Fragmentation within and between wetland reserves: the importance of spatial scales for nest predation in reed buntings

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Loss and fragmentation of habitat are important threats for the persistence of many plant and animal populations (Lawton and May 1995, Harrison and Bruna 1999, Reed 2004). Several mechanisms have been proposed to explain fragmentation-induced reductions in demographic rates of populations, an important one being increased nest loss due to predation and/or parasitism in small habitat patches (Brittingham and Temple 1983, Wilcove et al. 1985, Paton 1994). In birds, nest predation is a prime determinant of fitness and is hence considered to be a major force shaping avian population dynamics (Sæther and Bakke 2000). For instance, birds nesting in fragmented landscapes may experience elevated nest predation rates due to an unfavorable habitat edge to patch size ratio (Brittingham and Temple 1983, Wilcove et al. 1985, Paton 1994), although this finding is far from general (Lahti 2001). Chalfoun et al. (2002) and Stephens et al. (2003) found that the probability of
detecting an effect of fragmentation on nest predation depended on the spatial scale, i.e. increased from the edge, to the patch and to the landscape scale.

Most research on fragmentation effects in birds has involved forested areas (Andrén 1995), while studies focusing on wetlands are relatively rare (Lahti 2001, Chalifon et al. 2002, Batáry and Bándi 2004). This is surprising given that wetlands are among the most fragmented and threatened ecosystems of the world (Keddy 2000). In central Europe, reed (Phragmites sp.) inhabiting species experience fragmentation at multiple scales: reed habitats are mostly confined to nature reserves scattered in the landscape, and in addition, reed beds themselves often occur only patchily within these nature reserves (i.e. the remaining wetland fragments). Because reed is used frequently as thatching material, reed beds are cut annually in several regions of Europe, with negative effects on reed inhabiting arthropod (Schmidt et al. 2005) and bird communities (Poulin and Lefebvre 2002). It has been suggested, therefore, to leave a mosaic of uncut reed to provide habitat for arthropod and bird species sensitive to reed cutting. The size and shape of these reed patches may be critical, because selective cutting potentially increases fragmentation within reed habitats, which may elevate predation risk for bird species nesting in reed beds.

In Switzerland, commercial reed harvesting is of minor importance. In the recent years however, management of wetland reserves, particularly in the Canton Zurich, has focused on a) promoting species living outside reed beds such as orchids (Orchidaceae) or dragonflies (Odonata), b) preventing natural succession and c) fighting exotic plant species (e.g. Solidago sp.). Consequently, most areas containing reed are mown annually, sometimes even when the birds are still breeding (unpubl.). At most locations, the intensive management leaves only narrow bands of old reed along water bodies and in some sites, no reed is left at all (unpubl.).

Here we examined whether the probability of nest predation in the reed bunting (Emberiza schoeniclus), a small ground-nesting passerine breeding mostly in the transition zones along standing or slow-flowing bodies of water (Glutz von Blotzheim and Bauer 1997), was related to factors operating at four spatial scales. These scales were chosen to investigate factors, which separately or in concert may influence nest predation probability, and which reflect conditions ranging from the immediate vicinity of a nest to factors relating to landscape features. On the nest scale, we assessed the influence of habitat structure of a nest’s immediate neighborhood on probability of nest predation and predicted predation probability to depend on vegetation density, water cover and on nest height. On the edge scale, we explored if nest predation rate was related to proximity to habitat edges (“edge effect on nest predation hypothesis”, Gates and Gysel 1978, Yahner and Wright 1985, Lahti 2001), size and/or shape of the reed patch containing the nest. We expected that predation rates were highest close to the reed edges and were enhanced when patches were small and/or the ratio between edge length and patch size was large (Chalifon et al. 2002). On the site scale, we examined if probability of nest predation within a site (i.e. nature reserve) was related to site size and/or fragmentation within sites (Wilcove et al. 1985, Faaborg et al. 1995), predicting predation rate to be elevated when sites were small and fragmentation within sites was high. Finally, we investigated whether nest predation rate depended on fragmentation on the landscape level (Stephens et al. 2003). We expected nest predation to be positively related to distances between nature reserves (a measure of landscape fragmentation) and negatively to distances between nature reserves and forests (a measure of predation pressure by forest-related predators).

Given that some techniques of the current wetland management in Europe cause increased fragmentation of reed areas, the spatial scale determining nest predation in reed inhabiting birds has to be known in order to develop alternative management scenarios to prevent and/or counteract population declines.

**Material and methods**

**Study species**

Reed buntings mostly breed at the edges of Phragmites reeds, and the presence of old reed is the most important cue for territory establishment when males return from the wintering grounds (Surmacki 2004). Reed buntings defend mating and nesting territories (type B territories, Nice 1941), which may range in size from 96 to 7500 m² (Glutz von Blotzheim and Bauer 1997). Territories in continuous old reed habitat are usually densely packed, while in fragmented reed habitats, the distribution of territories reflects the availability of old reed patches (unpubl.). Nests are usually placed in old reed habitat (Glutz von Blotzheim and Bauer 1997, Widmer 2001, but see Okulewicz 1989 cited in Surmacki 2004), but with progressing breeding season, some nests are also placed along ditches or in sedge meadows adjacent to old reed patches. In central Europe, reed buntings usually nest twice per season, but when nests fail up to five breeding attempts per season can be made (unpubl.). Clutch size averages 4–6 eggs and declines with season; predation and flooding are the main reasons for nest losses (Glutz von Blotzheim and Bauer 1997). Though the overall distribution of reed buntings in Switzerland has not changed in the recent years, some peripheral areas along the edge of the range have been abandoned (Antoniazza 1998). In the Canton Zurich, where this study took place (see Study sites), population size in
eight wetlands has not significantly changed between 1975 and 2002 (Weggler et al. 2004); however, the species has declined locally between 1993 and 2000 for reasons yet unknown (Weggler and Widmer 2001).

