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Habitat selection of two *Acrocephalus* warblers breeding in reed beds near Malacky (Western Slovakia)

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The study was carried out in 1999 and 2000 at three sites near Malacky, W Slovakia: Jakubovské rybníky fishponds, Jakubovské štrkovisko gravel pit and Vojenské rybníky fishponds. The aim of our research was to study the selection of breeding habitats of two *Acrocephalus* warblers: the great reed warbler (*Acrocephalus arundinaceus* L., 1758) and the reed warbler (*Acrocephalus scirpaceus* Hermann, 1804). Environmental plant variables characterising the nest sites of both species were measured on 37 great reed warbler nests and 101 reed warbler nests. Discriminant analysis was used to investigate the interspecific and intraspecific differences in nest site selection of these species. The breeding habitats of the great reed warbler differed from the nest sites of the reed warbler ($P < 0.001$). The breeding habitats of the great reed warbler had a very similar structure in all areas and DFA did not separate them. However, the breeding habitats of the reed warbler differed according to site (P_1, $P_2 \ll 0.001$). Our results showed that the reed warbler is more flexible in nest site selection than the great reed warbler.

Key words: great reed warbler, *Acrocephalus arundinaceus*, reed warbler, *Acrocephalus scirpaceus*, breeding, habitat selection.

Introduction

It is necessary to investigate the ecological demands of species so that their consistent protection can be secured. Birds have the biggest demands during the breeding season. Among sympatric species the breeding habitats differ in plant structure, composition of surroundings, food supply, microclimate and interspecific and intraspecific relationships. The two most important ecological factors influencing habitat selection are food supply and plant composition (Cody, 1985; Wiens, 1989; Ille & Hoi, 1995).

High-stalk littoral macrophyte stands represent acute bounded, relatively uniform small habitats enabling detailed studies of habitat demands of bird species nesting there. Typical breeders in this habitat are *Acrocephalus* warblers. Populations of the great reed warbler have declined in W and C Europe (Kux, 1987; Cramp, 1992; Kloubec, 1995; Trnka, 1999) while the numbers of reed warbler breeding pairs seem to be stable (Kloubec, 1995). The cause of this variation has not been explained but it could be caused by changes in breeding habitats (non-specific reasons could cause changes in the quality of reed).

Table 1. Characteristics of individual ponds.

Site	Average depth (m)	Total size of pond (ha)	Total size of macrophytes		Size of study plot	
			(ha)	%	(ha)	%
JRF-1	1.5	32.11	0.99	3.08	0.19	19.30
JRF-2	1	12.55	2.09	16.65	0.53	25.36
JRF-3	1	18.12	1.85	10.21	0.32	17.30
JŠGP	> 50	27.21	0.06	0.23	0.02	31.34
VRF-2	1.8	8.56	1.50	17.52	0.15	10.00
VRF-3	1.8	12.74	6.03	47.36	0.60	9.90
VRF-4	1.8	15.80	2.27	14.95	0.47	20.70

Key: JRF 1–3 – Jakubovský rybník fishpond, Nos 1–3; JŠGP – Jakubovské štrkovisko gravel pit; VRF 2–4 – Vojenský rybník fishpond, Nos 2–4.

The great reed warbler and reed warbler are suitable model species for the study of habitat selection. Their nests and bordered individual nest sites are relatively easy to find. These species are sympatric and reciprocal interspecific competition among them can be demonstrated (Catchpole, 1973; Hoi et al., 1991; Honza et al., 1999). Some authors have published detailed studies about them (Leisler, 1981; Van der Hut, 1986; Hoi et al., 1991, 1995; Graveland, 1998; Ivanitskii et al. 2002; Poulin et al. 2002).

The aim of this study was to find out the interspecific differences in habitat selection in habitats of C Europe, primarily to detect the intraspecific differences among three different sites, and to compare the adaptability of species to individual changes in quality of breeding habitats. Based on the results of great reed warbler habitat preference we also tried to determine the properties of potentially available breeding areas for this endangered species.

