

Nest predation in European reedbeds: different losses in edges but similar losses in interiors

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A b s t r a c t. Higher nest predation at habitat edges is a major problem for conservation biology. We studied nest predation using artificial nests resembling great reed warblers' nests at edges and interiors of reedbeds in four large wetlands in Europe: Lake Hornborga (Sweden), Lake Neusiedl (Austria), Lake Velence (Central-Hungary) and Kis-Balaton marshland (West-Hungary). Nest losses showed great local and temporal variation, and in general there was larger nest predation at the edges than in the interior reedbeds. Predation rates of artificial nests along different reedbed edges showed great variation. In contrast, predation rates of interiors were more similar across all experiments, with less variation. This may indicate the existence of a habitat-specific predation rate with less variation in interiors of large habitats, while edges are more exposed to the influences of other factors, which resulted in higher variation of predation rates among study sites. Therefore, reedbed conservation should prefer large stands if considering only passerine nest predation, because (1) nest survival seems to be higher in interior than at edges, and (2) because interiors are less variable, i.e. more stable than edges. The designation of reedbeds cannot rely on reedbed edges, where predation can change due to factors not related to the reed habitat at all.

Key words: artificial nests, edge effect, habitat fragmentation, great reed warbler, variability

Introduction

Landscape heterogeneity has attracted great interest in ecology and conservation biology. Heterogeneous landscapes are characterised by a large amount of habitat edges. Habitat edges may influence the occurrence, abundance, and behaviour of species (e.g., Hoi et al. 1991, Murcia 1995, McCollin 1998, Batáry & Báldi 2004). Characteristic for edges is the higher level of nest losses due to predation and brood parasitism (Paton 1994, Rothstein & Robinson 1994, Andrén 1995, Robinson et al. 1995, Hartley & Hunter 1998, Batáry & Báldi 2004). Nest predation is a key factor in community organisation (Martin 1996, Hoi & Winkler 1994), reproductive success (Major & Kendall 1996) and thus the survival of threatened bird species. After the pioneering works by Gates & Gysel (1978) and Wilcove (1985) numerous studies have investigated nest predation along edges (reviews are Paton 1994, Andrén 1995, Söderström et al. 1998, Batáry & Báldi 2004). The debate on the role of edges on nest predation is still continuing, probably as a result of variation in the results. Batáry & Báldi (2004), in their review, found variation regarding location, landscape and nest characteristics. They also showed that nest predation at edges is significantly higher for deciduous forests and wetlands, but not for fields and coniferous forests (Batáry & Báldi 2004). The variation among

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habitat types, therefore, questions any extrapolation on edge effect in relation to nest predation from one habitat to another. For example, Woodward et al. (2001) found that the ecological trap hypothesis (Gates & Gyse 1978) might not be valid for shrubland birds. This hypothesis states that, in habitat edges, the complex vegetation attracts birds for nesting, however, they are trapped by increased predation along edges. The results of Woodward et al. (2001) indicate the existence of differences depending on habitat type. Recently, mainly forest edges were studied in relation to nest predation, but there is a need to examine more habitats to find general rules. Reedbeds, for example, are rarely considered in this context (but see Picman et al. 1993, Jobin & Picman 1997, Poulin et al. 2000, Hoi et al. 2001).

To understand variation of nest predation rate among habitats, it is also necessary to study variation within a habitat, e.g. in different locations. In this study we compared nest predation of the edge and interior of four European reedbeds in Austria, Hungary and Sweden. We chose this habitat because it is more similar in structure at different areas than e.g. forests. Reedbeds are of conservation concern because they are declining in Western Europe (Ostendorp 1989, Hawke & José 1996) and harbour a unique and specific biota (Hawke & José 1996). This includes bird species declining in Western Europe, such as bittern (*Botaurus stellaris*), sedge warbler (*Acrocephalus schoenobaenus*), great reed warbler (*A. arundinaceus*) and Savi's warbler (*Locustella luscinioides*) (Hagemeyer & Blair 1997). Our aim in this study was to describe nest predation patterns and its variance in reedbed edges and interiors using artificial passerine nests, and to evaluate the results for conservation purposes.