**Study sites**

This study is part of an ongoing project on the significance of small sites for local population dynamics in the reed bunting carried out in 21 nature reserves scattered over an area of 200 km$^2$ in the southeastern part of the Canton Zurich, Switzerland. This set of 21 nature reserves represents all the sites, which are potentially suitable for reed buntings (presence of old reed) in the 200 km$^2$ area. These wetland reserves range in size from 1.9 to 247.2 ha (median 10.5 ha, inter-quartile range 4.2–16.7 ha). Because we were interested in potential influences of distance between nests and water bodies or reed edges on nest predation, we here only considered sites that were located at distinct water bodies (ponds or lakes, five sites in total, Table 1). For the same reason we excluded nests that were placed outside reed areas. We classified the sites according to the number of breeding pairs in either large sites (>20 breeding pairs) or small sites (≤3 breeding pairs). In the small sites, all breeding pairs were monitored, whereas in the large ones, at least 10 breeding pairs per year were surveyed. Number of breeding pairs (averaged over the four study years, cf. Table 1) was highly correlated to the area of old reed, both when examining only the five sites considered in this study (Spearman rank correlation coefficient $r_s = 0.7$, $n = 5$) and when taking all 19 sites with at least one breeding pair in one year of study into account (Pearson correlation $r > 0.75$ in each year, $n = 19$).

Habitat in the study sites is mowed in fall, except for reed along water bodies; hence, all reed patches considered in the analyses have not been cut for several years (hereafter referred to as “old reed patches”). All sites are surrounded by agricultural fields, meadows and forests.

Locations of the study sites and spatially referenced information of the following variables were incorporated into ArcView GIS 3.3 (Anon. 1992–2002): location and identity of nests, location and area of old reed patches, location of water bodies, total area of the nature reserve (i.e. site), and location of forest stands closest to each site. Area of reed patches and nest locations were recorded using hand held GPS (Garmin GPS-12XL with RXMAR Decoder, Trimble GeoExplorer 3, Leica GS50). Precision of GPS locations after differential correction was ≤2 m.

Location and borders of water bodies and of forests, respectively, were manually digitized in ArcView GIS 3.3 (Anon. 1992–2002) from a spatially referenced map of the Canton Zurich (tiff- and tfw-formats, 1:5000), while total area of each nature reserve (i.e. site) was extracted from ArcView shapefiles containing all cantonal nature reserves and their plant communities. Both the spatially referenced map of the Canton Zurich and the shapefiles were made available to us by the cantonal office for nature conservation.

**Monitoring of nests**

From March to July 2002–2005, all territories were visited at least twice per week by two observers to assess pairing and breeding status of the reed buntings and to locate nest sites, aiming at a full record of all nesting attempts in the surveyed territories. Territories were monitored from ladders to find nests, which can be detected by observing females building the nest or leaving and returning during incubation. Nests were found on average 6.81 (±SE = 0.52, $n = 183$ nests with known or inferred laying date) days after the first egg is laid; 17.5% were located when parents were feeding nestlings. Intervals between subsequent nest checks were 2–4 d. Nest visits at artificial (Eger 2004) and real nests (unpubl.) do not affect predation risk in this species. A nest was considered predated when its content had disappeared before or at banding date (nestling day 7–8) and other factors such as flooding could be excluded. Abandoned nests still containing eggs or dead nestlings were not considered predated. Nests that failed for reasons other than predation were not considered in the analyses. Since the young start to fledge after day 9 (Glutz von Blotzheim and Bauer 1997), nests were not checked after young had been banded to avoid premature fledging.

<table>
<thead>
<tr>
<th>Site, coordinates, wetland size (ha)</th>
<th>2002</th>
<th>2003</th>
<th>2004</th>
<th>2005</th>
<th>Size category</th>
<th>Old reed area (ha)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Feldbach, 8°47'33&quot;E/47'14&quot;18&quot;N, 2.7</td>
<td>2, 3</td>
<td>3, 4</td>
<td>1, 1</td>
<td>2, 1</td>
<td>Small</td>
<td>0.383</td>
</tr>
<tr>
<td>Seeewidsee, 8°44'45&quot;E/47'15&quot;24&quot;N, 5.2</td>
<td>2, 2</td>
<td>1, 1</td>
<td>1, 1</td>
<td>2, 5</td>
<td>Small</td>
<td>0.364</td>
</tr>
<tr>
<td>Greifensee, 8°41'52&quot;E/47'19&quot;26&quot;N, 44.1</td>
<td>10, 17</td>
<td>14, 12</td>
<td>11, 14</td>
<td>11, 16</td>
<td>Large</td>
<td>0.972</td>
</tr>
<tr>
<td>Lützelsee, 8°46'21&quot;E/47'15&quot;36&quot;N, 54.7</td>
<td>13, 13</td>
<td>13, 5</td>
<td>11, 9</td>
<td>12, 14</td>
<td>Large</td>
<td>1.314</td>
</tr>
<tr>
<td>Pfäffikersee, 8°37°30&quot;E/47'20&quot;43&quot;N, 247.2</td>
<td>10, 15</td>
<td>11, 15</td>
<td>12, 15</td>
<td>10, 14</td>
<td>Large</td>
<td>2.581</td>
</tr>
</tbody>
</table>
Exposure time

