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**Nest predation in Reed Buntings *Emberiza schoeniclus*: an experimental  
study**

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*Running title: Nest predation in Reed Buntings*

Predation is a major cause of nest failure in many bird species. High levels of nest loss may be a consequence of habitat fragmentation, leading to increased amounts of edge habitat. Yet the evidence for generally high nest predation rates along edges in fragmented landscapes is ambiguous. Using real nests of Reed Buntings *Emberiza schoeniclus* in which artificial Reed Bunting and real Quail eggs were placed, we experimentally tested for edge effects on nest predation in highly fragmented reed *Phragmites* sp. habitats in the Swiss lowlands. We also examined seasonal patterns of predation and the impacts of nest visits by observers. We found evidence for an edge effect at the water-sided reed edge, with nests located closer to the water being more likely to be predated than those further away. Predation probability increased from early to late season, suggesting that nest predation may be density dependent. Probability of nest predation was only weakly influenced by whether or not a nest was visited. Our results suggest that the intensive reed management currently applied in Swiss nature reserves may result in unnaturally high levels of nest losses in the Reed Bunting, because reed bands are not wide enough to allow nest placement at a safe distance from reed edges.

Predation is the main cause of nest failure in many bird species (Ricklefs 1969, Martin 1993). In open-nesting songbirds, annual nest losses due to predation can substantially differ within and among species (Winkler 2004), with extreme values exceeding 90% (Møller 1988, Hanski & Laurila 1993, Hoover *et al.* 1995). High levels of nest loss may have implications for the persistence of populations (Robinson *et al.* 1995), given the importance of nest success in avian population dynamics (Ricklefs 1969, Sæther & Bakke 2000). It has been argued that nest failure rates due to nest predation and/or parasitism increase with increasing habitat fragmentation (Brittingham & Temple 1983, Wilcove *et al.* 1985, Paton 1994, Hartley & Hunter 1998). Fragmentation generally increases the amount of edge habitat relative to core habitat and may hence facilitate predators' access to nests located close to edges. Many studies have reported increased nest predation along habitat edges (Paton 1994, Hartley & Hunter 1998, Batáry & Báldi 2004). In contrast, reviews by Andrén (1995) and Lahti (2001) suggest that nest predation rates in birds are not generally elevated near habitat edges in fragmented landscapes. The potential impact of edge effects in birds has been studied mainly in species inhabiting forested areas (Paton 1994, Andrén 1995). Far less is known about edge effects in wetland species (Lahti 2001, Batáry *et al.* 2004), although wetlands have been strongly affected by destruction and fragmentation (Keddy 2000). Moreover, results of the few studies on nest predation in wetlands are ambiguous (Hoi & Winkler 1988, Honza *et al.* 1998, Kristiansen 1998, Báldi & Batáry 2000, Batáry *et al.* 2004, Batáry & Báldi 2005a).

Patterns of nest predation often vary seasonally. Nest predation rates have variously been shown to decrease (Hansson *et al.* 2000, Roos 2002, Schäfer 2002, Conner & Perkins 2003), remain constant (Gates & Gysel 1978, Honza *et al.* 1998) or increase over the breeding season (Schaub *et al.* 1992).

Explanations for seasonal variation in nest predation rate focus on changes in the availability (density dependence) and visibility (vegetation density or cover) of nests (Hoi & Winkler 1988, Ferguson 1993, Hoi & Winkler 1994, Honza *et al.* 1998, Hoi *et al.* 2001, Roos 2002, Batáry *et al.* 2004). Whatever the reasons for seasonal changes in nest predation risk, temporal patterns of nest predation may have important implications for individual fitness and life history evolution (Martin 1995).

Nest predation rates reported in the literature may be inflated because of nest visits by human observers. Researchers may leave tracks when visiting nests and may thereby attract predators. In addition, human and/or parental activity during nest visits may attract the attention of predators (Skutch 1985). Whether or not observers affect reproductive performance of their study subjects is unclear: some studies suggest negative effects of visitation on nest survival (Bart & Robson 1977, Lenington 1979, Major 1990, Whelan *et al.* 1994, Tryjanowski & Kuzniak 1999, Gutzwiller *et al.* 2002), while others found minimal or no negative effects (Hoi & Winkler 1988, Reitsma *et al.* 1990, Hoi & Winkler 1994, O'Grady *et al.* 1996, Mayer-Gross *et al.* 1997, Ortega *et al.* 1997).

