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Reedbed structure and habitat preference of reed passerines during the post-breeding period

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Abstract: Post-breeding habitats of nine passerine species were studied in the permanently flooded reed beds of ponds near the village Pusté Úľany (SW Slovakia) in 2002. Structural features of reed beds and the abundance of all birds studied were sampled at two sites and eight study plots. The reed bed structure and abundance of four passerines differed considerably between the individual study plots. The variations in vegetation structure were also caused by winter reed burning in the SE part of study area. Stems in burnt reed beds were smaller and thinner than unburnt. Abundance of the reed warbler and to a lesser extent sedge warbler was higher in tall reed beds, while the bearded tit preferred thick reed stems. Position of reed beds along the shore – open water gradient was an important factor in terms of abundance at the study plots in the case of the reed bunting. This species showed a strong preference for the reed bed edge with open water. Horizontal distribution of other species seems to be random, however, the birds with the exception of Savi's warbler preferred the upper stratum of reed bed in vertical distribution. Our field data corroborate with those found in experimental studies concerning with ecomorphological characteristics of birds. Some inconsistencies, however, could also be caused by other factors (e.g. foraging preferences). Comparison of breeding and post-breeding habitat requirements of the studied bird species confirmed a more or less random distribution of the majority of species in the post-breeding period. Some variation was found in the cases of only the reed warbler and bearded tit.

Key words: *Acrocephalus* warblers, *Locustella luscinioides*, *Panurus biarmicus*, *Emberiza schoeniclus*, *Remiz pendulinus*, habitat selection.

Introduction

Common reed is the most abundantly represented species of tall-stalk littoral growths in wetland ecosystems. It represents an important habitat for many bird species, especially passerines, the abundance and spatial distribution of which is influenced above all by vegetation structure and food supply (Thomas, 1984; Van Der Hut, 1986; Kouki et al., 1992; Martínez-Vilalta et al., 2002; Poulin et al., 2002). The high uniformity of reed beds offers the opportunity for a more detailed study of habitat requirements of individual bird species associated with this assemblage. The breeding habitat selection of *Acrocephalus* warblers and less frequently of the reed bunting, bearded tit and other species has been studied by various authors (Price, 1969; Catchpole, 1972, 1974; Dyrcz, 1980; Leisler, 1981; Anselin & Meire, 1989; Ille et al., 1996; Graveland, 1998; Poulin et al., 2000, previously cited works and others). However, few works involved in the study of habitat selection of reed passerines in the post-breeding period have been carried out. Spatial distribution of *Acrocephalus* warblers in reed beds has been studied, for example, by Bairlein (1983), Baccetti (1985), Pambour (1990), Honza & Literák (1997), Gyurácz & Bank (2000). As the horizontal and vertical distribution patterns of birds are highly influenced by the structure of the reed bed, this study is focused on the quest for answers to the question 'How do the structural features of reed beds influence abundance and spatial distribution of the individual passerine species in the post-breeding period?' It should contribute to a deeper knowledge of the ecology of the studied bird species and their protection at stopover sites during autumn migration.

Material and methods

The study was carried out in an undisturbed fishpond system near the village Pusté Úľany (NW part of Podunajská nížina lowland, SW Slovakia, 48°14′ N and 17°35′ E) in 2002. Four ponds extend over an area of about 30 ha and are surrounded by large areas of water and terrestrial reed beds (*Phragmites australis* – 20 ha) and less reedmace (*Typha* sp. – 5 ha). Two sites densely covered with permanently flooded homogeneous common reed (*Phragmites australis*) were selected in the largest of these ponds. The reed bed located in the SW part of the pond (site 2) was burnt in winter 2001, and only a few small patches of reed were left unburnt. The