We calculated the number of days a nest was known to be active (hereafter referred to as exposure time), which can be used in Mayfield logistic regression (Aebischer 1999, Hazler 2004) to assess predation probability while accounting for the number of days a nest has been exposed to predators. This approach avoids potential underestimation of predation rates due to nests that failed before they were found. Exposure time for successful nests (i.e. nests fledging at least one young) was the difference between banding date and the date the nest was found to be active. For predated nests, we first calculated the midpoint (rounded to the nearest day) between the date when failure was detected and the latest date the nest was recorded active; exposure time was then calculated as the difference between this midpoint date and the date at which the nest was found to be active (Manolis et al. 2000).

Mayfield logistic regression and model structure

The dependent variable in all analyses was nest fate (0 if successful and 1 if predated while under observation) per exposure time. We used a trial/events approach (Anon. 2002–2003, Hazler 2004), in which nest fate (0 or 1) was the numerator and number of nest days (exposure time) the denominator in a binomial model. A prerequisite of logistic regression is that observations are independent. Our study comprises data gathered within five study sites and hence nest fates may be more similar within than between sites, potentially causing overdispersion and an underestimation of standard errors of parameter estimates (Allison 2001, Burnham and Anderson 2002). One remedy for this problem is the use of hierarchical models (Singer 1998, Porter and Umbach 2001). We specified a random effect that nests territories within sites using the GLIMMIX procedure in SAS (Anon. 2002–2003). This model structure invokes estimation of variance components within the specified levels (here within sites) rather than across the entire dataset, thus accounting for potential intercorrelations (Littell et al. 1994). Further, we specified territories as a repeated effect (r-side effect in GLIMMIX terminology, (Anon. 2002–2003)) to account for repeated observations within territories, but included an additional repeated term to account for multiple observations of the same nest (i.e. a nest predated in the nestling stage appears as successful in the egg stage, successful nests appear as not predated in both stages). We found that only nest stage significantly influenced predation probability ($p = 0.023$, $n = 265$).

### Table 2. Spatial scales and associated original variables.

<table>
<thead>
<tr>
<th>Scale</th>
<th>Variable name</th>
<th>Definition</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nest scale</td>
<td>Nest height</td>
<td>From ground/water surface to the nest rim (cm)</td>
</tr>
<tr>
<td></td>
<td>Water depth</td>
<td>Depth (cm) of water below the nest</td>
</tr>
<tr>
<td></td>
<td>Vegetation height</td>
<td>Height (cm) of dead leaves above the nest</td>
</tr>
<tr>
<td></td>
<td>Reed stems at 0.5 m</td>
<td>Number of reed stems at the height of 0.5, 1.5 and 2.5 m, respectively</td>
</tr>
<tr>
<td></td>
<td>Reed stems at 2.5 m</td>
<td>Number of reed stems at the height of 0.5, 1.5 and 2.5 m, respectively</td>
</tr>
<tr>
<td></td>
<td>Number of tussocks</td>
<td>Number of sedge tussocks</td>
</tr>
<tr>
<td></td>
<td>Vegetation cover</td>
<td>% per 1 m$^2$ covered by vegetation in steps of 25%</td>
</tr>
<tr>
<td></td>
<td>Water cover</td>
<td>% per 1 m$^2$ covered by water in steps of 25%</td>
</tr>
<tr>
<td>Edge scale</td>
<td>Distance to water</td>
<td>Distance (m) of a nest to the closest water body</td>
</tr>
<tr>
<td></td>
<td>Distance to reed edge</td>
<td>Distance (m) of a nest to closest land sided reed edge</td>
</tr>
<tr>
<td></td>
<td>Reed patch size</td>
<td>Size (m$^2$) of reed patch containing the nest</td>
</tr>
<tr>
<td></td>
<td>Reed patch shape</td>
<td>Shape of reed patch, expressed as the ratio of the circumference (m) of the reed patch containing the nest and the area of that patch (m$^2$)</td>
</tr>
<tr>
<td>Site scale</td>
<td>Site size</td>
<td>Binary variable small versus large, cf. Table 1</td>
</tr>
<tr>
<td></td>
<td>Total reed area</td>
<td>Reed patch area (ha) summed over all monitored reed patches in a site</td>
</tr>
<tr>
<td></td>
<td>Reed shape</td>
<td>Ratio of total reed edge length$^D$ and total reed area</td>
</tr>
<tr>
<td>Landscape scale</td>
<td>Distance between sites</td>
<td>Distance (km) of a study site to the nearest nature reserve with reed habitat</td>
</tr>
<tr>
<td></td>
<td>Distance to forest</td>
<td>Average of the distances (km) from all nests in a site to the nearest forest edge</td>
</tr>
</tbody>
</table>

$^A$ Measured at the nest.
$^B$ Measured in 0.25 m$^2$ plots centered on the nest.
$^C$ Measured in 1 m$^2$ plots centered on the nest.
$^D$ Sum of the circumferences (m) of all reed patches within the monitored area of a site.
and we therefore created two data sets, one referring to the egg stage (n = 177 nests), the other to the nestling stage (n = 120).