In Central Europe, Reed Buntings *Emberiza schoeniclus* are typically inhabitants of transition zones along standing or slow-flowing bodies of water and prefer mature reed *Phragmites* sp. as nesting habitat (Blümel 1995). These

wetland habitats are now highly fragmented and in Switzerland, where the study was conducted, current management regimes often leave only narrow bands of reed a few meters wide along lakes. Predation is the main source of nest failure in Reed Buntings (Cramp & Perrins 1994, Glutz von Blotzheim & Bauer 1997, own obs.), but it is unclear whether or not the current management regimes and the associated increase in reed edge habitat increase nest predation.

In this paper, we present results of a nest predation experiment using Reed Bunting *Emberiza schoeniclus* nests collected after the previous breeding season within which we placed artificial and real eggs. The goals of the study were threefold. First, we assessed whether the probability of nest predation is a function of proximity of a nest to a habitat edge (the 'edge effect on nest predation hypothesis'; Gates & Gysel 1978, Yahner & Wright 1985, Lahti 2001). In the presence of an edge effect, a positive relationship between nest success and distance from the habitat edge would be expected. Second, we assessed seasonal changes in the nest predation rate to determine whether there is an increase of predation probability as the season progresses, due to density dependence (Hoi *et al.* 2001, Roos 2002), or a decrease in nest predation associated with denser vegetation and so lower nest visibility. Third, we assessed whether human visits to nests influenced the probability of nest predation. In the presence of a visitor effect, we predicted that the probability of nest predation would increase if nests were visited regularly.

## **METHODS**

### **Study sites**

The study was undertaken at two locations in the Swiss lowlands (Canton Zurich) in 2003: lake "Pfäffikersee" (47°21'00"N, 8°47'18"E, 540 m a.s.l., hereafter referred to as PF) and lake "Greifensee" (47°22'21"N, 8°39'54"E, 440 m a.s.l., hereafter referred to as GR). Both lakes are bordered by almost continuous but narrow bands of mature reed, which themselves are bordered on the landward side by wetland plant communities consisting mainly of sedge (Cyperaceae) meadows. Agricultural fields and meadows surround the wetlands. Within these wetlands, we selected two study sites in which the mature reed bands ranged in thickness from 10 to 20 m and which matched each other as closely as possible in reed density, availability of sedge tussocks and vegetation cover.

### **Experimental nests**

We used Reed Bunting nests collected in the previous season and placed within them one reared Japanese Quail *Coturnix japonica* egg and four artificial eggs (cf. Batáry *et al.* 2004). Studies using artificial nests with only quail eggs may lead to an underestimate of predation rates, because small mammals are not able to break the shell of quail eggs (Roper 1992, Haskell 1995, Maier & DeGraaf 2000, Rangen *et al.* 2000). On the other hand, the use of plasticine eggs, common in nest predation experiments (e.g. Stuart-Smith & Hayes 2003), may elevate nest predation rate, because the smell of plasticine may attract small mammals (Maier & DeGraaf 2000, Rangen *et al.* 2000). To avoid plasticine, we coated confectionery eggs with coloured parafin, which is scentless, to mimic Reed Bunting eggs in size and shape as closely as

possible. Prior to the experiment, these eggs were tested for weather resistance by placing them at various locations in a nearby forest and were found to comply with the requirements of the study, showing no deformation when exposed to sunlight and rain for 13 days, a period corresponding to the incubation period of Reed Buntings.

