

SPECIES-SPECIFIC DISTRIBUTION OF REED-NESTING PASSERINE BIRDS ACROSS REED-BED EDGES: EFFECTS OF SPATIAL SCALE AND EDGE TYPE

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We studied the distribution of breeding passerine birds across reedbed edges in Hungary. Our aim was to investigate the effects of edge. Therefore, we studied the birds' distribution at two spatial scales, across four different reed edges (a reed – water edge, a reed – boat path edge, a reed with bushes – dike edge and a gradually changing edge), where the vegetation structure and the landscape position (depending on the extent of open water) were different. Reed-nesting birds were censused by the line transect method in three wetlands (Lake Velence: 1992–1994; Kis-Balaton: 1991; Macska-sziget (island), Szigetköz: 1994–1995). We found different edge effects at different spatial scales. At the landscape scale there were no differences at the community level between edge and interior community structure parameters (species number, total and species density), but at the species level, the density of Bluethroat *Luscinia svecica* was 3.5 times higher in the interior than in the edge habitat, whereas the density of Great Reed Warbler *Acrocephalus arundinaceus* was 12 times higher in the edge than in the interior habitat. At the local scale, when only the first 40 m from the edge was considered, the Reed Warbler *A. scirpaceus*, Savi's Warbler *Locustella luscinioides*, Bearded Tit *Panurus biarmicus* and partly the Sedge Warbler *A. schoenobaenus* showed strong significant edge (0–5 m) preference for both reed – water and reed – boat path – reed edges. Eight out of 14 species showed different patterns of edge avoidance/preference at the three edges of similar landscape position, which reflects the crucial role of vegetation structure at the edge. Reed-nesting passerine species responded individualistically to edges. The general pattern of edge preference on the local spatial scale may be a result of lower nest predation in the edges mediated by the vegetation structure.

Key words: breeding bird communities, edge effect, habitat selection, landscape ecology, reedbed, vegetation structure

INTRODUCTION

The distribution of animals across the junctions of different landscape elements is a key issue of ecology. In addition, the description of edge effects and fragmentation has emerged recently as a critical research area in conservation biology (SOULÉ & KOHM 1989), and ornithology (NEWTON 1995). However, our knowledge is still in its infancy (LIDICKER & KOENIG 1996). It has been suggested that greater wildlife diversity is due to the greater structural complexity of

edge vegetation (YAHNER 1988), via better food availability and concealment. Most of the edge studies on which this is based were conducted at forest edges, and the effects of other edges on bird distributions generally have been lacking from the literature (ROSENBERG & RAPHAEL 1986, MURCIA 1995). Although TSCHARNTKE (1992) reviewed the effects of fragmentation of reedbeds, he cited only one study dealing with birds. We found only one other paper published recently on fragmentation of reedbeds and the occurrence of birds (CELADA & BOGLIANI 1993).

We define edge effect as the distribution of population and community structure parameters across the edge. The edge is the outer boundary of the reedbed. In our study we used three approaches to detect edge effect: first, the overall patterns were investigated at two spatial scales: the local and the landscape scales (see details in methods). We carried out our study at the two scales that were emphasised by YAHNER (1988) and MOSKÁT *et al.* (1992). Second, reedbed edges in different landscape positions were compared. Third, we compared three reedbed edges with different vegetation structures.

Our main goal was to analyse the distribution of breeding passerine bird species across reedbed edges. We investigated the following questions: (1) are there any differences between edge and interior reed-nesting passerine bird communities? (2) Are there any differences between the distribution of these birds at two levels of spatial scales (landscape and edge levels)? (3) How can the type and landscape position of reed edges influence the distribution of birds across the edge? Finally, as a synthesis of the previous questions, we describe the distribution of individual bird species across a heterogeneous reedbed.

MATERIALS AND METHODS

Breeding passerine birds were censused at three study sites in Western Hungary. Lake Velence (47°10'N 18°32'E) has a reedbed of 1000 ha. The vegetation at this study site was almost entirely reed *Phragmites australis*. We counted birds from a boat within the reedbed along narrow (2–3 m) boat paths (hereafter called interior sharp edges), using a line transect method. The routes for the interior habitats were at least 200–300 m from the edge of the reedbed. Reedbed – water edges (sharp edges) were also surveyed by boat (Fig. 1a). Considering the standard 25+25 m wide belts on both sides of the transect in interior and 25 m wide belt on one side in edge habitats, 15 ha in the former and 12.25 ha in the latter were censused in the breeding seasons of 1992 and 1994. Some parts of the routes (11.5 ha in interior and 4.5 ha in edge habitats) were censused both

in April and May in the same year. For density estimation, we considered only the greater density value of a particular route. The other routes were censused only in May.