Daily nest predation rates can be estimated by fitting an unconditional model, i.e. a model that includes as fixed effect only the intercept, with

\[ \hat{Y} = \left(1 + \exp(\hat{\beta}_0)\right)^{-1} \]

where \( \hat{Y} \) is the daily nest predation rate and \( \hat{\beta}_0 \) = intercept of the unconditional model (after Hazler 2004). All analyses were done with SAS (Anon. 2002–2003).

**Variables potentially influencing predation rate**

We measured variables relating to four spatial scales to examine at what scale(s) nest predation is most prevalent. The nest scale was defined as the immediate neighborhood of a nest and thus includes variables describing the micro-habitat of the nest site inside a reed patch (Table 2). The importance of micro-habitat variables in the context of avian nest predation has repeatedly been shown (Weidinger 2002, Müller et al. 2005). In contrast to the nest scale, variables relating to the edge scale capture effects of a nest’s location relative to the edge of reed patches as well as effects of the size and shape of reed patches containing the nest on nest predation probability. The location of nests relative to habitat edges can be an important determinant of nest success in birds (see review in Lahti 2001, Batary and Baldi 2004). The site scale reflects the configuration of reed bunting nesting habitat (old reed) in a site (here in a nature reserve), referring to the arrangement of all reed patches in a site, independently from the location of nests. The landscape scale finally relates to factors acting above the level of the site by examining the influence of variables related to the configuration of sites in the landscape on nest predation probability. One of these variables measures isolation (nearest neighbor distance, Bender et al. 2003), while the other quantifies the probability of nest predation due to predators from forests (distance to forests), such as red fox *Vulpes vulpes*. In the following, we describe the different scales and the associated variables in detail (Table 2).

**Nest scale**

At each nest, we measured nest height above ground/water (to the nest rim) (hereafter referred to as “nest height”), depth of water below the nest (“water depth”), and height of dead leaves above the nest (“vegetation height”) to the nearest 1 cm. On square plots of 0.25 m² centered on each nest, we counted the number of reed stems at the height of 0.5, 1.5 and 2.5 m (hereafter “reed stems at 0.5 m”, “reed stems at 1.5 m” and “reed stems at 2.5 m”, respectively) and the number of sedge tussocks (“number of tussocks”).

**Edge scale**

Variables referring to the edge scale were distances between a nest and the closest water body (“distance to water”) and land sided reed edge (“distance to reed edge”), respectively, as well as the size (“reed patch size”) and shape (“reed patch shape”) of the reed patch containing the nest. Distance to the water was calculated with ArcView GIS 3.3 (Anon. 1992–2002) as the nearest distance from the nest to the water border; distance to land sided reed edge was measured in the same manner in the field using a meter stick. Reed patch shape was expressed as the ratio of the circumference (m) of the reed patch containing the nest and the area of that patch (m²) (Helzer and Jelinski 1999). Circumference and area of reed patches were calculated with ArcView GIS 3.3 (Anon. 1992–2002). All variables were standardized and subjected to PCA as described for the nest scale. Both in the egg and nestling stage, factor 1 (hereafter “reed factor”) was related to reed stems at 0.5, 1.5 and 2.5 m, respectively, factor 2 (“vegetation factor”) combined nest height, vegetation height and vegetation cover, factor 3 (“water factor”) was associated to water depth and water cover, and finally, factor 4 represented the number of tussocks (“tussock factor”).

**Site scale**

Site size was entered as categorical variable (“site size”, small versus large, Table 1). We used two measures of reed fragmentation within sites: 1) the monitored area.
(ha) of reed patches within a site (“total reed area”, includes reed patches without nests) and 2) the ratio of the total length of the reed edge (i.e. the sum of the circumferences of all reed patches within the monitored area of a site) and the total monitored area of reed patches within a site (“reed shape”). These two variables were standardized (see nest scale) and reduced to a single factor by PCA. This factor explained 87.3% of the variation in the data set of the egg stage (n = 177) and 87.6% of the nestling stage (n = 120) and is hereafter referred to as “site fragmentation factor”. Reed shape was positively, total reed area negatively related to this factor. Note that in small sites, where all breeding pairs were monitored, all old reed patches were taken into account, while in large sites the area defended by the monitored reed bunting pairs (at least 10 pairs annually) was considered (see Study sites).

Landscape scale
For each study site, we calculated the distance (km) to the nearest nature reserve with reed habitat (“distance between sites”) and the average of the distances (km) from all nests in a site to the nearest forest edge (“distance to forest”) with ArcView GIS 3.3 (Anon. 1992–2002).

Model selection
In a first step, we calculated a priori specified models for each spatial scale. These models contained the scale-specific variables and all their combinations (all subsets approach). Burnham and Anderson (2002) recommend that specific models rather than all possible combinations of predictor variables should be used. Although this approach is preferable, it cannot be applied when the information available about the system is scarce, as it is the case here (Stephens et al. 2005). Models were then ranked within each spatial scale using the Akaike information criterion (AIC, Akaike 1973). This measure of model performance optimizes the trade-off between goodness of fit of the model on the one hand and the number of parameters needed to explain variation in the dependent variable on the other hand (Burnham and Anderson 2002). We used AICc, which is a derivate of AIC corrected for small sample sizes. The model with the lowest AICc value in a set of candidate models denotes the best model. Based on AICc values, a weight can be calculated for each model indicating the degree to which it is supported by the data. Weights of all candidate models sum up to 1 and high weight indicates better support. Candidate models were evaluated in the following way: models with \( \Delta \text{AICc} < 2 \) compared to best model (with smallest AICc) were judged to have considerable support by the data. Competing models with \( \Delta \text{AICc} < 2 \) compared to the best model, but differing by one parameter only, were evaluated with regard to their log-likelihood value. This value measures the information content of a model while AICc also considers the number of parameters involved. If log-likelihood of a model containing the parameter \( X_1 \) is almost equal to a model including \( X_1 \) and \( X_2 \), then \( X_2 \) does not contribute much to explain variation in the data set (Burnham and Anderson 2002).