Study Area and Methods

The study was conducted in two wetlands in Hungary, one in Austria and one in Sweden. Lake Velence, Hungary (24 km², 47° 10' N 18° 32' E) is a shallow lake with a reedbed (*Phragmites australis*) of ca. 1000 ha; marshland Kis-Balaton, Hungary (150 km², 46° 42' N, 17° 21' E) is more heterogeneous than Lake Velence, consisting of reedbeds, cattail (*Typha* sp.) stands, sedge meadows, bushes and small forest patches. It has ca. 2500 ha of reedbeds, largely at the study site. Lake Neusiedl, Austria (320 km², 47° 45' N, 16° 42' E) is a shallow lake, similar to Lake Velence, with 17800 ha of reedbeds. Lake Hornborga, Sweden (34 km², 58° 19' N, 13° 33' E), is a shallow lake with about 1500 ha of reedbeds (for details about the areas see Báldi & Kisbenedek 1999, Hertzman & Larsson 1999, Moskát & Báldi 1999, Batáry et al. 2004). We placed out nests made of chicken wire and lined with dry grasses and reed flowers. In size and appearance the nests resembled great reed warbler nests. Artificial passerine nests give sufficient information for comparative purposes (Major & Kendal 1996). The predation rate of such dummy nests proved to be similar to real great reed warbler nests (Batáry & Báldi 2005). The nests were fixed to two reed stems at 30–60 cm high, similarly to the real great reed warblers nests (Batáry & Báldi 2005), except that at Lake Hornborga the nests were placed at 20–40 cm height due to the shorter reeds. Each nest contained one fresh Japanese quail and one plasticine egg; the latter was similar in size to the great reed warbler eggs. Nests were placed at the edge (0–2 m), and interior (>50 m) of reedbeds. Exposure times were different (Table 1). A nest was predated if at least one of the eggs was missing or damaged. We calculated the daily survival of nests (=1–daily predation rate) and its variance using Mayfield's method, a maximum likelihood estimator (Johnson 1979).

Table 1. Summary of experiments using artificial nests to assess nest predation in reedbed interiors and edges in Europe. The water depth in the reedbeds was more than 20 cm. The surrounding landscape was marshland for all experiments, except for experiment 5, where the adjoining landscape was a mixture of dry reedbeds, sedges, fields, and bushes.

Experiment	Location	Date	Exposure (day)	Treatment	Edge type	No. of nests	No. of lost nests (%)
1	Lake Velence	June 98	12	edge	reedbed – open water	25	14
			12	interior		25	16
2	Lake Velence	Apr 99	4	edge	reedbed – open water	30	12
			4	interior		30	14
3	Lake Velence	May 99	4	edge	reedbed – open water	30	25
			4	interior		30	16
4	Lake Hornboga	June 98	7	edge	reedbed – open water	22	16
			6	interior		23	5
5 & 6	Kis-Balaton	May 99	3	edge	reedbed – dike	15	0
			3	interior I		15	3
			3	interior II		15	7
7	Lake Neusiedl	Apr 01	3	edge	reedbed – open water	39	33
			3	interior		38	14
8	Lake Neusiedl	May 01	2	edge	reedbed – open water	40	11
			2	interior		40	5
9	Lake Neusiedl	June 01	3	edge	reedbed – open water	40	30
			3	interior		39	9