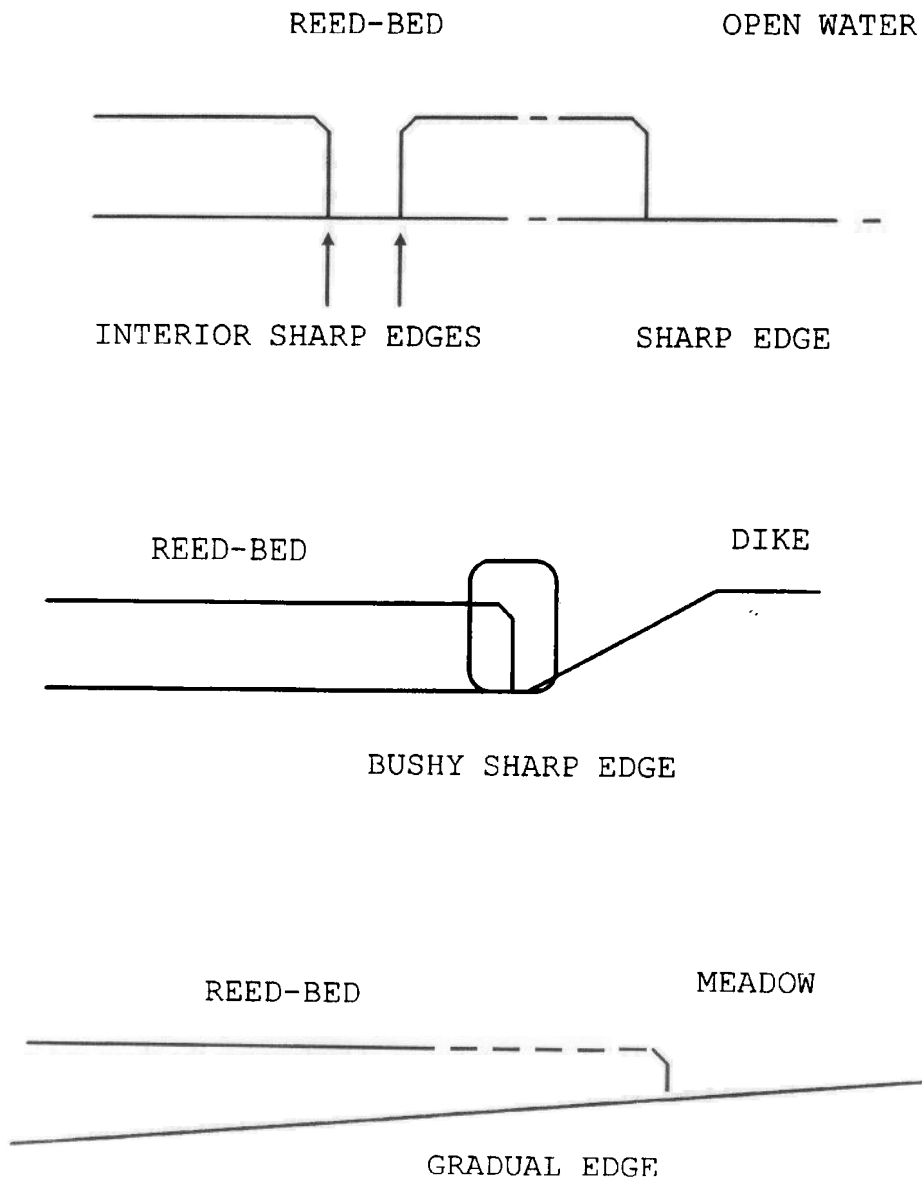


Fig. 1. Different kind of reedbed edges studied: sharp edge, and interior sharp edge at Lake Velence (1a), bushy sharp edge (1b) at Kis-Balaton marshland study areas, and gradual edge at Maeska-sziget (1c)

The marsh Kis-Balaton (46°42'N, 17°21'E) is a reconstructed marshland of 15,000 ha in Western Hungary. The area was more heterogeneous than at Lake Velence, consisting of managed (burned or mowed) parts and some bushes within the reedbed, and a planted bush line of willow (*Salix* spp.) and alder (*Alnus* sp.) at the very end of the reedbed, bordering the grassy dike side (hereafter called bushy sharp edge, Fig. 1b). There were small forest patches on the other side of the dike, about 60–100 m away. We conducted bird censuses by the line transect method along the surrounding dikes of the area. The census route was 8.5 km long (21.25 ha, considering a 25m belt from the reedbed edge) but for this comparison we included only the unmanaged reedbeds, covering 7.6 ha. Bird censuses were repeated eight times in April and May, 1991 (see BÁLDI & MOSKÁT (1995) and MOSKÁT & BÁLDI (1999) for details). The data were pooled.

The third study site was situated in the U turn of a dead-branch of the Danube River in the Szigetköz Region, Western Hungary (47°51'N, 17°27'E). The area of the reedbed was ca. 70 ha. We censused 5.5 ha of reedbed edge by the line transect method. The inner part of the U turn formed an island (Macskasziget (island)), which was regularly mowed. The census route was on the edge of unmowed reedbed on the island. The edge was clearly different from the former ones, where there were sharp edges at the end of the reedbeds. At this third site, the ground rose gradually to form a low, sparse reed stand with sedge at the edge, which gradually changed to denser and taller, "healthier" reed stands (hereafter called gradual edge, Fig. 1c). The exact edge of the reedbed was at the end of the mowed parts. There were altogether four censuses: in April and May in 1994 and 1995. The data were pooled.

At all three sites, all birds detected either visually or acoustically were recorded (mainly acoustical records). The lateral distance of each observed bird from the edge was estimated. For the density estimations, which were calculated only for data from Lake Velence, we used only the observations within the standard 25 m wide belts. The data analysis was carried out in three steps. First, the bird communities of interior and edge habitats were compared (the landscape scale), only for data from Lake Velence. Second, we analysed the data on a much finer (local) spatial scale to detect possible differences between different scales. For this purpose, the abundance of birds in relation to the distance from the edge was examined in 5 m zones within the first 40m from the edge at all study sites. This analysis was performed for the interior (interior sharp edges at the boat paths) censuses, as well. Third, the distribution of birds across the sharp and interior sharp edges at Lake Velence were compared with similar data obtained from marshland Kis-Balaton (bushy sharp edge) and Szigetköz (gradual edge), to detect the effects of different edge types.