Parameter estimates and associated standard errors (SE) were averaged over the set of candidate models within each scale, by multiplying with the weight of the particular model and summing over the entire set of models that contained the particular parameter (Burnham and Anderson 2002).

Effects of some variables may depend on the presence of variables from other spatial scales. We therefore built a posteriori specified models combining the most relevant variables of each spatial scale. The relative importance of a variable can be estimated by summing the weight of the models in which the variable occurs (Burnham and Anderson 2002). Variables with a summed weight > 0.70 were selected to be entered in the final across-scale models. Both steps, i.e. a) model specification at each spatial scale separately and b) across scales, were done for data referring to the egg and the nestling stages separately.

Results
Daily nest predation rate was 0.02 in the egg stage and 0.01 in the nestling stage, resulting in an overall nest predation probability of 0.44 for a clutch of five eggs from date of the first egg until young are eight days old (reached banding age).

Nest scale
In the egg stage, the best model included the effects of the PCA factors “vegetation factor” and “water factor”, while the second and third best models additionally contained either the “reed factor” or the “tussock factor” (Table 3, Appendix 1). Log-likelihoods of all three models were almost identical; we hence concluded that the latter two factors did not contribute much additional information. The difference in AICc values from the best to the unconditional model was 7.1, indicating that the best model explained a substantial amount of variation in predation probabilities. Model-averaged parameter estimates revealed that predation probability declined with increasing vegetation cover, vegetation height and nest height (“vegetation factor”), while increasing water depth and water cover around the nest (“water factor”) elevated predation probability (Table 4).
In the nestling stage, variables measured at the nest scale were only of minor importance. The best models did not explain substantially more variation in predation probability than an unconditional model (Table 3). This is further reflected by both small estimates and large SEs and low relative importance of these variables (Table 4).

### Edge scale

In the egg stage, the best model included the “nest location factor” and the “land edge factor” (Table 3). Difference in AICc to the unconditional model was 5.6 (Appendix 1) and hence, these variables were important predictors of nest predation probability. Model-averaged parameter estimates indicated that nests located more distant from the land sided reed edge (“land edge factor”) as well as in larger reed patches with a smaller edge/area ratio and more distant to the water reed edge (“land edge factor”) as well as in larger reed patches with a smaller edge/area ratio and more distant to the water reed edge (“land edge factor”) were less likely to be predated than other nests (Table 4).

### Table 3. Results from generalized linear mixed models separately examining nest predation probability in the egg stage (n = 177 nests) and the nestling stage (n = 120) in relation to four spatial scales. Models with ΔAICc < 2 compared to best model (with smallest AICc) are shown (for all candidate models examined, Appendix 1). LL = Log-likelihood, K = number of parameters in model including the intercept, ΔAICc = AICc value corrected for small sample size, ΔAICc = difference in AICc to the best model, Weight = Akaike model weight. For definition of variable names mentioned under superscripts, see Table 2. “None” refers to the unconditional model (intercept only, K = 1).

<table>
<thead>
<tr>
<th>Stage</th>
<th>Scale</th>
<th>Variables in models</th>
<th>LL</th>
<th>K</th>
<th>AICc</th>
<th>ΔAICc</th>
<th>Weight</th>
</tr>
</thead>
<tbody>
<tr>
<td>Egg</td>
<td>Nest</td>
<td>Vegetation(^1), water(^2)</td>
<td>-168.75</td>
<td>3</td>
<td>343.64</td>
<td>0.00</td>
<td>0.36</td>
</tr>
<tr>
<td></td>
<td>Edge</td>
<td>Nest location(^6)</td>
<td>-169.52</td>
<td>3</td>
<td>345.18</td>
<td>0.00</td>
<td>0.66</td>
</tr>
<tr>
<td></td>
<td>Site</td>
<td>Site fragmentation(^1)</td>
<td>-172.48</td>
<td>2</td>
<td>349.02</td>
<td>0.00</td>
<td>0.47</td>
</tr>
<tr>
<td></td>
<td>Landscape</td>
<td>Distance sites(^8), distance forest(^9)</td>
<td>-167.52</td>
<td>3</td>
<td>341.17</td>
<td>0.00</td>
<td>0.59</td>
</tr>
<tr>
<td>Nestling</td>
<td>Nest</td>
<td>None</td>
<td>-69.39</td>
<td>1</td>
<td>140.82</td>
<td>0.00</td>
<td>0.24</td>
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<tr>
<td></td>
<td>Edge</td>
<td>None</td>
<td>-69.39</td>
<td>1</td>
<td>140.82</td>
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<td>Site</td>
<td>Nest location(^6)</td>
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<td>141.17</td>
<td>0.35</td>
<td>0.29</td>
</tr>
<tr>
<td></td>
<td>Landscape</td>
<td>Distance sites(^8), distance forest(^9)</td>
<td>-66.89</td>
<td>2</td>
<td>137.87</td>
<td>0.00</td>
<td>0.52</td>
</tr>
</tbody>
</table>