### **Experimental design**

We laid out 30 nests in PF and 16 nests in GR, respectively. Sample sizes in PF and GR reflected the length of the reed bands suitable for nest placement (see below). Nests were placed at locations where natural nests of Reed Buntings are usually found, i.e. on tussocks or underneath clusters of dead sedges. The nests were set from 0 to 8 m from the land-sided reed edge. This distance range was chosen because the majority of real Reed Bunting nests were located within 8 m of the reed edge at adjacent sites at PF and GR during the previous season (own obs.). Fifty percent of the nests were randomly set out between 0 and 4 m from the land-sided reed edge, and the remaining nests were placed randomly between 4 to 8 m. When setting out the nests, we alternated between these two distance groups to avoid spatial autocorrelation with respect to distance to the land-sided reed edge, i.e. two adjacent nests never belonged to the same distance group. The horizontal distance between two nests was 15 m, which corresponds to the average distance between nests of Reed Buntings found in nearby study sites (own unpubl. data). Thus, density of artificial nests did not differ between the sites PF and GR and the length of the reed band fitted with experimental nests was 450 m in PF and 240 m in GR,



respectively. The nests were set out on 2 May, when clutches of the first brood of the local breeding population of Reed Buntings were found, and collected after 13 days, which equals the average incubation time in this species (Cramp & Perrins 1994, Glutz von Blotzheim & Bauer 1997, own obs). Fifty percent of the nests within each distance class (<4 m and 4–8 m from the land-sided reed edge, respectively) were randomly assigned to be visited. These nests were visited on the 3<sup>rd</sup>, 7<sup>th</sup> and 10<sup>th</sup> day after nests were set out, i.e. approached by one observer checking its contents to mimic a nest control, as done in our study of Reed Bunting population dynamics. Nests not assigned to visitation were not checked until the end of the experiment. All nest checks were done by M. Eger. To examine potential seasonal effects on nest predation rate, the experiment was repeated from 13 June onwards, when successful pairs initiated their second clutch in the study area. All nest locations were shifted by 7.5 m in one direction for the second experiment; hence, each nest was set out at a new location without changing its distance relative to the land-sided reed edge.

### **Habitat measurements**

To account for parameters potentially influencing nest predation rate, we measured the following variables when the nests were recollected: nest height above ground (cm), height of dead leaves above the nest (cm), percentage vegetation cover, percentage water cover, reed density (number of reed stems at 1.5 m above ground), number of tussocks and the shortest distance to open water. Percentage vegetation and water cover, respectively, were estimated in plots of 1 m<sup>2</sup> centred on each nest (four categories: 0–25%, 26–50%, 51–75%,

or 76–100% cover). Reed density and number of tussocks were counted in plots of 0.25 m<sup>2</sup> centred on the nest (cf. Aebischer *et al.* 1996). Distance to lake water (hereafter referred to as distance to the water-sided reed edge) changed during the course of the experiment owing to changes in water level of the lakes. To account for this temporal variation, distance to water was put into one of the following categories: <5 m, 5–10 m, 10–15 m, and 15–20 m. Because reed edges were not parallel, distance to water-sided reed edge was not correlated with distance to the land-sided reed edge (Table 1).

### **Statistical analyses**

We distinguished between two different predation events: nest predation had occurred when any egg was missing or showed bite or claw marks, whereas quail egg predation occurred when the quail egg was missing or damaged. This was done to allow distinction between small and large predators, because quail eggs may be too large to be consumed by small-mouthed predators such as rodents (Batáry *et al.* 2004). In no case was only the quail egg predated, hence nest predation rate was always equal to or higher than quail egg predation rate.

Our main goal was to examine the influence of distance to the land-sided reed edge, season, and visitation on nest predation probabilities (see Introduction) while simultaneously accounting for other factors potentially influencing predation rates. We hence determined as a first step the parameters with the greatest impact on nest and quail egg predation rates and used the resulting models in a subsequent step to assess the impact of the experimental variables, i.e. distance to land-sided reed edge, season, and visitation on

predation rates. Step one was achieved by generalized linear models using Proc Genmod in SAS (SAS Institute Inc. 2002-2003), fitting nest or quail egg predation as a binary dependent variable and the habitat measurements described above as independent variables. All habitat variables were treated as continuous variables. Although vegetation and water cover as well as distance to the water-sided reed edge were recorded in categories, higher values indicate higher cover or larger distances, respectively. Entering these variables as continuous allows detection of potential linear relationships with nest predation probability, rather than only exploring differences between classes. Study site (GR or PF) was entered as a fixed effect. We calculated models with all possible linear combinations of predictor variables using maximum likelihood for parameter estimation. No interactions were included to avoid overfitting of models. The best model was then selected using Akaike's Information Criterion, AIC (Akaike 1973, Burnham & Anderson 2002) corrected for small sample sizes (AICc, Burnham & Anderson 2002). Because our aim was to find the most influential variables to be used as covariates in the final model rather than determining effect sizes, we did not perform a model selection for this step (also see McElligott *et al.* 2002). The model with the lowest AICc value can be viewed as the most parsimonious one, explaining the most variation in the data set with a minimum of explanatory parameters (Anderson *et al.* 2000, Burnham & Anderson 2001, Burnham & Anderson 2002).