We used only data from the main belt (<25 m) for comparing bird communities in the edge and interior habitats, where densities of birds (number of in-

dividuals/10 ha) were calculated. Chi-square tests, *t*-tests and G-tests of homogeneity were applied to evaluate the differences in the distribution of birds at the edges of the three study sites.

RESULTS

We observed the same eight passerine bird species in the interior and edge habitats at Lake Velence (Table 1). The total density values of edge and interior habitats were similar: 113.6 individuals/10 ha along the edge, and 102.0 individuals/10 ha in the interior habitats. (Density was simply calculated as the number of observed birds within the main-belt (25 m) and then standardised to number per 10 ha.) The distribution of density values among species, however, significantly differ in the edge and interior habitats (likelihood ratio $\chi^2 = 16.159$, *df* = 7, *p* < 0.05). This is mainly the result of the unequal densities of two species in the edge and interior habitats: the Bluethroat *Luscinia svecica* avoided the edges (ca. 3.5 times larger density in interior habitats), and the Great Reed Warbler *Acrocephalus arundinaceus* preferred the edges (ca. 12 times greater density in the edge). There were no large differences in the other species. The contribution of these two species to the total χ^2 value is ca 75%.

The distribution of the number of individuals in relation to the distance from the edge (0–40 m) showed significant deviation from the homogeneous distribution in the Bearded Tit *Panurus biarmicus*, Great Reed Warbler, Savi's Warbler *Locustella luscinioides*, Reed Warbler *A. scirpaceus* and the Sedge Warbler *A. schoenobaenus* (Fig. 2) at the sharp edge. The Bearded Tit, Great Reed, Savi's and Reed Warblers showed clear preference for the first 5 m of the reedbed. The pattern of Sedge Warbler's distribution fluctuated in relation to the distance from the edge, without clear edge preference. The only species with homogeneous dis-

Table 1. Density of passerine bird species (number of individuals/10 ha) in interior (0–25 m of the interior sharp edge) and edge (0–25 m of the sharp edge) reed-bed habitats at Lake Velence

Species	edge (12.25 ha)	interior (15 ha)
<i>Acrocephalus arundinaceus</i>	8.2	0.7
<i>Acrocephalus melanopogon</i>	2.5	2.0
<i>Acrocephalus schoenobaenus</i>	20.4	15.3
<i>Acrocephalus scirpaceus</i>	28.6	23.3
<i>Emberiza schoeniclus</i>	5.7	4.0
<i>Locustella luscinioides</i>	24.5	30.0
<i>Luscinia svecica</i>	2.5	8.7
<i>Panurus biarmicus</i>	21.2	18.0