1. PCA-factor related to “vegetation cover”, “vegetation height” and “nest height”; 2. PCA-factor related to “water cover” and “water depth”; 3. PCA-factor related to “reed stems at 0.5, 1.5 and 2.5 m², respectively; 4. PCA-factor related to “number of tussocks”; 5. PCA-factor related to “distance to reed edge”; 6. PCA-factor related to “distance to water”; 7. PCA-factor related to “reed patch size” and “reed patch shape”; 8. PCA-factor related to “total reed area” and “reed shape”; 9. “distance between sites”; 9. “distance to forest”.

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### Table 4. Model-averaged estimates ± SE and weights for variables of scale-specific models. For variable names see Table 3. Weights are calculated by summing the Akaike weights of all models containing the focal variable (Appendix 1). Modeled was the probability that predation occurred. In bold: variables selected to be included in the across-scale models. N = number of nests.

<table>
<thead>
<tr>
<th>Scale</th>
<th>Variable</th>
<th>Egg stage, n = 177</th>
<th>Nesting stage, n = 120</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Estimate ± SE</td>
<td>Weight</td>
</tr>
<tr>
<td>Nest</td>
<td>Vegetation</td>
<td>-0.37 ± 0.26</td>
<td>0.94</td>
</tr>
<tr>
<td></td>
<td>Water</td>
<td>0.19 ± 0.19</td>
<td>0.76</td>
</tr>
<tr>
<td></td>
<td>Reed</td>
<td>-0.03 ± 0.10</td>
<td>0.31</td>
</tr>
<tr>
<td></td>
<td>Tussocks</td>
<td>-0.01 ± 0.06</td>
<td>0.27</td>
</tr>
<tr>
<td>Edge</td>
<td>Land edge</td>
<td>-0.28 ± 0.30</td>
<td>0.78</td>
</tr>
<tr>
<td></td>
<td>Nest location</td>
<td>-0.24 ± 0.22</td>
<td>0.83</td>
</tr>
<tr>
<td>Site</td>
<td>Site fragmentation</td>
<td>-0.18 ± 0.23</td>
<td>0.68</td>
</tr>
<tr>
<td></td>
<td>Site size</td>
<td>0.04 ± 0.37</td>
<td>0.33</td>
</tr>
<tr>
<td>Landscape</td>
<td>Distance sites</td>
<td>2.21 ± 1.21</td>
<td>0.99</td>
</tr>
<tr>
<td></td>
<td>Distance forest</td>
<td>1.02 ± 1.56</td>
<td>0.58</td>
</tr>
</tbody>
</table>
model (Table 3). Hence, the variables measured at this scale did not considerably affect predation probability.

Site scale

In the egg stage, the “site fragmentation factor” constituted the best model, followed by a model that additionally included “site size”. ΔAICc of both models was <2 compared to the unconditional model, which indicated that both variables did not predict predation probabilities well.

In the nestling stage, the “site fragmentation factor” again turned out as the best predictor variable, but again, explanatory power was low. The same also applied for “site size” (Table 3).

Landscape scale

In the egg stage, the best model included “distance between sites” and “distance to forest”; the difference in AICc values to the unconditional model was 9.6, meaning that this model explained a substantial amount of variation in predation probabilities (Table 3, Appendix 1). However, “distance to forest” did not substantially improve explanatory power as indicated by the log-likelihoods being almost equal between this and the second best model containing “distance between sites” only. Model-averaged parameter estimates revealed that the larger the distances between sites and to the nearest forest, the more likely nests were predated (Table 4).

In the nestling stage, “distance between sites” again appeared to be the best predictor of predation probability at the landscape scale, followed by “distance to forest” (Table 3). ΔAICc of the best and the unconditional model was 3.0 (Appendix 1), which is considerably lower than in egg stage, but still indicated that the model with “distance between sites” had substantial support by the data. Again, “distance to forest” did not explain much additional variation as denoted by the small difference in the log-likelihood values of the models with and without this variable (Appendix 1). In contrast to the egg stage, nest predation probability decreased with distance between sites (Table 4).

Across spatial scale comparisons

In the egg stage, the best models in the scale-specific analyses consisted of variables from the nest scale, the edge scale and the landscape scale (Table 4). Based on their weight summed over the candidate models for each scale, we chose to enter the PCA factors “vegetation factor”, “water factor” (nest scale), “land edge factor”, “nest location factor” (edge scale) and the variable “distance between sites” (landscape scale) in across-scale models. Correlation coefficients among these variables were $r_s < 0.48$ (Spearman rank correlations, n = 177) and tolerance values > 0.64 in all cases, indicating that multicollinearity was not a concern. Model selection yielded new candidate models, the best of which being considerably better then the best scale-specific model (Table 3 and 5). The top-ranking model included the PCA factors “vegetation factor”, “land edge factor”, “nest location factor” and the variable “distance between sites” (Fig. 1). ΔAICc of this model compared to the unconditional model was 12.7 (Appendix 2). Most high-ranking models contained the “land edge factor” and the “vegetation factor”, resulting in a summed weight of 0.76 and 0.78, respectively, for these factors (Table 6). “Distance between sites” also was given a high weight, followed by the “nest location factor”. Finally, the “water factor” only appeared in lower ranking models, and it had both a relatively low summed weight and a small model-averaged estimate, compared to its SE.