The experimental variables (distance to land-sided reed edge, season and visitation, the latter two as binary categorical variables) were then added to the models containing the covariates identified as being most influential in the

previous step separately and in combination, resulting in seven candidate models in total. This was done separately for both nest predation and quail egg predation. A model selection after Burnham & Anderson (2002) was then undertaken, first calculating Akaike model weights, which indicate the degree to which a model is supported by the data. Weights of selected models sum up to unity and higher weights denote better explanatory power. The effect sizes of parameters over all models were then estimated using model averaging: parameter estimates of each model were multiplied by the weight of the particular model, and the products summed over all selected models that contained that particular parameter to give the weighted average of parameter estimates (Burnham & Anderson 2002, Johnson & Omland 2004). Similarly, standard errors (SE) were calculated for parameter estimates following Burnham & Anderson (2002). Model averaging usually results in effect sizes similar to those estimated by one model, but standard errors are often inflated. Effects were considered meaningful if, after model averaging, standard errors were still smaller than effect sizes. Multicollinearity was examined using tolerance values (Allison 2001); all values were  $> 0.6$  indicating low intercorrelation among predictor variables (Table 1). Sample size was 92 nests in all models. All analyses were done using SAS 9.1.3 (SAS Institute Inc 2002-2003).

## RESULTS

### Nest predation

Overall nest predation rate was 62.0% ( $n = 92$ ), with 88.3% of all nests at PF and 12.5% at GR being predated. Among predated nests that were visited, artificial eggs disappeared first; any loss of the quail egg was only recorded on second or third checks. The model that best explained nest predation in relation to the habitat covariates included only distance to the water-sided reed edge and reed density, indicating that predation probability declined with increasing distance to the water-sided reed edge (estimate  $\pm$  se =  $-1.54 \pm 0.83$ ) and slightly increased with reed density ( $0.04 \pm 0.09$ ,  $n = 92$ ). The difference in AICc values between this and the second best model (which included only distance to water) was  $>2$ , denoting considerably less support for the second best model.

The subsequent model selection procedure highlighted the importance of distance to the water-sided reed edge, the effect size and standard error remaining almost unchanged when calculated by model averaging, i.e. combining the information of all seven models together (estimate  $\pm$  se =  $-1.10 \pm 0.98$ , Fig. 1). Predation rate tended to be lower in the first than in the second experiment (52.2% versus 71.7%, respectively,  $-2.25 \pm 1.48$ ). For all other parameters, standard errors were larger than effect sizes, indicating the low importance of these variables. Likelihood of predation tended to be positively associated with reed density ( $0.02 \pm 0.34$ ) and with distance from the land-sided reed edge ( $0.03 \pm 1.00$ ) and was slightly lower in visited than in unvisited nests (58.7% versus 65.2%, respectively,  $0.39 \pm 1.20$ ).

### **Quail egg predation**

Predation rate of the quail egg was 18.5 % ( $n = 92$ ); 26.7% of the nests at PF and 3.2% of the nests at GR were predated. Predation probability increased with nest height (estimate  $\pm$  s.e. =  $0.20 \pm 0.06$ ), but declined with height of dead leaves ( $-0.09 \pm 0.03$ ). The second best model additionally included distance to the water-sided reed edge, and the difference in the AICc values to the best model was 1.7.

Model selection revealed that quail egg predation was most closely tied to season, with again lower predation probabilities in the first than in the second experiment (6.5% versus 30.4%, respectively, estimate  $\pm$  s.e. =  $-2.20 \pm 0.72$ , Table 2). The covariates selected in the first step received weak support after model averaging (nest height: estimate  $\pm$  s.e. =  $0.08 \pm 0.27$ , height of dead leaves:  $-0.06 \pm 0.20$ ), as did distance to land-sided reed edge, which tended to be positively associated with probability of quail egg predation ( $0.38 \pm 0.64$ ). Finally, visited nests tended to be predated slightly more often than those not visited (84.8% versus 78.2%,  $0.56 \pm 0.68$ ).

