the risk of nest predation. However, such assessment may not be the only or not even the correct mechanism. Testing these questions experimentally, therefore, should be a major challenge for future studies.

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Kykeneekö pajusirkku ennakoimaan pesäsaalistusriskin asettuessaan pesimäreviirilleen?

Lintu saattaa minimoida pesäsaalistusriskiä asettumalla reviirille, joilla on alhainen pedon kohtaamisriski. Yksilön kyky arvioida pesäsaalistuksen riskiä pesimäreviirille asettumisen hetkellä, ja reviirin valinta tämän arvioinnin mukaan, on kuitenkin huonosti tunnettu. Tutkimme tätä olettamusta tekopesillä, joita sijoiteltiin 29 pajusirkun (*Emberiza schoeniclus*) reviirille ja 29 satunnaisesti valittuun pisteeseen samassa ympäristössä. Arvioimme samalla alueiden tärkeimmän pajusirkun pesäsaalistajan, ruskosuohaukan, yksilöiden jakautumista. Pajusirkun reviireillä olleet tekopesät joutuivat vähemmän saalistetuiksi kuin satunnaispisteissä olleet (vastaavasti 14 ja 41 %), mikä oli samansuuntainen kuin havaittujen ruskosuohaukkojen suhteellinen runsaus (keskiarvot vastaavasti 3,7 ja 5,8). Tulokset viittaavat siihen, että pajusirkut kykenevät arvioimaan saalistusriskin asettuessaan reviireilleen.

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