In the nestling stage, “distance between sites” (landscape scale) turned out to be the most important predictor of nest predation probability. Performance of models related to the other spatial scales was rather poor (Table 3), and we hence did not calculate across-scale models for the nestling stage.

Discussion

This study shows that the probability of nest predation in the egg stage is related to multiple factors acting on various spatial scales. Predation probability in the nestling stage was only tied to the variable “distance between sites”, measured at the landscape scale. This may indicate that the most vulnerable nests are already

<table>
<thead>
<tr>
<th>Models</th>
<th>LL</th>
<th>K</th>
<th>AICc</th>
<th>Δ AICc</th>
<th>Weight</th>
</tr>
</thead>
<tbody>
<tr>
<td>Vegetation, land edge, nest location, distance sites</td>
<td>−163.85</td>
<td>5</td>
<td>338.05</td>
<td>0.00</td>
<td>0.16</td>
</tr>
<tr>
<td>Vegetation, land edge, nest location</td>
<td>−165.13</td>
<td>4</td>
<td>338.49</td>
<td>0.44</td>
<td>0.13</td>
</tr>
<tr>
<td>Vegetation, land edge, distance sites,</td>
<td>−165.53</td>
<td>4</td>
<td>339.30</td>
<td>1.25</td>
<td>0.08</td>
</tr>
<tr>
<td>Vegetation, water, land edge, nest location</td>
<td>−164.56</td>
<td>5</td>
<td>339.48</td>
<td>1.43</td>
<td>0.08</td>
</tr>
<tr>
<td>Vegetation, water, land edge, nest location, distance sites</td>
<td>−163.69</td>
<td>6</td>
<td>339.88</td>
<td>1.83</td>
<td>0.06</td>
</tr>
</tbody>
</table>

Table 5. Results from generalized linear mixed models examining nest predation probability in the egg stage (n = 177 nests) across spatial scales. Models with ΔAICc < 2 compared to best model (with smallest AICc) are shown (for all candidate models examined, see Appendix 2). For details on variable names and abbreviations, see Table 3. No across-scale models have been calculated for the nestling stage.
depredated in the egg stage (Martin et al. 2000). Unless stated otherwise, our discussion focuses on nest predation occurring in the egg stage.

**Nest scale**

Probability of predation declined with increasing vegetation cover, height of dead leaves above the nest and nest height above ground, summarized in the “vegetation factor”. This might reflect a) that well-camouflaged nests are less likely to be detected by predators (Martin 1995, Widmer 2001, Weidinger 2002, Müller et al. 2005), although the effect of camouflage on nest predation may depend on the species studied (Howlett and Stutchbury 1996), and b) that nests are probably more likely to be attacked from the ground than from the air. The latter is consistent with our experience from field work, where we never observed potential aerial predators such as crows (*Corvus* sp.) invading reed patches along the water border. That higher water cover and depth was coupled with an elevated predation probability may indicate an association of predators with water, which is corroborated by effects evident on the edge scale (see below).

**Edge scale**

Nests located closer to a water body, in smaller reed patches, and in patches with a higher relative amount of edge habitat (all variables represented by the PCA factor “nest location factor”) were more likely to be preyed upon than other nests. Further, predation probability increased when nests were located close to the land sided reed edge (“land edge factor”). These results provide evidence for edge effects operating at the level of the reed patch containing the nest. Increased amounts of edge habitat make a patch more accessible to predators (see Lahti 2001 and Batáry and Baldi 2004 for recent reviews). Red foxes, for instance, are predators of reed bunting nests (unpubl.), and this species is known to search along linear structures for prey (Seymour et al. 2004), but other potential predator species such as cats (*Felis* sp.), polecats *Mustela putorius*, grey herons *Ardea cinerea*, little bitterns *Ixobrychus minutus* or rails may also benefit from increased edge length. That predators

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**Figure 1.** Scale-dependent factors affecting daily nest predation probability in the egg stage. Symbols are predicted values from a multiple logistic regression with vegetation (referring to the nest scale), distance to land edge, nest location (both variables of edge scale) and distance between sites (landscape scale) as independent variables. N = 177.

**Table 6.** Model-averaged estimates $\pm$ SE and weights (see Table 4) for variables of across-scale models of the egg stage ($n = 177$). No across-scale models have been calculated for the nestling stage.

<table>
<thead>
<tr>
<th>Variables</th>
<th>Estimate $\pm$ SE</th>
<th>Weight</th>
</tr>
</thead>
<tbody>
<tr>
<td>Vegetation factor</td>
<td>$-0.27 \pm 0.27$</td>
<td>0.78</td>
</tr>
<tr>
<td>Land edge factor</td>
<td>$-0.30 \pm 0.31$</td>
<td>0.76</td>
</tr>
<tr>
<td>Distance between sites</td>
<td>$0.77 \pm 0.93$</td>
<td>0.68</td>
</tr>
<tr>
<td>Nest location factor</td>
<td>$-0.17 \pm 0.22$</td>
<td>0.64</td>
</tr>
<tr>
<td>Water factor</td>
<td>$0.04 \pm 0.11$</td>
<td>0.35</td>
</tr>
</tbody>
</table>
are less efficient in finding nests located in patches of increasing size (1–10 ha) has recently been demonstrated by modeling (Seymour et al. 2004) and in field studies (Byrkjedal 1980, Crabtree et al. 1989, Burger et al. 1994, Hansson et al. 2000, Sovoda et al. 2000).

