NEST SIZE INFLUENCES NEST PREDATION RISK IN TWO COEXISTING *ACROCEPHALUS* WARBLERS

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The risk of nest predation may be related to nest size, in which case predation might cause selection for smaller nests, but body size forces larger species to build larger nests. This study attempts to find out whether nest size influences predation rate in two coexisting congeneric birds, the Reed Warbler *Acrocephalus scirpaceus* and the Great reed Warbler *A. arundinaceus* that differ in body size. Abandoned nests of both species, each containing one quail egg and one plasticine egg, were placed in the same type of habitat and at the same height. Nest size affected predation probability of the experimental nests since predation rate was lower in the smaller Reed Warbler, than in the Great Reed Warbler. Condition of eggs after predation did not differ between species which suggests that they share the same predators. Most marks on the plasticine eggs were produced by rodents. To test whether the scent of plasticine or quail eggs could attract predators, we performed a parallel experiment using empty Sherman traps and traps baited with a quail egg and a plasticine egg placed in the same area as nests. Capture success was similar in both types of trap and thus the scent of the eggs did not attract the predators. We discuss the implications of these findings for the interactions between these warbler species during the breeding season.

Key-words: Acrocephalus - experimental nests - habitat selection - nest predation - nest size - wetlands

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INTRODUCTION

Nest predation has been suggested as an important constraint on nest size (Collias & Collias 1984; Slagsvold 1989a), but body size forces larger birds to build larger nests, which may be more easily detected by predators. Thus, larger species may suffer higher risk of predation that would need to be compensated by selection of different habitats, greater investment in nest defense or communal breeding (Martin 1992; Hogstad 1995; Cresswell 1997). Nest predation may also have an effect on the assemblage of bird communities through a density-dependent predation rate (Martin 1988b, 1993, 1998). This mechanism promotes coexistence of bird species that differ in their nesting habits. Nesting microhabitat differentiation has been studied mainly in forests and is assumed to be of two types: horizontal differentiation produced by the use of different plant species for building nests, and vertical differentiation produced by the different height of nest placement (Martin 1993). However, in habitats with simpler structure, the range of different microhabitats for nesting may be greatly reduced (Burger 1985). This may be particularly true in reedbeds, that are frequently dominated by just one plant species, the Common Reed *Phragmites australis*, that forms large monospecific stands (Hara *et al.* 1993).

In Europe, the main group of passerines specialised in breeding in marsh vegetation belongs to the genus *Acrocephalus* (Cramp 1992). They present some degree of morphological adaptation of leg and foot to food searching in different vegetation structures, which favours habitat segregation (Leisler *et al.* 1989), but there is considerable nesting habitat overlap between some species, especially the Reed Warbler *Acrocephalus scirpaceus* and the Great Reed Warbler *A. arundinaceus* (Catchpole 1973; Hoi *et al.* 1995). The Great Reed Warbler (GRW hereafter) is three times heavier than the Reed Warbler (RW hereafter) and builds nests that are more than 4 times greater in volume than Reed Warbler nests. In this paper we test if greater nest size increases predation risk for nests placed in the same reed habitat, and explore the consequences that different nest size may have for these two coexisting bird species. Owing to the possible strategies that the larger species could adopt to reduce predation risk, it is unlikely that observational studies would detect either intra or inter-specific relationships between nest size and predation rate. Thus, several studies have used experimental nests in an attempt to overcome this problem and some have found an increase in predation rate with nest size (Møller 1990; Cresswell 1997; Sieving & Willson 1998), although others have not (Slagsvold 1989b). We used abandoned nests of both species to test the effect of size on predation risk. Egg and nest condition after predation is used to assess whether they share the same predator species.

METHODS

The study was performed at the Hondo Natural Park (Alicante, SE Spain, 38°11'N, 0°42'W), formed by a system of ponds and channels built over a pre-existing natural wetland to regulate water flux and to store water for irrigation. The Park has an area of about 2400 ha, which includes large extensions covered by reeds. During the breeding season of 1997 we collected nests when their breeding cycle had finished. These species build open cup nests, supporting the structure by embracing several reed stems. Both use the same vegetal material and thus nests have similar colour and appearance (Cramp 1992, own observations). Nests were collected by cutting the reed stems that held them at about 30 cm above and below nest insertion.