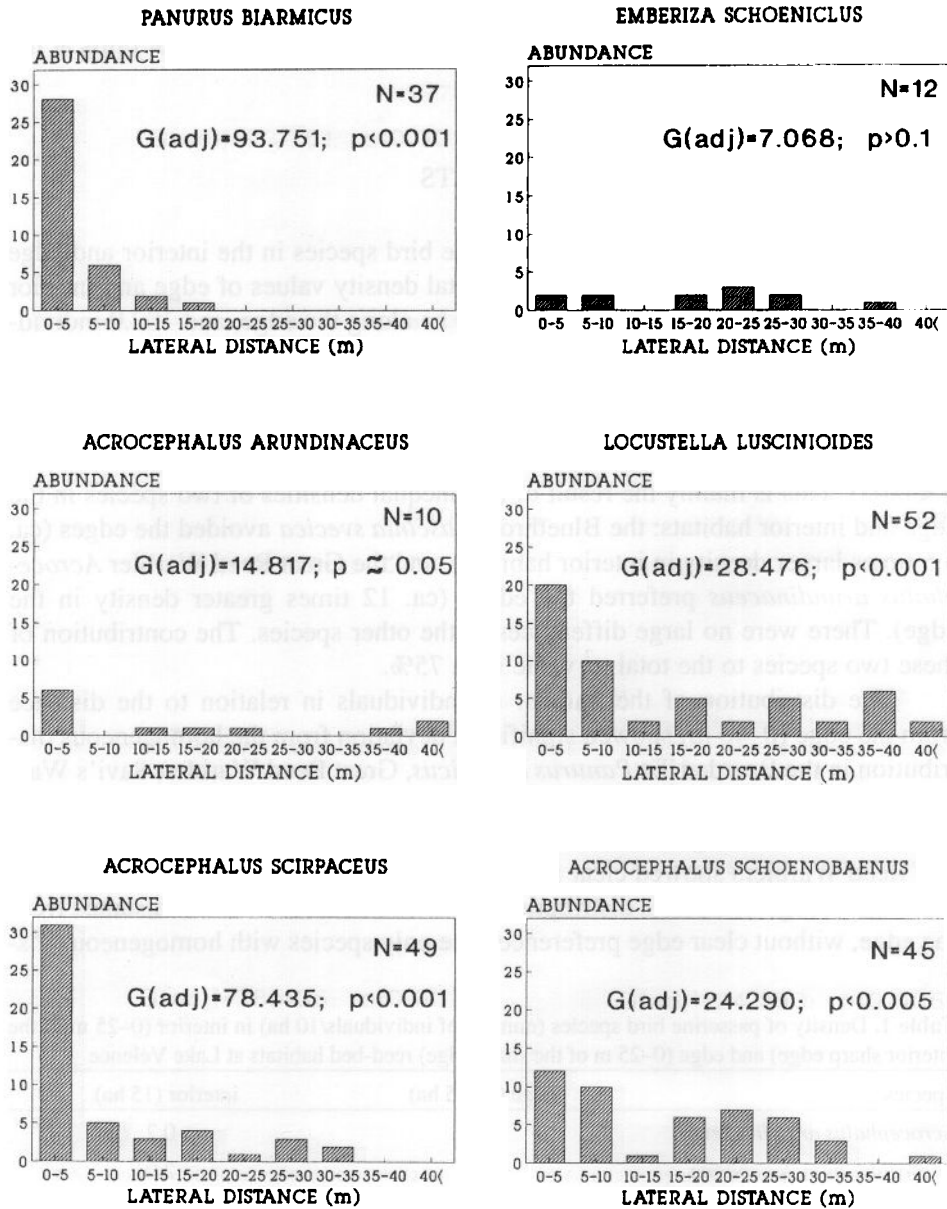


Fig. 2. Distribution of the number of individuals of the six most abundant passerine bird species at Lake Velence across sharp edges. For analysis we used the 0–40 m zone (to which the N refers), but on the figures we presented the number of birds beyond 40 m, because it can give important additional information on the edge preference of species

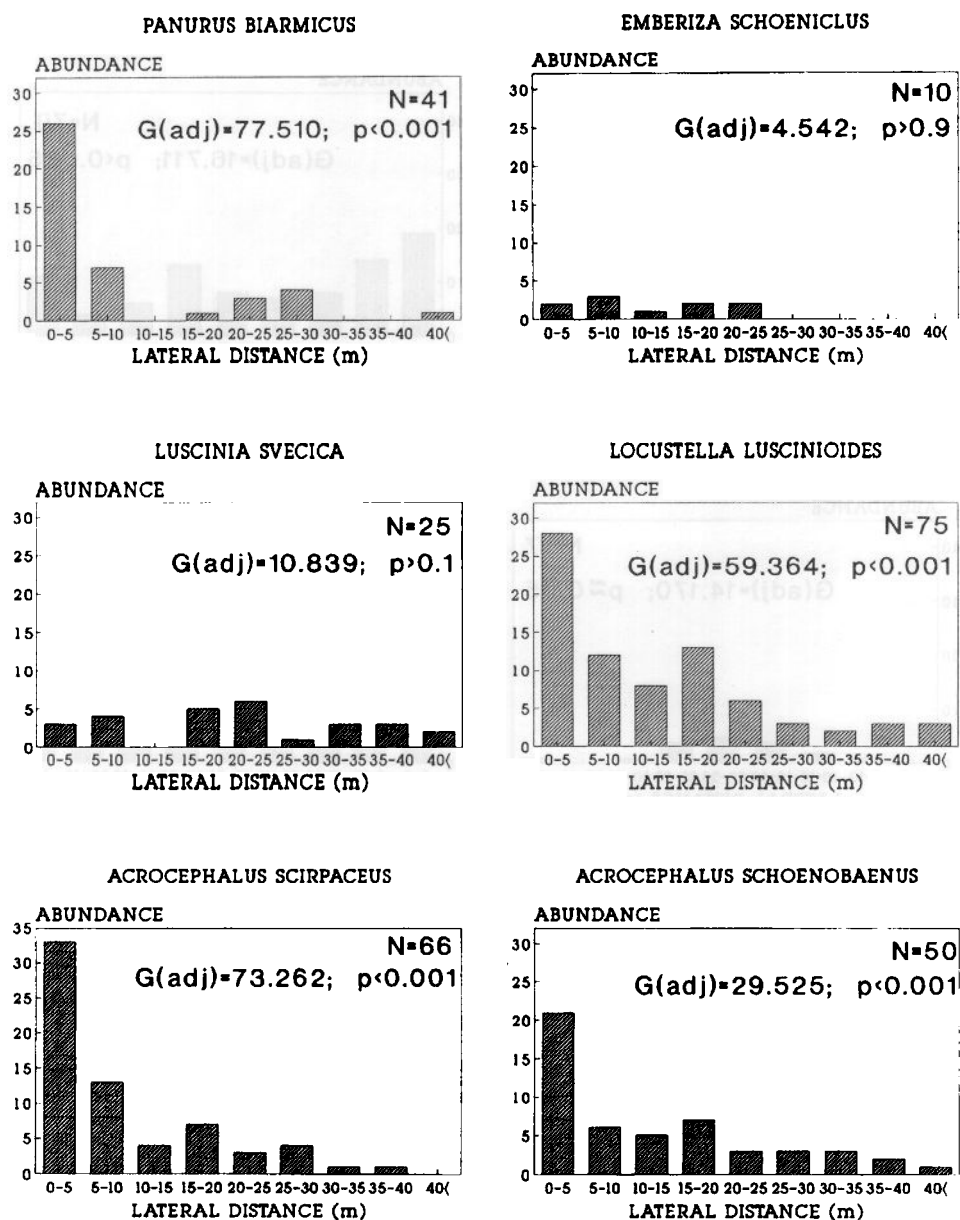


Fig. 3. Distribution of the number of individuals of the six most abundant passerine bird species at Lake Velence across interior sharp edges. For analysis we used the 0–40 m zone (to which the N refers), but on the figures we presented the number of birds beyond 40 m, because it can give important additional information on the edge preference of species