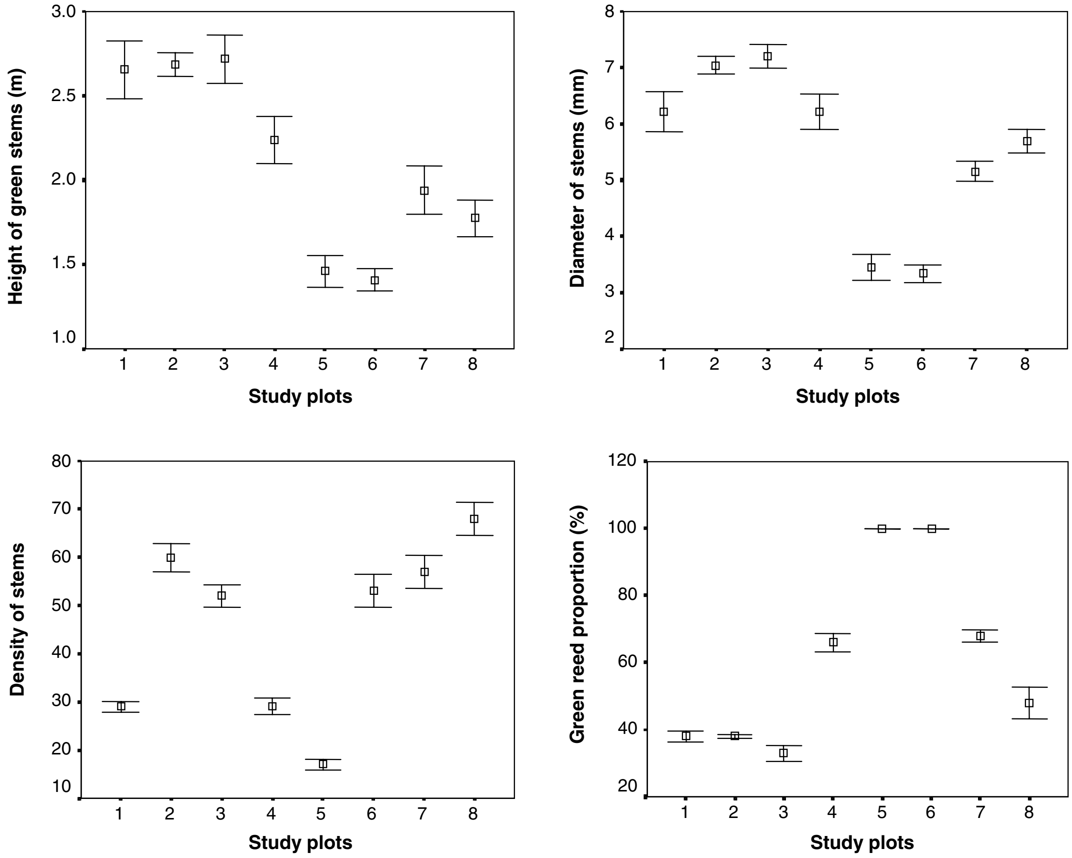

Fig. 1. Means and standard errors of selected environmental variables at study plots.

reed bed located in the NE part (site 1), however, has been never harvested or burnt. In both reed beds four smaller study plots with expected different density, height and diameter of stems stretching from the bank as far as the open water surface were sampled. Inside each plot a single mist net was located along the 10 m long and 1 m wide transect.

Reed structure in each transect was estimated at the end of July, i.e. after the period of reed growth. Density, diameter and proportion of dry (old) and green (this year) reeds were determined by counting and measuring all stems within a square, while density was counted in three squares of 0.5 × 0.5 m located at the centre of each transect and 0.5 m away from the right side of its edge. Only the height of green reed was measured within the same squares. The birds were caught using 10 m long and 2.5 m high mist-nets. The bottom shelves of all nets were set at the same height (0.3 m) above the water level. The distance of each mist-net from open water was also noted. Birds were captured once at 5-day intervals from 15 July to 31 August at each site. All nets were opened 5 h before sunset and operated 5 h after sunrise under rainless and windless conditions. Nets were visited every 60 min and captured birds were identified, sexed, aged and ringed. The capture position of each bird was also recorded (lower and upper positions represent the two bottom and two top shelves respectively).