Two areas where the study species usually build nests were selected for the experiment: one was located by the shore of one of the dikes that delimit the ponds of the Hondo (afterwards, Shore Group), and the other was located in a reedbed that emerges in front of the dike, 10-15 m from the shore, forming a long island of reeds (afterwards, Island Group). 75 RW nests and 25 GRW nests were placed in the Shore group. Nests were placed every 25 m along the shore, with one GRW nest for every 3 RW nests. As the number of GRW nests available was small, nests of this species were not used in the Island Group. In this area, 40 RW nests were also placed at 25-m intervals, starting in front of the first RW nest in the Shore group. Natural densities in our study area ranged between 2.9 and 17.6 pairs ha^{-1} for RW and between 0.9 and 4.3 pairs ha^{-1} for GRW (Pinheiro 1999), thus distances between experimental nests were within the range of natural nests. The average ($\pm$ SD) size of the RW nests (diameter x height) was 71.1 $\pm$ 6.76 mm (range 55-90 mm) x 75.8 $\pm$ 14.06 mm (range = 50–145 mm) and of GRW nests 113.6 $\pm$ 11.20 mm (range 90-133 mm) x 138.9 $\pm$ 26.95 mm (range = 90-210 mm).

All nests were placed from a canoe at chest height (1.3 m above water level) and at about 0.4 m from the external edge of the reedbed, a location that is within the range of natural nests of both species. In a sample of natural nests of the same study area mean ($\pm$ SD) nest height was 1.76 $\pm$ 0.72 m for the RW (0.44-3.70, $n = 80$) and 0.98 $\pm$ 0.38 m for the GRW (0.49-1.64 m, $n = 14$). The distance to the edge of the reedbed presented an asymmetric distribution in both species, with an average of 0.71 $\pm$ 0.51 m for the RW (median 0.49 m, 0-2 m, $n = 80$) and 0.51 $\pm$ 0.49 m for the GRW (median 0.28 m, 0-1.5 m, $n = 14$). Nests were fixed to the vegetation by attaching the extremes of the stems included in its structure to

the same number of reed stems, using brown and dark green adhesive tape. A quail egg (approx. 34 x 26 mm) and a plasticine egg (approx. 22 x 16 mm), painted with grey and brown spots to resemble the general pattern of GRW and RW eggs, were placed in each nest. The plasticine egg was attached to the nest with fishing line. Shore Group nests were distributed on 28th June 1997 and Island Group nests on 7th July 1997. Nests were visited after 7 and 14 days. On day seven, the quail egg in surviving nests was replaced with a fresh egg. A nest was considered to have been depredated if either of the two eggs appeared damaged or was missing. Condition of the nests after predation was classified as: intact (no perceivable alteration), having a hole in the side, tilted or torn (seriously damaged). The condition of the quail egg was classified as intact, scratched (presumably by rodents), pieces of broken shell, and missing. The condition of the plasticine egg was classified as intact, with rodent-tooth marks, missing and "other causes" (this category included eight eggs in RW nests: five eggs were hanging out of the nest, caught by the fishing line, but without marks; and three eggs had unidentified marks).

In order to find out whether predators were attracted to the experimental nests by the scent of the plasticine or quail eggs, we performed an experiment using Sherman traps (7.5 x 9 x 23 cm). The traps were new and washed with hot water. 30 empty traps, and 30 traps containing one plasticine and one quail egg, in exactly the same manner as the experimental nests, were placed in the field. The traps were set in the morning along the same shore of the dike where the Shore Group of experimental nests had been placed, 30 m apart and alternating empty traps with baited traps. Traps were examined and removed the next morning. This experiment was repeated twice (8th July and 24th July 1997) washing traps out with hot water in between.

We fitted a hierarchical log-linear model (Freeman 1987) to the data from the mammal trapping experiment. Significant interactions in the log-linear models were selected by backward elimination of effects. First a saturated model, including all possible interactions, was adjusted to the data. Then, the significance of removing the higher order interaction was assessed with the Likelihood Ratio test. All statistical analyses were performed using the SPSS package (Norusis 1994).

RESULTS

Predation of experimental nests

The percentage of RW nests depredated (Table 1) did not differ between nests on the shore and the island, during either the first week ($\chi^2_1 = 0.87$, $P = 0.351$) or the second week ($\chi^2_1 = 0.146$, $P = 0.703$). Experimental RW nests were preyed upon less than GRW nests after one week, considering only Shore Group nests (RW: 73.3%; GRW: 96.0%; $\chi^2_1 = 5.81$, $P = 0.016$) and when all exper-

Table 1. Number of experimental nests found depredated in each visit. The percentage of nests that were preyed upon between consecutive visits is shown in parentheses as well as the percentage of nests surviving at the end of the experiment.