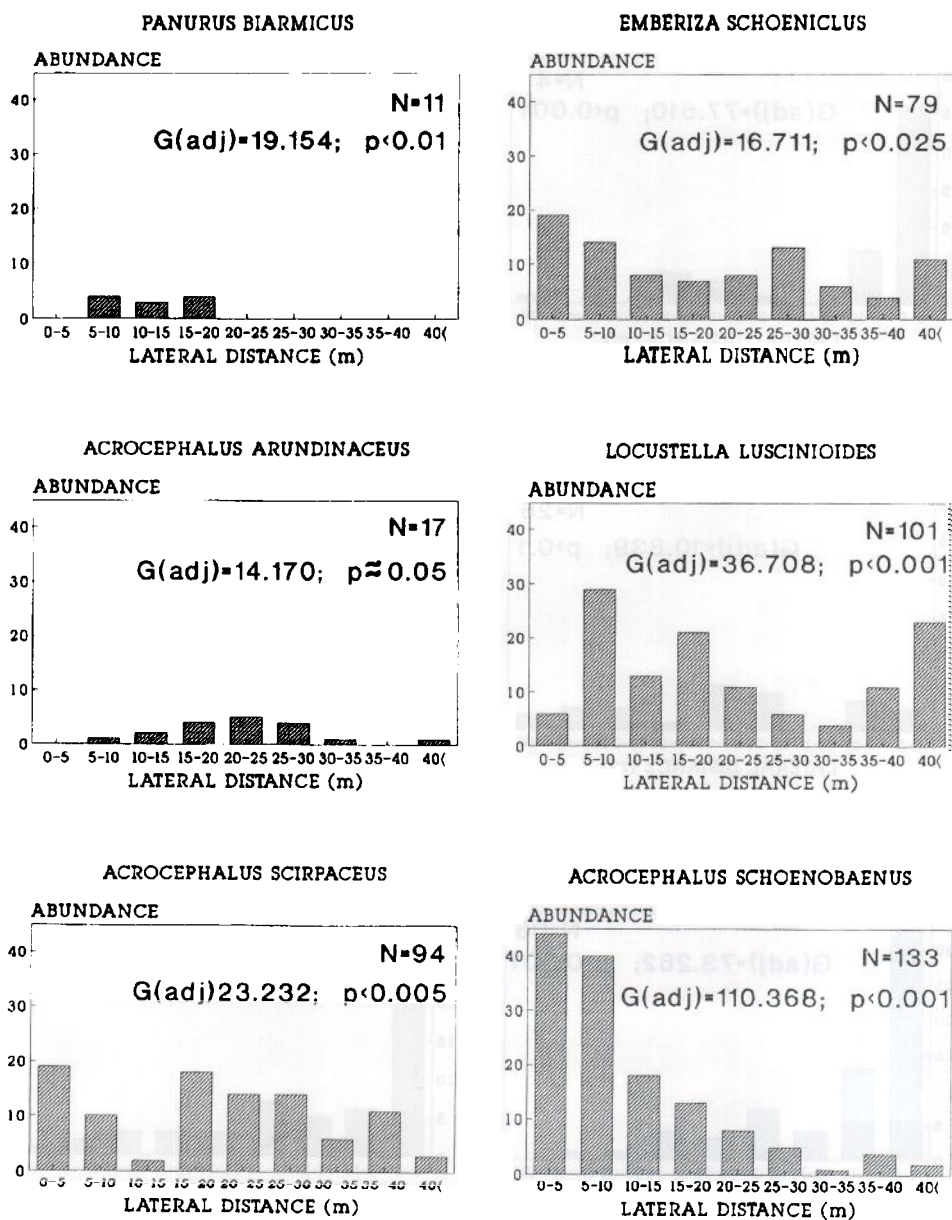


Fig. 4. Distribution of the number of individuals of the six most abundant passerine bird species at Kis-Balaton across bushy sharp edge. For analysis we used the 0–40 m zone (to which the N refers), but on the figures we presented the number of birds beyond 40 m, because it can give important additional information on the edge preference of species

Table 2. Comparison of the distribution of passerine birds across edges in three edge types. (The 5 m wide zones were used, see Figs 2–5) χ^2 values, degree of freedom and two-tailed significances are given. – : too few values at least at one of the sites for calculation

Species	sharp edge – bushy sharp edge	sharp edge – gradual edge	bushy sharp edge – gradual edge
<i>Acrocephalus arundinaceus</i>	17.137 7 $p < 0.05$	–	–
<i>Acrocephalus schoenobaenus</i>	20.814 7 $p < 0.01$	5.806 7 NS ($p > 0.5$)	25.854 7 $p < 0.002$
<i>Acrocephalus scirpaceus</i>	34.273 7 $p < 0.001$	3.727 6 NS ($p > 0.5$)	15.400 7 $p < 0.05$
<i>Emberiza schoeniclus</i>	5.131 7 NS ($p > 0.5$)	7.972 7 NS ($p > 0.1$)	4.140 7 NS ($p > 0.5$)
<i>Locustella luscinioides</i>	30.614 7 $p < 0.001$	19.674 7 $p < 0.02$	21.266 7 $p < 0.01$
<i>Panurus biarmicus</i>	23.092 3 $p < 0.01$	–	–

tribution was the Reed Bunting *Emberiza schoeniclus*. Therefore, four from the six abundant species occurred mostly in the first 5 m of the reedbed, showing a well defined overall edge preference at the local scale. Very similar patterns were observed for the five common species in the interior sharp edge habitats, where the censuses were made along narrow boat paths, no wider than 2–3 m (Fig. 3). The Bluethroat *Luscinia svecica*, which was very rare at the sharp edge did not showed significant relation to the edge.