We used effect sizes to estimate the differences between pairs of experiments. This method was necessary because there were differences among the experiments (e.g. sample size, edge type), therefore it was not possible to enter them together into a conventional statistical analysis, e.g. ANOVA. Hedge's *d* was used as effect size, which performs well even for small ($N < 5$) sample sizes (Rosenberg et al. 2000). The effect sizes were signed arbitrarily as positive if predation was higher in the edge than in the interior. In addition to the usual comparison between edge and interior predation pressure, we were also interested in the variation of predation rate at edges and at interiors. For this question we also calculated effect sizes comparing all possible edge experiments in pairs. Similar analysis was made for all possible interior experimental pairs. The effect size of nest predation edge effect in the paired interior-interior and edge-edge comparisons cannot be signed; therefore, we used the absolute values of effect sizes. This did not show a direction of the effect, but we were interested in the magnitude of variation among edges and among interiors, therefore it fulfilled our requirements. Having the effect sizes, we reached a common statistical background for all individual experiments, which can be entered into the summary meta-analysis. The meta-analysis technique was used to quantitatively synthesise the results, applying the MetaWin 2.0 program (Rosenberg et al. 2000). The meta-analysis uses the effect sizes of the individual experiment as a common statistical measure and summarises these across the studies (Gurevitch & Hedges 1999). Normality was tested using the normal quantile plot. We accepted the normal distribution of data because the points were inside the confidence bands. We used a fixed-effects model for the comparison of edge-interior experiments, because the estimate of the pooled variance was zero, but a mixed-effects model for the edge-edge and interior-interior comparisons, because the variance was larger than zero (Rosenberg et al. 2000).

Results

Altogether 230 (46.4 %) of the 496 artificial nests were depredated. Nest losses showed great variation regarding site and time (Table 1). The general pattern of increased nest losses in reedbed edges emerged (Table 2). The meta-analysis revealed an interesting pattern, the variation of effect sizes of edges was almost an order of magnitude larger than in the interiors; this is indicated by the limits of the 95% CIs of the edge-edge and interior-interior comparisons (Table 2). Therefore, an interesting pattern of survival rate was found, with less variation in the interior of reedbeds and higher variation at their edges (Fig. 1).

Table 2. Summary of the meta-analyses on daily nest survival rates in European reedbed edges and interiors. E: effect size; CI: confidence interval.

Comparison	df	E	95% CI **
Edge – interior	8	0.7323	0.0613 to 1.4033
Edge – edge *	14	4.2222	2.1751 to 6.2693
Interior – interior *	20	1.5217	1.2567 to 1.7868

*The absolute value of effect sizes was used in these meta-analyses, because we were interested whether there is any difference between edge-edge and interior-interior comparisons. It is not possible to decide, even arbitrarily, which from the two edges (or interiors) should have higher nest losses.

**The 95% confidence limits indicate a significant effect size at $P=0.05$, if it did not bracket zero.

We identified 32 individual predators from the eggshell remains and marks in the plasticine eggs, and found 12 empty nests in the 1999 experiments at Lake Velence and Kis-Balaton. The predator community was rather poor at Kis-Balaton, with only small passerines destroying the eggs (8 cases). At Lake Velence, however, a diverse predator community was responsible for the losses (Table 3). There was no great difference between the interior and edge predators, although birds seem to be more frequent in the interior. Empty nests may be attributed to large predators (B a y n e & H o b s o n 1999), supported by our observations of broken reed shoots and damaged nests at 6 of the 12 cases. Potential species are the marsh harrier (*Circus aeruginosus*) and otter (*Lutra lutra*).

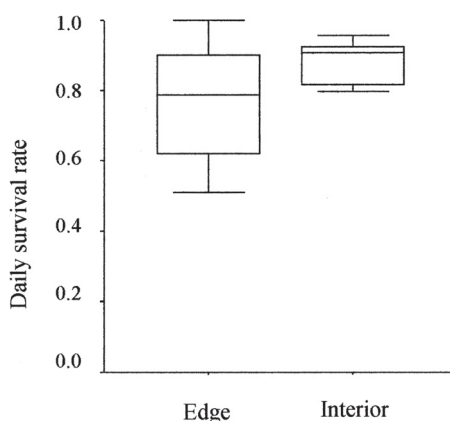


Fig. 1. Mayfield's survival rates of artificial nest experiments in edge (N=8) and interior (N=9) of reedbed habitats in Austria, Hungary and Sweden. Medians, quartiles and ranges are plotted. Note the large variation of rates in edge, and small in interior sites.