### **DISCUSSION**

This study suggests that probability of predation on artificial Reed Bunting nests is lower at the beginning than towards the end of the breeding season, most markedly so with regard to quail egg predation. Whether or not a nest was visited and its location relative to the land-sided reed edge were only of minor importance. However, nests placed further from water were less likely to be predated than nests close to the water's edge.

### **Edge effects**

Some studies have reported higher nest predation rates of wetland birds along edges than in the core of reed habitats (Hoi & Winkler 1988, Kristiansen 1998, Batáry *et al.* 2004, Batáry & Báldi 2005a), while others either found no effects (Honza *et al.* 1998) or yielded inconsistent results (Báldi & Batáry 2000). Two recent reviews on edge effects and avian nest success mirror these equivocal patterns (Batáry & Báldi 2004, Lahti 2001). This lack of agreement may reflect differences between species in their responses to habitat fragmentation and edge effects as well as differences in the habitat types studied, or it may be a consequence of methodological differences (e.g. experimental vs empirical approaches, studies on natural vs artificial nests, see Faaborg 2004, Villard & Pärt 2004 for a discussion of the latter). Further, Chalfoun *et al.* (2002) and Stephens *et al.* (2003) highlighted the importance of the spatial scale at which fragmentation is studied (edge, patch or landscape), and study duration for the probability of detecting edge effects in relation to nest predation.

Our results indicate the presence of edge effects operating from the water-sided rather than the land-sided reed edge. This implies that artificial nests were mostly predated by species living in proximity to the lake border. We have observed Water Rails *Rallus aquaticus* to predate real Reed Bunting nests containing nestlings and suspect Coots *Fulica atra* and perhaps Little Bitterns *Ixobrychus minutus* to do the same. Hansson *et al.* (2000) reported Water Rails and Bitterns *Botaurus stellaris* to be important predators of both artificial and real nests of the Great Reed Warbler *Acrocephalus arundinaceus*. Other bird

species suspected elsewhere to be important predators of nests inside reed beds (Hansson *et al.* 2000, Batáry *et al.* 2004) either did not occur in our study sites (e.g. Marsh Harrier *Circus aeruginosus*, Bittern) or were never observed to search for nests in reed beds (corvids *Corvus* sp., gulls *Larus* sp.), despite four years of intensive field work. Among species preying on nests close to the land-sided reed edge are Red Fox *Vulpes vulpes* (own obs.) and perhaps Polecat *Mustela putorius* and feral cats. We found faeces of voles (*Microtus arvalis* or *Apodemus flavicollis*) in eight predated nests and small paraffin wax splinters in another eight, indicating that these small rodents may be responsible for some of the nest losses. However, it is still unclear to what extent mice and voles indeed are predators of natural nests (Maier & DeGraaf 2000, Stuart-Smith & Hayes 2003).

The considerable difference between overall predation rate (62.0%) and quail egg predation rate (18.5%) suggests that most predation events were caused by animals that were unable to swallow or break quail eggs. This finding again points at small bird or mammalian species as the main predators of artificial nests in our study; it further shows that using only quail eggs in the nest experiment may lead to an underestimation of predation rate, as found in other studies (Roper 1992, Haskell 1995, Maier & DeGraaf 2000, Rangen *et al.* 2000). On the other hand, the use of artificial nests may also induce higher predation rates than in natural nests. In our study area in 2003, 27.1% of 118 natural Reed Bunting nests were predated, while additional 11.0% of the losses occurred for unknown reasons (own unpubl. data). These figures imply that the overall predation rate of 62.0% for artificial nests overestimates natural



predation rate. Also, artificial eggs were always predated before the quail egg, again pointing at an easier detectability of artificial eggs. Discrepancies in predation rate of natural and artificial nests have also been reported in some studies (Wilson & Brittingham 1998, Zanette 2002, Stuart-Smith & Hayes 2003, Batáry & Báldi 2005b, Burke *et al.* 2004), whereas others found similar predation rates for natural and artificial nests (Crabtree *et al.* 1989, Major 1990, Ammon & Stacey 1997).