The distribution of the common species across the bushy sharp edges at the marshland at Kis-Balaton showed different patterns (Fig. 4). The Sedge Warbler showed strong edge preference and the Reed Bunting weak edge preference. The Reed and Savi's Warblers also showed edge preference, as in the case of sharp and interior sharp edges, but they tend to avoid the 0–5 m edge of the reedbed, where the bushes were present. The Great Reed Warbler and the Bearded Tit presented a more pronounced avoidance of the bushy zone, although the sample sizes were small.

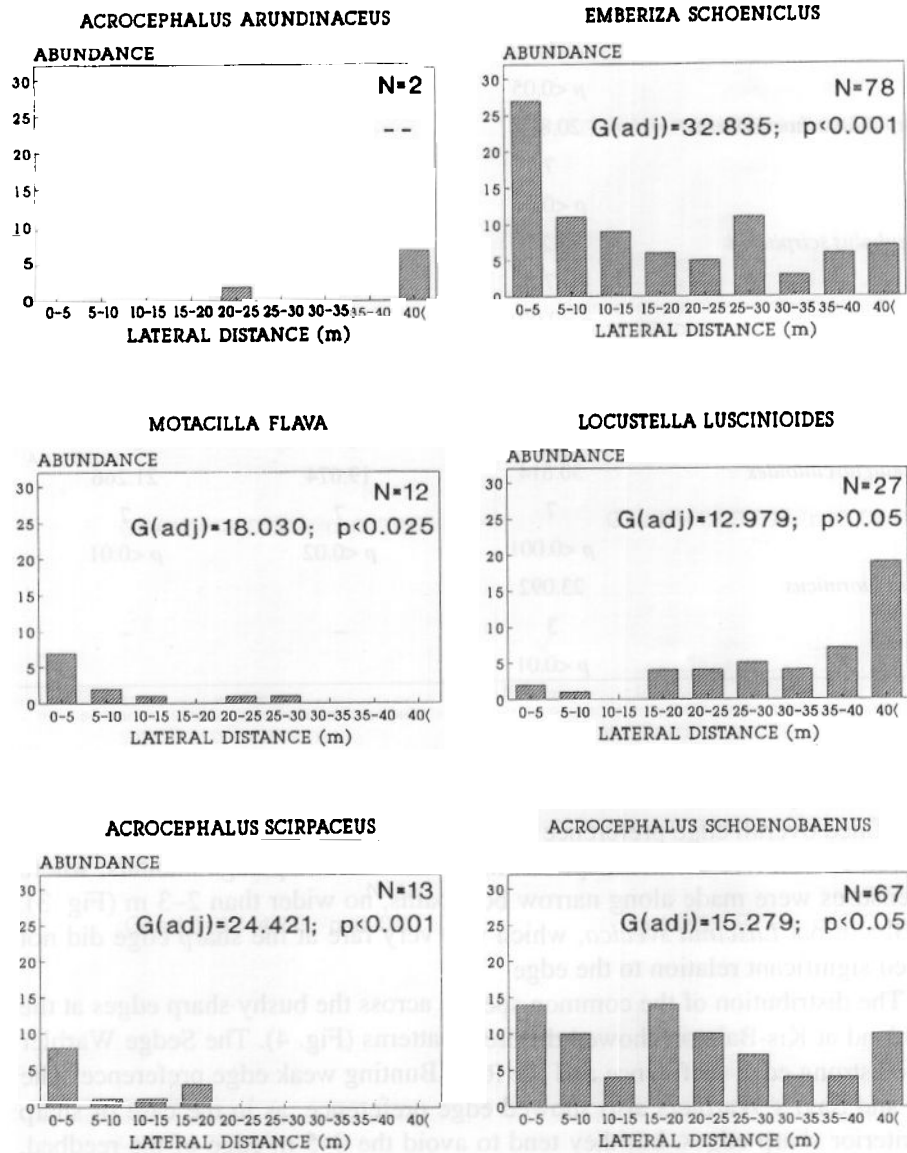


Fig. 5. Distribution of the number of individuals of the six most abundant passerine bird species at Macska-sziget across gradual edge. For analysis we used the 0–40 m zone (to which the N refers), but on the figures we presented the number of birds beyond 40 m, because it can give important additional information on the edge preference of species

There were six common species at the sharp and interior sharp edges at Lake Velence and the gradual edges at Macska-sziget, the Moustached Warbler *A. melanopogon* and the Bluethroat were absent from Macska-sziget. The Reed Warbler, Reed Bunting and the Yellow Wagtail *Motacilla flava* showed edge preference at this site (Fig. 5, the Yellow Wagtail, *Motacilla flava*, was included, as the sixth most abundant species at Macska-sziget). The latter two species preferred the reed – meadow edge, while the few Reed Warblers were observed on some sites where the reed was tall, e.g. near channels. The Savi's and the Great Reed Warblers avoided the gradual edge, they were observed further inside the reedbed, beyond the 40 m limit of this analysis (Fig. 5).