	Found depredated after		Surviving	
	7 days	14 days		
Reed Warbler				
Shore	55 (73.3)	18 (90.0)	2	(2.7)
Island	26 (65.0)	12 (85.7)	2	(5.0)
Total	81 (70.4)	30 (88.2)	4	(3.5)
Great Reed Warbler				
Shore	24 (96.0)	1 (100)	0	-

imental nests were considered (RW: 70.4%; GRW: 96.0%; $\chi^2_1 = 7.16$, $P = 0.007$). As predation on experimental nests was so high, very few nests survived until the end of the experiment, so that predation rates during the second week could not be compared by species. We did not find any evidence of clumping of nest predation (Runs test; Shore nests: $z = -1.577$, $P = 0.115$; Island nests: $z = -0.247$, $P = 0.805$). Marks on the plasticine eggs could have revealed the identity of the predators. However, 56.6% of the plasticine eggs disappeared, and another 9.6% of the plasticine eggs were intact or we were unable to identify the predator. Condition after predation of both kind of eggs did not differ between species (plasticine egg, $\chi^2_3 = 1.92$, $P = 0.590$; quail egg, $\chi^2_3 = 1.80$, $P = 0.615$). Rodent marks were found on 33.8% of the plasticine eggs (Table 2, data for both species pooled). The quail egg was missing in half of the nests (50.7%). Those that remained appeared to be mainly intact (68.7%) or had only scratches on the shell (20.9%), and only 10.4% were broken. The state of the experimental nests after predation differed between species ($\chi^2_3 = 16.97$, $P = 0.001$). The GRW nests appeared torn (44%) or tilted (16%) more often than RW nests (20.7% and 2.7%). On the other hand, RW nests remained intact (49.5%) or had holes in the sides (27%) more often than GRW nests (36% and 4% respectively, Table 2).

Mammal trapping

During the first trapping night mammals were captured in 56% of empty traps and 50% of the traps baited with a plasticine and a quail egg, while during the second night these figures were 37.9% for empty traps and 66.7% for baited traps. Mice were the most frequent captures (*Mus musculus* 79.6%, *Apodemus sylvaticus* 5.6%) and some shrews (*Crocidura russula*) were captured only in the second night (14.8% of total captures). To find out whether the probability of capturing a mammal depended on the contents of the trap (empty or with plasticine and quail eggs), we performed a log-linear analysis, excluding closed traps. The third order interaction (Trap Night × Trap Content × Trapping Result) was non-significant (Likelihood Ratio Test. $\chi^2_4 = 3.25$, $P = 0.517$) as was the interaction between trap content and trapping result ($\chi^2_4 = 4.28$, $P = 0.369$), but the interaction between trapping night and trapping result was highly significant ($\chi^2_4 = 21.14$, $P = 0.0003$). Thus, the number and species of mammals trapped did not differ between empty traps or those that contained plasticine and quail eggs.

DISCUSSION

The proportion of experimental RW nests that were preyed upon during the first week of exposure (70.4%) was significantly lower than the pro-

Table 2. Condition of experimental nests and eggs after predation. Percentages are shown in parentheses.

Plasticine Egg	Intact	Rodent marks	Missing	Other
GRW	1 (4)	9 (36)	15 (60)	0
RW	4 (3.6)	37 (33.3)	62 (55.9)	8 (7.2)

Quail Egg	Intact	Scratched	Broken shells	Missing
GRW	11 (44)	3 (12)	1 (4)	10 (40)
RW	35 (31.5)	11 (9.9)	6 (5.4)	59 (53.2)

Nest	Intact	Hole in side	Tilted	Torn
GRW	9 (36)	1 (4)	4 (16)	11 (44)
RW	55 (49.5)	30 (27)	3 (2.7)	23 (20.7)

portion of GRW nests (96.0%). Thus, these results clearly show that, when nests of both species are placed in the same type of reeds and at the same height, the probability of being visited by a predator is higher for the larger nests of the larger species. To our knowledge, this is the first study to show this result in an interspecific comparison using real abandoned nests. Sieving & Willson (1998) found a similar result using two sizes of artificial nests (diameter 14 cm vs. 8.5 cm, height 6.5 cm vs. 3.5 cm) similar in size to those of these two warbler species: larger nests suffered more predation than smaller ones in the same locations (ground or shrub), both in coniferous and deciduous forests.

Marks left on the plasticine eggs identified rodents as the main predators involved, but unfortunately, most (56.4%) of the plasticine eggs disappeared from the nests. The Sherman traps experiment showed that the success of capture did not differ in baited and non-baited traps and so plasticine and quail egg scents did not attract rodents to traps. Thus, there is no reason to believe that potential predators were attracted to nests by the scent of the eggs. Bayne & Hobson (1999) arrived at the same conclusion in another experiment and Hoi & Winkler (1994) experimentally found no effect of human scent on predation rates. The condition after predation of both plasticine and quail eggs was very similar in experimental nests of both warbler species which suggests that predators of nests of both species were the same. Nest condition after predation differed between them, with GRW nests usually more severely altered than RW nests. This does not necessarily mean that different predators attacked the nests, but rather, that since GRW nests were more easily detectable, they were visited more often by predators than RW nests, and so the nest structure was disturbed more. Abundance of rodents may fluctuate between years and so their predation pressure. We do not have data about the relative abundance of these mammals along several years, but the fact that about 50% of traps captured mice suggests that rodent abundance was high, at least in the study year. It is possible that in years or places with lower predator abundance the difference in predation risk between small and big nests would be smaller.