Our findings indicate that at least some predators invade reed patches from the water sided edge. This parallels the outcome of a nest predation experiment, which we had performed in our study area, where predation probability declined with increasing distance to the water sided reed edge (Eger 2004). In our study area, water rails *Rallus aquaticus* depredate real reed bunting nests (unpubl.), and coots *Fulica atra* and little bitterns may also belong to the predator guild.

If experienced birds preferentially settle in large reed patches and sites, and young birds have to content with small ones, then the increased predation probability of nests located in small reed patches with a higher relative amount of edge habitat may reflect differences in the quality of the breeding individuals rather than of the habitats. We found no evidence of settlement patterns reflecting differences in individual quality estimated from standard morphological measurements (length of wing and tarsus, body mass). Body mass of females, who are responsible for nest site selection and nest building in reed buntings, was higher and tarsus length shorter in small than large sites (Pasinelli et al. unpubl.). Age of reed buntings cannot be determined from plumage in spring. However, philopatry of adult females and males (i.e. percentage of adult females and males returning to breed in the same site from one year to the next, respectively) did not differ between small and large sites, and breeding dispersal is rare (unpubl.). These findings indicate that large sites did not host more individuals of older age and/or of increased quality than small sites.

**Site and landscape scale**

Variables measured at the site scale were not closely tied to predation probability. This was not due to low variance in the parameters measured, because values for the variable “total reed area” ranged from 390.4 to 25809.1 m² (mean = 7332.2 m², SD = 9640.4 m², n = 5) and for “reed shape” from 0.062 to 0.411 m² (mean = 0.211, SD = 0.130, n = 5). On the other hand, the landscape scale variable “distance between sites” was the only one affecting predation probability both in the egg and the nestling stage, albeit in contrasting ways. Reviews suggest that in birds, predator effects are most prevalent when tests are conducted at the landscape scale (Chalfoun et al. 2002, Stephens et al. 2003, Batáry and Báldi 2004), because predators may benefit from habitat fragmentation by agriculture where they are provided with additional food resources (Andrén 1995, Marzluff et al. 1998, Dijak and Thompson III 2000). However, the studies considered in these reviews are biased towards fragmentation of forests or grassland habitats in the northern hemisphere. In these habitats, potential predator species such as raccoons *Procyon lotor* or weasels *Mustela nivalis* may become more abundant when landscapes contain an increased proportion of agricultural fields. In Switzerland however, mammalian predators, except for red foxes, generally avoid farmland (ermines *Mustela erminea*, Meia 1995, weasels, Güttinger 1995). We interpret the positive correlation between nest predation probability and distance between sites found in the egg stage as an effect of predators assembling in the few remaining hunting grounds (here wetlands), reminiscent of crowding effects in insects, birds and small mammals as a consequence of fragmentation (reviewed in Debinski and Holt 2000).

**Spatial and temporal levels of nest predation**

Our study supports the conclusions of Chalfoun et al. (2002) and Stephens et al. (2003) that nest predation in relation to habitat fragmentation should be studied at multiple spatial scales. Across-scale models were ranked highest, meaning that they were the best models to explain variation in nest predation probability. The overall best model, containing the “vegetation factor”, the “land edge factor”, the “nest location factor” and the variable “distance between sites”, revealed nest site selection to be critical for nest success, because it showed that predation probability was reduced for nests located in the interior of large patches with dense vegetation. Natural selection should thus favor females selecting nest sites towards the center of habitat patches, unless the distribution of suitable sites for nesting is not homogeneous within patches. The micro-habitat structures determining nest site selection in reed buntings are poorly known, however.

Our results further imply that studies of nest predation should distinguish between the egg and nestling stage whenever possible, a fact that is often not considered (Chalfoun et al. 2002, Stephens et al. 2003, Batáry and Báldi 2004). The most vulnerable nests are often predated already in the egg stage (Martin et al. 2000). Hence, if only the egg stage is considered, as in most nest predation experiments, the importance of factors with the potential to affect also better protected nests (those surviving the egg stage) may be underestimated. Nest losses are more detrimental in the nestling than in the egg stage, because the reproductive investment lost is higher and the likelihood of a replacement brood may be reduced.
Implications for conservation of reed-inhabiting bird species

Given the strong evidence of edge effects operating at the level of the reed patch containing the nest, conservation measures in favor of the reed bunting should result in an increase in reed patch size with reduced edge length. This would allow the birds to select nest sites farther from edges than it is currently possible. Further, reed patches should be spared from mowing for several years, because the intensive mowing prevents the development of dense ground vegetation (Carex sp., Juncus sp., Polunin et al. 2002), which we have shown to be of central importance for nesting success of reed buntings.

We suggest that these measures represent a simple, but effective strategy to improve breeding conditions for the reed bunting and perhaps other reed-inhabiting passerines (for example Acrocephalus and Locustella warblers, Graveland 1999, Kube and Probst 1999, Hansson et al. 2000, Hoi et al. 2001, Batáry et al. 2004). In addition, old reed reed patches may also serve as sources for arthropods to re-colonize nearby reed patches (Tscharnkte 1992). Hence, both arthropod and bird communities would profit from a change in the current reed management strategies.

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