Five of the six abundant common species showed significantly different distribution across edges comparing the sharp and bushy sharp edges (Table 2), even after sequential Bonferroni corrections. The Savi's Warbler showed different distributions at the sharp and gradual edges (Table 2). Nine common reed-living bird species were observed at the bushy sharp and gradual edges (Table 3). Three wetland species occurred at Kis-Balaton, which were absent from Macska-sziget (Moustached Warbler, River Warbler *L. fluviatilis* and Penduline Tit *Remiz pendulinus*), and one species was censused only at Macska-sziget (Yellow Wagtail). The differences among the distributions of the abundant common species across the reed edge were significant in four cases, except the Reed Bunting (Table 2).

We observed only reed-nesting bird species at the Lake Velence study site, which is a homogeneous reedbed. However, at the two other sites, several passerine species were censused that do not depend upon the reed stands (Table 3). Their presence may be attributed to the landscape structure. At Kis-Balaton and Macska-sziget, not only reed stands and open water occurred in the censused areas, but several other habitat types, too, such as meadows, bushes and trees. In addition to the reed-nesting passerines, there were bush-preferring species (e.g. Robin *Erithacus rubecula*, Red-backed Shrike *Lanius collurio*), meadow species (e.g. Goldfinch *Carduelis carduelis*), and visitors from the nearby forest patches (e.g. Chaffinch *Fringilla coelebs*, Tree Sparrow *Passer montanus*) in these two study sites. However, the great majority of overall bird abundance (number of individuals) consisted of reed-living birds: 90.7% at Kis-Balaton and 91.5% at Macska-sziget. Although the forest- and meadow-living species were rare visitors in the reedbed edge, some characteristic bush and meadow species belonged to the bird community of the census area. They were thought to breed in the line of bushes at the reed edge.

Table 3. The presence-absence data of the observed passerine bird species at the three study sites. We omitted the interior sharp edge data from this table, because at the Kis-Balaton and Macskasziget study sites no interior parts were censused

Species	sharp edge	bushy sharp edge	gradual edge
<i>Acrocephalus arundinaceus</i>	+	+	+
<i>Acrocephalus palustris</i>		+	+
<i>Acrocephalus melanopogon</i>	+	+	
<i>Acrocephalus schoenobaenus</i>	+	+	+
<i>Acrocephalus scirpaceus</i>	+	+	+
<i>Aegithalos caudatus</i>		+	
<i>Carduelis carduelis</i>		+	
<i>Emberiza schoeniclus</i>	+	+	+
<i>Erithacus rubecula</i>		+	+
<i>Fringilla coelebs</i>		+	
<i>Lanius collurio</i>		+	+
<i>Locustella fluviatilis</i>		+	
<i>Locustella naevia</i>		+	+
<i>Locustella luscinioides</i>	+	+	+
<i>Luscinia megarhynchos</i>			+
<i>Luscinia svecica</i>	+		
<i>Motacilla alba</i>		+	+
<i>Motacilla flava</i>			+
<i>Muscicapa striata</i>		+	
<i>Panurus biarmicus</i>	+	+	+
<i>Parus major</i>		+	
<i>Passer montanus</i>		+	+
<i>Phylloscopus collybita</i>		+	
<i>Phylloscopus trochilus</i>		+	
<i>Remiz pendulinus</i>		+	
<i>Saxicola torquata</i>			+
<i>Saxicola rubetra</i>			+
<i>Sylvia atricapilla</i>		+	+
<i>Sylvia communis</i>		+	
<i>Sylvia nisoria</i>			+
<i>Sylvia curruca</i>			+

DISCUSSION

Opinions on how animal communities respond to forest edges are widely divergent (REESE & RATTI 1988, MURCIA 1995, BÁLDI 1996). Indeed, there are many studies on the effects of forest edges on bird communities, but the results are diverse. For example, HELLE & HELLE (1982), HANSSON (1983) and FULLER & WHITTINGTON (1987) found a much greater density in the edge. In contrast, LOVEJOY *et al.* (1986) found 60 percent fewer birds in the edge than in interior forests. Similarly, MARTIN (1983) found a lower density on small islands than on large islands, perhaps a consequence of impoverished edges. The confusion is not surprising: pattern may vary even in individual species. For example, the Robin has been shown to avoid deciduous forest edges (MOSKÁT & FUISZ 1994), to prefer edges (BÁLDI & KISBENEDEK 1994, BÁLDI & MOSKÁT 1994), and to occur irrespective of edges (FULLER & WHITTINGTON 1987). However, this is not surprising, because the edge effect depends on many factors. The three main factors are the (1) spatial scale (as in many aspects of ecology, WIENS (1989a)), (2) edge type (i.e. vegetation structure and landscape position of the edge), and (3) census methodology. We demonstrated in the present study that differences in edge effect do exist between different spatial scales and edge types in reed habitats. It is easy to accept that methodology may also have serious effects, since different bird census techniques usually give different results even in the same habitat and study area (MOSKÁT 1987). However, we used the same census technique in all the three habitats, and the censuses were made by the same person (AB); therefore methodological problems should be excluded here. In addition, one main point of our results, namely the edge-preference patterns of *Acrocephalus* warblers, which were observed by the line transect method, was confirmed by a mist-netting study (CSÖRGŐ 1995a). CSÖRGŐ found that, at the reed belt along the bank of Lake Balaton (ca. 5 km from the Kis-Balaton study area), the distribution of birds was similar to our observations: 43% of the Great Reed Warblers, 22% of the Reed Warblers and 11% of the Sedge Warblers were captured in the first 12 m from the water along a 144 m long mist-net line in July. The netting effort did not differ among mist-nets. Although more detailed investigations are needed to clarify the influence of methods on edge studies, it seems that for reed habitats the patterns are robust enough to be clearly detectable by different census techniques.