Data were inspected for normal distribution and log transformed if necessary. Simple comparisons between two variables were performed using the *t*-test or the Mann-Whitney *U*-test. The proportion of green stems was compared using the Chi-square test (χ^2). The one-way ANOVA or Kruskal-Wallis tests were used for comparison of vegetation structure or bird abundance at reed bed plots. For selection of factors affecting bird abundance, multiple regression analysis was performed. Moreover, using this method it was possible to identify relationships among the tested variables.

Results

Reed structure

The reed bed structure differed considerably between the two sites (Tab. 1). Reed was significantly taller and thicker at site 1 (t = 11.6 and 12.1, df = 189 and 363, $P < 0.0001$, respectively), although the proportion of green stems was larger at site 2 ($\chi^2 = 15.9$, df = 1, $P = 0.0001$). Likewise, the reed density also tended to be higher at site 2, but the difference was not statistically significant ($n_1 = 170$, $n_2 = 195$, $U' = 6.0$, $P = 0.561$).

As predicted, significant differences in reed bed structure were not only found between the NE and SW parts of the pond but also among the study plots, which exhibited great variation in all measured variables (Fig. 1). There were statistically highly significant differences in height and diameter ($F_{7,183} = 25.6$ and $F_{7,357} = 42.6$, $P < 0.001$, respectively) and minor differences in density and proportion of stems ($H' = 20.3$ and 21.8, df = 7, $P = 0.005$ and 0.003, respectively) between transects at both sites. However, no relationships were found between the position of study plots and the

Table 1. Mean and standard error (SE) of selected environmental variables at study reedbed sites.

Environmental variables	Reedbed site 1		Reedbed site 2	
	Mean	SE	Mean	SE
Reed density (all stems/square)	42.50	7.96	48.75	11.04
Green reed height (m)	2.56	0.07	1.59	0.05
Reed diameter (mm)	6.81	0.12	4.70	0.12
Green reed proportion (%)	43.75	4.02	79.00	6.76

Table 2. Number of birds captured for each species at the two reedbed sites.

Bird species	Site 1	Site 2	Total
Savi's warbler^{ns}	36	23	59
Moustached warbler^{ns}	10	3	13
Sedge warbler**	142	30	172
Marsh warbler^{ns}	21	23	44
Reed warbler*	185	110	295
Great reed warbler*	28	11	39
Bearded tit*	73	23	96
Penduline tit*	17	2	19
Reed bunting^{ns}	45	82	127

Key: * $P < 0.05$, ** $P < 0.01$, *ns* – non significant (*t*-test and *U*-test).

reed bed structure with respect to open water – shore gradient.

Bird abundance

During the study period, a total of 864 reed passerine birds were mist netted. Overall bird abundance was significantly higher in tall and thick reeds at site 1 (557 *vs.* 307 captures, $t = 3.8$, df = 18, $P = 0.001$) where the numbers of sedge warbler and to a lesser extent great reed warbler, reed warbler, bearded tit, and penduline tit were greater than in short and thin reeds at site 2 (Tab. 2). Only the reed bunting and marsh warbler abundance tended to be higher at site 2, but the differences were not significant.

As shown in Fig. 2, various bird species were also mist netted in different numbers at various reed bed plots. However, these differences were significant only in four species, namely the reed and sedge warblers ($H'_7 =$ 19.2 and 35.2, $P = 0.007$ and 0.0001 respectively), reed bunting ($H'_7 = 27.2$, P = 0.0001) and bearded tit (H'_7 = 22.9, P = 0.002). It was followed by the analysis of relationships only between the reed bed structure and abundance of the above-mentioned species.

Preferences of species for reed bed structure

As previously stated, four of the nine reed passerines exhibited the tendency to clump their distribution in some parts of reed bed. Because the differences in all vegetation variables were significant between the eight study plots, they (as independent variables) were submitted along with the selected bird abundance data (as dependent variable) to multiple regression analysis.