The greater detectability of GRW nests implies that this species should invest more in nest defence or be more selective in nesting microhabitat location to reduce the cost of nest defence and the risk of predation. There is evidence that GRW selects safer nest sites than RW. Graveland (1998) used discriminate analysis to compare the characteristics of nest habitat in both species and found that GRW nested farther from the shore than RW, in wider belts of reeds growing further out in the water, where water was deeper. Graveland (1998) also found that when reeds in water were common GRW selected for higher reed density and stem height and concluded that the RW uses types of reeds that are abundant in his study area while GRW selects a much scarcer type of reed. An experiment by Hansson *et al.* (2000) also stresses the importance of selection on GRW nest placement. They found that the attractiveness of a territory (measured as the average ranking for occupation over several years) affected nest predation probability, both in experimental and real nests, as expected: nests in less attractive territories were depredated more often. Other factors may also contribute to explain the difference in nesting habitat between these species. In particular, GRW may need stronger reed stems than RW to support their nests (Graveland 1998) and if reeds growing in islands were thicker than reeds growing in the shore this could explain the selection for nesting farther from the shore. However, in our study area the reed diameter is similar in both locations or even thicker in the shore (unpubl. data). The observation by Leisler (1981) that GRW nesting in water reed deserted their nests when the water level dropped also supports the importance of nest predation risk for the nesting microhabitat selection in this species.

Nests of the warbler species studied are exposed to the same predator community, but RW are much more abundant than GRW and their nests are sometimes separated by less than 10 m (Cramp 1992), so that they represent a more abundant resource for nest predators than GRW nests.

Since predators looking for the abundant, though less detectable, RW nests would easily find any GRW nest in the same area, it would pay to the GRW to chase away RW, behaviour commonly observed in this species (Hoi *et al.* 1991, Honza *et al.* 1999), or even to prey upon their nests. Martin (1988a, 1993) suggested that overlapping in nest sites increases the risk of nest predation in coexisting species, and that this would be an important selection pressure in the evolution of differentiation of nesting habitats, a hypothesis that has been supported by several experiments (Martin 1988b, Hoi & Winkler 1994, Martin 1996, Schmidt & Whelan 1998). However, those experiments compared differing nest placements (ground, shrub or canopy), not size. Our results, and those of Sieving & Willson (1998), suggest that when coexisting species differ in body size, and thereby in nest size, asymmetry in the effect of species density on each other could exist. We hypothesize that the use of the same nesting places would be more negative for the larger species. We expect this to be most likely when the success in nest defence is weakly affected by the body size of the parents (i.e., predators are larger than defending parents) and the habitat structure is relatively simple, such as reedbeds.

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SAMENVATTING

Het risico van nestpredatie zou beïnvloed kunnen worden door de grootte van het nest, omdat grotere nesten meer opvallen. Als dat klopt, zou nestpredatie kunnen resulteren in selectie voor kleinere nesten. Maar soorten met een groter lichaam zijn gedwongen om grotere nesten te bouwen. Het hier gepresenteerde onderzoek is gericht op de vraag of nestgrootte de kans op nestpredatie beïnvloedt in twee samen voorkomende rietvogels die verschillen in lichaamsgrootte, de Kleine Karekiet *Acrocephalus scirpaceus* en de Grote Karekiet *A. arundinaceus*. Verlaten nesten van beide soorten werden verzameld en vervolgens geplaatst op dezelfde hoogte in hetzelfde rietveld. Elk nest kreeg twee eieren, een kwartelei en een ei van klei. Het ei van klei was met een draadje vastgebonden aan het nest en bedoeld om tandafdrukken en andere sporen van predatoren vast te leggen. Uit de resultaten blijkt dat nesten van de Grote Karekiet vaker werden gepredeerd dan nesten van de Kleine Karekiet. Nestgrootte lijkt dus inderdaad van invloed op de mate van nestpredatie. De eieren van gepredeerde nesten van beide soorten lieten dezelfde sporen zien. De predatoren betroffen in beide gevallen dus waarschijnlijk dezelfde soorten. De meeste sporen op de eieren van klei waren van muizen afkomstig. Om te testen of de geur van de klei of de kwarteleieren de predatoren had aangetrokken, hebben de auteurs een experiment gedaan waarin het vangsucces van deze dieren in Shermanvallen die al dan niet waren voorzien van eieren, werd vergeleken. Het vangsucces was in beide gevallen hetzelfde. De geur van de eieren trok de predatoren dus niet aan. De discussie gaat in op de gevolgen van de resultaten voor nestplaatsselectie en interacties tussen Kleine en Grote Karekieten in het broedseizoen. (IT)