The similar results of the line transect and mist-netting studies have important methodological considerations. The detectability is supposed to decline with the distance from the observer, which may be a factor accentuating any edge effect in the local scale analysis. However, detectability had no significant effect on the results of this study, because, (1) the mist-netting study, where detectability has no influence, showed similar distribution pattern, and (2) within a few ten

Table 4. Patterns of relative abundance of seven reed-nesting passerine bird species in reedbed edges of different landscape position and vegetation structure. Interior: density estimation in a 25+25 m wide main belt, 200–300 m from the edge; see study area section for the description of the edge types

Species	interior	interior sharp edge	sharp edge	bushy sharp edge	gradual edge
<i>Acrocephalus arundinaceus</i>	very few	very few	many	few	absent
<i>Acrocephalus schoenobaenus</i>	many	medium	medium	many	medium
<i>Acrocephalus scirpaceus</i>	many	many	many	medium	few
<i>Emberiza schoeniclus</i>	few	few	few	medium	many
<i>Locustella luscinioides</i>	many	many	many	medium	few
<i>Luscinia svecica</i>	many	many	few	very few	absent
<i>Panurus biarmicus</i>	medium	many	many	very few	absent

meters, the detectability of bird song is not declining (SCHIECK 1997). This assumption is based on two arguments: (1) most of the observations belong to acoustical records, and (2) visual detections are almost negligible due to the very dense structure of reed-stands.

The scale-dependent response to fragmentation of forest birds was shown by JOKIMAKI & HUITA (1996). Here we found differences in the response of the same species at different scales. The Great Reed Warbler showed similar edge preference at both the landscape and local scales at the Lake Velence study area. This pattern suggests a strong preference for reed edges and avoidance of interior reedbeds (Table 4). The Bluethroat preferred the interior of reedbeds, with no respect to small scale heterogeneities, like boat paths at the interior sharp edges. Thus, the Great Reed Warbler selected edges at both spatial scales, whereas the habitat selection of the Bluethroat avoided edges only at the larger scale. The Reed Warbler, Savi's Warbler and Bearded Tit showed edge preference at the local scale, both in sharp and interior sharp edges, but no obvious preference at the landscape scale. Therefore their observed distribution patterns may be a result of the occupation of the whole reedbed, but a local abundance in all edge types (Table 4).

The pattern of the dispersion of reed-living passerine birds across reedbeds is in accordance with the ecomorphology of these species. For example, the Reed, Savi's and Great Reed Warblers are well adapted to homogenous reeds (LEISLER 1975, LEISLER *et al.* 1989), therefore they avoided bushy and gradual edges. The Sedge Warbler is adapted to a more heterogenous habitat, therefore the edge preference at the bushy sharp edge, show the normal habitat selection of the species. A more detailed investigation is needed to understand edge effect in

the light of habitat selection and ecomorphology for all the reed living passerine birds.

What are the key factors which generated the edge preference of reedbed passerines at the local spatial scale? It should be noted that, although most marshland-nesting passerines have a relatively small territory (HUT 1986), the preference for the first 5 m of the edge reflects not to territory selection, but to within territory preferences, for example for nesting or foraging sites. CSÖRGŐ (1995b) found that >70% of the Great Reed Warbler nests were within 2 m of the edge. In general, there are two main candidate mechanisms determining bird reproductive success: food availability and suitable nest sites (MARTIN 1992, WIENS 1989b). In fact, the importance of both factors were demonstrated for *Acrocephalus* species: HOI *et al.* (1995) showed that prey abundance had a key role in determining mating system and male parental investment both at the intra- and at the interspecific levels, and SCHULZE-HAGEN *et al.* (1996) found that nest predation, which mainly depends on nest site, had significant effect on breeding success. However, the quality of both foraging and nesting sites depend on the vegetation and landscape structure. Dense vegetation, which occurs along edges, provides better nesting possibilities than scarce vegetation, and the expected increased nest predation rate in the edge (e.g. PATON 1994) was not supported for reedbeds. We conducted a nest predation experiment with a total of 50 artificial passerine nests, and daily depredation rate was slightly lower in the edge (4.7%) than in the interior (5.33%) of reedbed (BÁLDI, unpubl. data).

Although there is an inverse relation between vegetation density and prey abundance in homogenous reedbeds (ILLE & HOI 1995), edges harbour more insects than interior parts, in spite of the denser vegetation (HERBERT HOI, pers. comm.). Thus, both predation avoidance and food availability is better in edges of reedbeds, which may explain the general result of edge preference in our study.

An important point of our study is the demonstration of the individualistic response of bird species to the spatial structure of reedbeds. The reed-living passerine bird community is relatively species-poor and the species are more similar to each other than in a forest bird community, e.g. their body size is almost the same, except the Great Reed Warbler. In spite of their similarity, their distribution is different across the reedbed (Table 4). The individualistic responses of bird species to variations in environment was described on a continental scale (TAPER *et al.* 1995) and on a finer scale for forest birds (JOKIMAKI & HUITA 1996). Here we demonstrated it on a local scale for reedbed birds. Other studies also showed species-specific response of birds in edge habitats (PARISH *et al.* 1995).

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