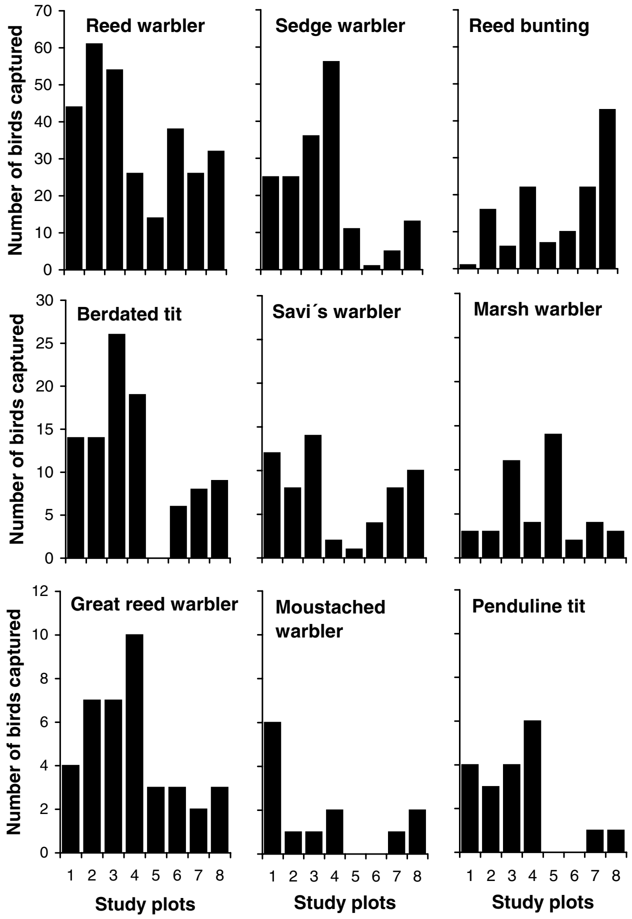

Fig. 2. Number of birds captured for each species at study plots.

Using the stepwise method, which excluded non-significant variables, the height of green reed was the only significant predictor of reed warbler abundance ($R^2 = 0.7$, $F_{1,6} = 7.5$, $P = 0.03$). This relationship was positive. In contrast, the abundance of the bearded tit was positively related to the diameter of stems (R^2 = 0.9, $F_{1,6} = 16.5$, $P = 0.007$). An interesting situation was that of the sedge warbler. Because all independent variables were put into the model ($R^2 =$ 0.9, $F_{5,2} = 198.2$, $P = 0.005$), height and diameter of reeds, the effect of which was identified as the most important for abundance of the above-mentioned species, were excluded from multiple regression analysis. After their exclusion the residual variables were considered non-significant ($F_{3,4} = 2.6$, $P = 0.245$). However, when testing the height and diameter of stems for sedge warbler separately, a closer correlation between height (P = 0.064) and abundance than between reed diameter ($P = 0.088$) and abundance was established, although both variables were again non-significant. The position of reed beds along the shore – open water gradient was an important factor, which influenced considerably the abundance of reed bunting at the study plots. This

Table 3. Interspecific comparison in vertical distribution of reed passerine birds at the study area.

	Sedge warbler	Moustached warbler	Marsh warbler	Reed warbler	Great reed warbler	Bearded tit	Penduline tit	Reed bunting
Sedge warbler	–	*ns*	*	***	*	*	**	***
Moustached warbler		–	*ns*	*ns*	*ns*	*ns*	*	**
Marsh warbler			–	*ns*	*ns*	*ns*	*ns*	**
Reed warbler				–	*ns*	*ns*	*ns*	***
Great reed warbler					–	*ns*	*ns*	***
Bearded tit						–	*ns*	***
Penduline tit							–	NS

Key: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, *ns* – non significant (χ^2-test).