Table 3. Nest predators identified from marks left on eggs and nests at the reedbed of Lake Velence.

Predator	Edge	Interior
Large birds *	5	10
Small birds	2	3
Large mammals	0	0
Small mammals **	1	3
Empty nests	8	4

* Large birds were Corvidae and marsh harrier (*Circus aeruginosus*).

** Small mammals were *Sorex araneus* and/or *Neomys* spp.

Discussion

We found a nest predation edge effect in this study, which strengthens the results of a recent review (B a t á r y & B á l d i 2004). However, some studies in open habitats suggest that predation rates are usually not increased near the edges (e.g., V i c k e r y et al. 1992, P i c m a n et al. 1993, P a s i t s c h n i a k - A r t s et al. 1998, S ö d e r s t r ö m et al. 1998, H o i et al. 2001, H o w a r d et al. 2001). H o n z a et al. (1998) and H a n s s o n et al. (2000) found no edge effect in nest predation in reedbeds. However, they studied real nests and only

within a few meters of the reedbed edges, known to have different patterns than the larger scale comparison we applied in the present study (B á l d i & K i s b e n e d e k 1999).

A more important result of this study was that predation rates in reedbed interiors varied less between study sites than predation at edges. The smaller absolute effect size and confidence limits of interior-interior, than edge-edge comparisons reveal small variations in nest predation rates in the interior, and large variations at the edge. Although larger means have larger variance (Z a r 1996), consequently larger nest predation rates in edges may result in larger variances, this pattern can be explained by reasonable ecological arguments. Reedbed interiors may be dominated by reedbed specific predators and, consequently, a more characteristic reedbed predation rate. Edges may have been influenced by local site-specific factors, which are dependent on landscape type and structure, proximity to predator nests and perches, geographic position, etc., and not the reed habitat (D o n o v a n et al. 1997, M o s k á t & H o n z a 2000, Š á l e k 2004). These factors may result in larger variation of nest losses among edges. Although we were intent on carrying out the experiments in similar reedbeds, in reality there is variation due to e.g., geographic location (Central-Europe, Scandinavia), landscape structure (reed patches at Lake Velence and Lake Hornborga, vs. large continuous reedbeds at Lake Neusiedl and Kis-Balaton), or surrounding habitat (dike and heterogeneous habitats at Kis-Balaton vs. water and reed elsewhere).

The identification of predators of nests is a necessary task to understand nest predation edge effect (C h a l f o u n et al. 2002). The little evidence suggests that the response of nest predators to fragmentation and habitat edges is complex, taxon-specific and context-dependent (C h a l f o u n et al. 2002). The large diversity of only 36 predation marks at Lake Velence also suggests that a diverse predator community is present, which indicates complex species interaction even in a simple landscape.

We can conclude three important guidelines for reedbed management. First, artificial nests seem to be reliable substitutes for real nests in the assessment of nest predation pressure (B a t á r y & B á l d i (2005). It is important, because the search for real nests can disturb breeding and damage the fragile reed habitat. Second, there is a general edge effect in nest predation, with higher predation rates at the edge than in the interior reedbeds - an argument to conserve large reedbeds. We should caution that conservation may have several aims, probably with contrasting management strategies. For example, in spite of larger nest predation, reedbed edges are preferred nesting and foraging sites of reedbed passerines (B á l d i & K i s b e n e d e k 1999). Third, since reed stands along edges are not “true” reed habitats due to the dominance of predation (and probably other) influences from the surroundings, large reedbeds should be protected, where interiors are less affected by the surrounding habitats. Considering that the “interior nests” in our experiments were usually further than 200m from the edges, the conservation of reedbeds larger than 13 ha is necessary, a considerably larger area than suggested by B á l d i (1999), based on vegetation edge effects.

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