That nests located close to the waterside reed edge are often predated is consistent with results from analyses on predation rates of real Reed Bunting nests (Pasinelli & Schiegg 2006). This is reassuring since it suggests that nest predation patterns observed in the artificial nest experiment are comparable to those of real nests (Andrén & Angelstam 1988, Hoi & Winkler 1988, Batáry *et al.* 2004, but see Burke *et al.* 2004).

### **Season**

Both overall nest predation and quail egg predation were lower early than late in the season. However, there was no significant difference in reed density (U-test,  $P = 0.14$ ,  $n = 92$ ) or in vegetation cover ( $P = 0.20$ ,  $n = 92$ ) between the two experimental periods. It seems therefore that nests in the second experiment were not better camouflaged than in the first one.

Predation rates in a number of different habitats have been found to depend on the density of nests, both in studies of natural and artificial nests (Hoi & Winkler 1988, Hoi & Winkler 1994, Hoi *et al.* 2001, Roos 2002, but see Honza *et al.* 1998). Frequency-dependent predation and the development of a

search image by the predator (Gendron 1986) may cause elevated predation rates when nest densities are high. Only Reed Warblers *Acrocephalus scirpaceus* bred in the reed bands at similar densities as the Reed Bunting in our study area, and Reed Warblers are likely to be predated upon by the same predator guild as the Reed Bunting (Glutz von Blotzheim & Bauer 1991). Our second experiment coincided with the first broods of Reed Warblers (Glutz von Blotzheim & Bauer 1991, own obs.) and was hence at a time when overall nest density was highest. Thus, the increase in nest predation rate over the season seems to support the hypothesis of density dependent nest predation.

### **Nest visits**

Visiting nests did not strongly affect predation rate, which is in line with other studies (Reitsma *et al.* 1990, Hoi & Winkler 1994, O'Grady *et al.* 1996, Mayer-Gross *et al.* 1997, Ortega *et al.* 1997, but see Bart & Robson 1977, Lenington 1979, Major 1990, Tryjanowski & Kuzniak 1999). Further, our results are equivocal, because nests visits seemed to diminish overall nest predation probability, while it slightly increased likelihood of quail egg predation. However, in both analyses the size of the visitation effect was small and standard errors were larger than effect sizes. Potential influences of nest visits on predation rates may depend on factors such as predator community, vegetation structure and placement of the nests. The main predators in our study area were probably avian predators that do not use olfactory cues or human tracks to find their prey. This is corroborated by the finding that predators invading from the water-sided reed edge play an important role as indicated by the relation

between nest predation rate and distance to water-sided reed edge (also see Pasinelli & Schiegg 2006).

### **Implications for conservation**

Hansson *et al.* (2000) suggested that Great Reed Warblers should avoid building their nests close to either the land-sided or the water-sided reed edge to minimise nest predation. Our results point into a similar direction with respect to the water-sided reed edge, hence underlining the importance of reed bands wide enough to enable the birds to avoid edges (Batáry & Báldi 2005a).

However, each autumn, reed grown during the year is cut in our study area to prevent encroachment by trees, to combat exotic plant species and to provide habitat for endangered plant and invertebrate species. As a consequence, only very narrow bands of reed are left along borders of lakes and other water bodies. These bands may not be wide enough to provide nest sites at sufficient distances from reed edges. Hence, the current management regime may result in unnaturally high levels of nest losses in the Reed Bunting and perhaps other reed-inhabiting species as well. Given the importance of nest predation rates in avian population dynamics (Robinson *et al.* 1995, Sæther & Bakke 2000), the local decline in population size of Reed Buntings in our study area (Weggler & Widmer 2001) may thus be a consequence of the intensive reed management in Swiss nature reserves.

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## Tables

**Table 1.** Spearman rank correlation coefficients ( $n = 92$ ) between explanatory variables. \* indicates correlations significant at  $P < 0.05$ . “Dead leaves” refers to height of dead leaves above the nest, “Dist. water” to distance to the water-sided reed edge, and “Dist. land” to distance to the land-sided reed edge.