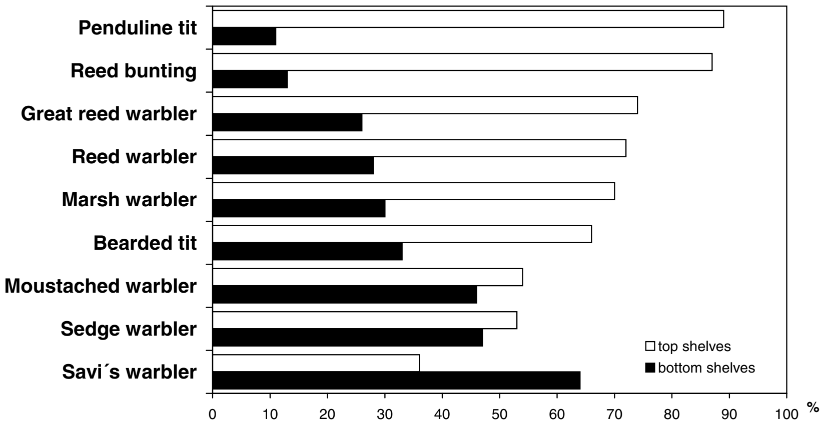

Fig. 3. Percentages of birds captured in two top and two bottom shelves for nine reed passerines.

species showed a significant edge preference for reed bed edge with open water ($R^2 = 0.8$, $F_{1,6} = 9.1$, $P = 0.024$). The vertical distribution of all species, except for Savi's warbler, which was captured predominantly in the two bottom shelves, indicated that most were found in the upper stratum of the reed bed (Fig. 3). Comparison with the other eight species showed significant differences in the sedge warbler and reed bunting (Tab. 3).

Discussion

Research into habitat patterns of reed passerines in the post-breeding period is complicated and runts into several methodological problems. Due to the disappearance of the majority of intraspecific (territorial) and interspecific relationships between the congeneric species (interspecific competition) bird communities in reed beds in the above-mentioned stage are less stable. The abundance of the individual species is, therefore, much more influenced by numerous other factors such as the autumn migration dynamic of migratory birds, dynamics and availability of food, weather conditions, situation of the site and other factors which can cause variation in the results. In spite of these methodological problems, our results achieved in the post-breeding period like the knowledge gathered by other authors in breeding period (e.g., Catchpole, 1974; Thomas, 1984; Martínez-Vilalta et al., 2002; Poulin et al., 2002; Prokešová & Kocian, 2004) confirmed a distinct correlation between the structure of reed beds and the abundance and distribution of some birds species even in the former period. Honza & Literák (1997) also predicted the effect of local conditions, structural features of the habitat and different availability of food on the horizontal distribution of birds in the post-breeding period. They, like other authors (Bairlein, 1983; Baccetti, 1985; Pambour, 1990), found a distinct preference for reed beds near open water by the reed warbler while sedge and marsh warblers were more associated with terrestrial reed. This study, was more focused on the spatial distribution of birds only in permanently flooded (aquatic) reed bed where no striking differences in preference for reed bed edge with open water by these and other bird species was observed except for the reed bunting. As this species is a generalist regarding habitat selection and feeding habitat (van der Hut, 1986), it was interesting to see its preference for the margin in our study area. However, the majority of individuals were captured in evening or early morning hours and therefore we assume that the reed bunting used the reedbed near the open water mainly for overnight rest. Results from Báldi & Kisbenedek (1999) obtained in breeding periods showing a strong significant edge (0–5 m) preferences for reed water and reed – boat path – reed edges again by the reed warbler but also Savi's warbler, bearded tit, and partially the sedge warbler, contradict our results. Obviously, in this case reed bed structure, changing along the shore-open water gradient and other circumstances including for instance, commercial exploitation of reed beds and other economic activities in these biotopes have also played an important role. The most important of these activities is the burning and cutting of reed. Báldi & Moskát (1995), Goc et al. (1997), Graveland (1999), Poulin & Lefebvre (2002), and Martínez-Vilalta et al. (2002) also confirmed their effects on the abundance and distribution of some bird species. Likewise, a distinct impact of winter burning of reed on overall abundance of birds in the post-breeding period at the sites in this study was found, as it was significantly higher in unburnt than in burnt areas.

In contrast to horizontal spatial distribution, a definite effect of reed bed structure on the vertical distribution of birds was not indicated, although as Honza & Literák (1997) predicted, a relatively high proportion of birds captured in the highest shelves of the ponds near Heřmanice (Czech Republic) compared to the results from Germany (Bairlein, 1983), Italy (Spina, in Honza & Literák, 1997) or France (Pambour, 1990) can be caused, apart from different food distribution, by taller reed. In general, the results of this study concerning the vertical distribution of individual species, especially *Acrocephalus* warblers in the post-breeding period are very similar to those mentioned above, as well as other authors (Gyurácz & Bank, 2000), although from the ecological and practical points of view this study differentiates only between the basal (two bottom shelves) and upper (two top shelves) strata of reed.

The horizontal and vertical distribution of birds in reed beds can also be affected by the distribution of food sources. According to Poulin et al. (2002), for example, food availability significantly correlates with overall passerine abundance. While Ditlhogo et al. (1992) detected differences only in a few invertebrates families between cut, burnt or left unmanaged reed beds. Poulin & Lefebvre (2002) found differences in abundance and distribution of arthropods between cut and uncut sites, where Diptera, Homoptera and Coleoptera were significantly more abundant at cut sites. These findings confirm the results of our simultaneous study at the same site concerning the effect of reed burning on arthropod abundance. Using the Malaise trap method we found significantly more abundance in the orders Coleoptera, Lepidoptera and Plecoptera at unburnt sites (Peterková et al., in litt.). Unfortunately, the abundance of aphids, which are an important food source to reed passerines during migration (Bibby & Green, 1981) were not investigated. Differences in vertical distribution of reed warblers can be attributed likewise to their niche segregation in food utilisation. While the moustached warbler obtains its food almost exclusively from vegetation at or near water surfaces and from water, the reed warbler gathers it from leaves in the bottom layer of reed beds, on trees or catches on the wing and the great reed warbler is a generalist in terms of food distribution. In contrast, Savi's warbler feeds predominantly on the ground in drier areas of reed-bed and sedge (Leisler, 1991; Cramp, 1992). It follows that food and its distribution in reed beds has an important role in the species-specific habitat preferences.

Comparison of habitat requirements of the studied bird species in breeding and post-breeding periods based on our data and the literature data is also interesting. While in the breeding period birds prefer certain species-specific habitats, distribution of the majority of species in permanently flooded reed beds was more or less random in the post-breeding period. The cause may be reduced samples of some species such as the great reed warbler which in the breeding period (Dyrcz, 1980; Leisler, 1981; Hoi et al., 1991; Graveland, 1998; Martínez-Vilalta et al., 2002; Poulin et al., 2002) tended to associate with taller and thicker reed than in the post-breeding period, although this relation was not significant. In contrast, in the case of the reed warbler, height of stems as an important factor, which influenced its abundance and distribution in breeding (Poulin et al., 2002; Martínez-Vilalta et al., 2002), as well as post-breeding periods, proved significant. Different preferences for reed bed structure were found in the bearded tit. While this species is associated with dense, thin and dry stem reed beds in the breeding period (Poulin et al., 2002), in the post-breeding period it preferred the thicker stem reeds that may be attributed to the limited skill of young birds (which represented as much as 90% of captured birds), for movement in thinner and denser reed beds.

Although the species-specific requirements for habitat structure are closely connected with the morphology of these species (Leisler et al., 1989), our results cannot be explained simply by morphological adaptations. We therefore assume that interaction between morphology and other factors such as territorial behaviour, inter-specific competition, food dispersion, position of study sites etc. can better predict habitat preferences.

Our results should contribute to the protection and management of reed beds at stopover sites of birds during their autumn migration, which has an important role on associated warblers communities.

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