	<b>Dead leaves</b>	<b>Veg. cover</b>	<b>Water cover</b>	<b>Reed density</b>	<b>Nb. of tuss.</b>	<b>Dist. water</b>	<b>Dist. land</b>
<b>Nest height</b>	0.11	0.18	-0.02	0.12	0.13	-0.27*	0.13
<b>Dead leaves</b>		0.27*	-0.07	-0.26*	0.32*	0.29*	-0.15
<b>Veg. cover</b>			-0.20*	-0.20*	-0.10	0.25*	-0.16
<b>Water cover</b>				0.13	0.18	0.16	0.06
<b>Reed density</b>					0.21*	-0.47*	-0.02
<b>Nb. of tussocks</b>						-0.25*	-0.34*
<b>Dist. water</b>							0.01

**Table 2.** Factors affecting predation probability in artificial Reed Bunting nests.  $\Delta AICc$  is the difference in  $AICc$  to the best model, weight indicates the relative support of a particular model compared to the other models, with higher values indicating better support. “Distance water” refers to distance to the water-sided reed edge, “distance land” to distance to the land-sided reed edge.

<b>Model</b>	<b>AICc</b>	<b><math>\Delta AICc</math></b>	<b>Weight</b>
<b>Nest predation (<math>n = 92</math>)</b>			
1. Season, visitation, distance land, reed density, distance water, site	51.76	0.00	0.32
2. Season, visitation, reed density, distance water, site	51.92	0.16	0.28
3. Season, distance land, reed density, distance water, site	52.56	0.80	0.20
4. Season, reed density, distance water, site	52.67	0.92	0.19
5. Visitation, distance land, reed density, distance water, site	58.58	6.82	0.00
6. Visitation, reed density, distance water, site	59.11	7.35	0.00
7. Distance land, reed density, distance water, site	59.21	7.45	0.00
<b>Quail egg predation (<math>n = 92</math>)</b>			
1. Season, visitation, distance land, , height dead leaves, nest height, site	55.51	0.00	0.63
2. Season, distance land, height dead leaves,	56.94	1.43	0.31

nest height, site

3. Season, visitation, height dead leaves, nest 61.53 6.02 0.03

height, site

4. Season, height dead leaves, nest height, site 61.77 6.26 0.03

5. Visitation, distance land, height dead leaves, 65.20 9.69 0.00

nest height

6. Distance land, height dead leaves, nest height, 66.63 11.12 0.00

site

7. Visitation, height dead leaves, nest height, site 69.86 14.35 0.00

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## Figure legends

**Figure 1.** Probability of nest predation (open bars) and quail egg predation (black bars) in % in relation to distance to water-sided reed edge. 1: <5m ( $n = 9$ ), 2: 5–10m ( $n = 20$ ), 3: 10–15m ( $n = 24$ ), 4: 15–20m ( $n = 39$ ).

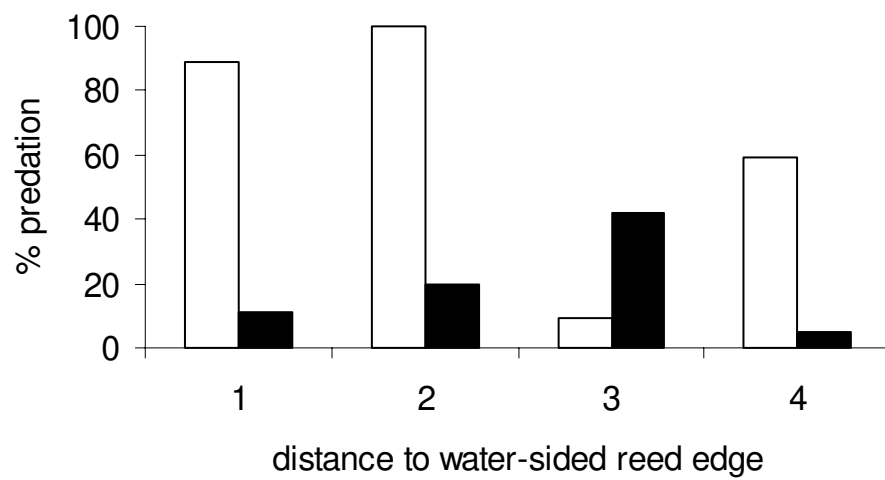


Fig. 1