Material and methods

The study was carried out during two breeding seasons in 1999 and 2000 at three sites near Malacky, W Slovakia: Jakubovské rybníky fishponds, Jakubovské štrkovisko gravel pit and Vojenské rybníky fishponds (Tab. 1). Jakubovské rybníky fishponds are a system of three ponds designated by the numbers 1, 2 and 3. Drainage canals from the Malina brook supply them with water. They are mainly surrounded by agricultural fields. They are the shallowest of all study sites and their water level does not fluctuate throughout the breeding season. Jakubovské štrkovisko gravel pit serves as a recreation area. The reed macrophytes represent a 10 m narrow edge along the shore. This edge is interrupted in many places because of the fishermen's cutting of the reed. Vojenské rybníky fishponds were also marked by numbers, the study being carried out only on three of them (No. 2, 3, and 4). They are situated in *Pineto-Quercetum* woods. They are deeper than the Jakubovské rybníky fishponds and their water level fluctuated throughout the year. Two study plots were randomly selected on each pond. Their size was determined to be sufficiently representative, taking into account our physical abilities. Their exact size and percentage of the whole size of reed beds are shown in Table 1. The total research area at all sites was 2.28 ha. The dominant littoral plant species at all sites was the reed (*Phragmites australis*). The nests (at least with one egg) of both warblers found on the study plots in May and June were used to estimate species density. The nests found in July were considered as a second brood and did not influence the density stated but were included in our study of habitat selection. Each year in July we measured the environmental plant variables around the nests. The measurements were made at the terminal phase of vegetation growth after the birds finished breeding. This is necessary for a statistical comparison of samples from different areas measured at different times. This method for measuring time was also recommended by Catchpole (1974). An earlier recording of vegetation near the nests during the breeding season could have caused the nesting pair to abandon the nest (Catchpole, 1974).

For the habitat selection study it was necessary to map as precisely as possible the plant composition and structure of the nest sites. In 5 × 5 m squares around the nest (the nest being localised in the centre of the square) we measured or estimated (second and third variable) the following variables:

1. Height of reed;
2. Ground coverage of reed: 1 – < 1%; 2 – 1–5%; 3 – 6–25%; 4 – 26–50%; 5 – 51–75%; 6 – > 75%;
3. Dispersion of reed: D1 – equal reed; D2 – unequal reed; D3 – clustered reed;
4. Number of plant species;
5. Horizontal coverage of vegetation: at a distance of 1 and 2 m from nest in each cardinal point

Table 2. Measured plant variables and their abbreviations used in statistical analyses.

Plant variables	Abbreviations
Average height of reed	PaH
Ground coverage of reed	PaC
Equal reed	PaD_1
Unequal reed	PaD_2
Reed made clusters	PaD_3
Number of reed stems	NstPa
Number of new reed stems	NnstPa
Number of old reed stems	NostPa
Diameter of new reed stems	DnstPa
Diameter of old reed stems	DostPa
Horizontal coverage of reed in layer up to 30 cm	hc0–0.3
Horizontal coverage of reed in layer from 0.31–1 m	hc0.31–1
Horizontal coverage of reed in layer from 1.1–3 m	hc1.1–3
Horizontal coverage of reed in layer over 3 m	hc>3
Number of plant species	Npsp

we assessed the presence (+) or absence (−) of contact of vegetation with vertical axis (fishing-line). We specified four height layers: 0–0.3 m; 0.31–1 m; 1.1–3 m; > 3 m.

In 50 × 50 cm squares we detected: 1. Number of reed stems; 2. Number of new reed stems; 3. Number of old reed stems; 4. Diameters of ten new reed stems; 5. Diameters of ten old reed stems.

All variables with their abbreviations are shown in Table 2.

Discriminant analysis was applied to determine which variables were important in selecting the nest site. Of the measured variables only the significant ones were used in DFA (Kruskal–Wallis test, $P < 0.05$). The two-group linear DFA was used to determine the interspecific differences in the choice of nest site. To find out intraspecific differences among the sites we used a three-group linear DFA (Hebák & Hustopecký, 1987; Koschin et al., 1992).

Results

Density of great reed warbler and reed warbler in the study areas

We found 41 nests of the great reed warbler and 130 nests of the reed warbler during the two years. All nests were built in reed. The density of both species is shown in Table 3. The values are estimated; they are accurate only for the study plots. When we compared the density of species in the three study areas, we found that the reed warbler was more numerous than the great reed warbler on Jakubovské rybníky and Vojenské rybníky fishponds, but the great reed warbler was more abundant than the reed warbler on Jakubovské štrkovisko gravel pit.

Table 3. The average density of species on individual ponds.

Site/Density (p/ha)	*A. arundinaceus*	*A. scirpaceus*
JRF-1	15.7	13.1
JRF-2	1.8	22.6
JRF-3	3.1	29.7
JŠGP	485.6	200.0
VRF-2	10.0	90.0
VRF-3	1.7	4.2
VRF-4	0	14.9

Comparison of great reed and reed warbler's nest sites

Nine significant variables (Kruskal-Wallis test, $P < 0.05$) were used in DFA of all measured variables (Tab. 2): PaH, PaD_1, PaD_3, DnstPa, DostPa, hc0–0.3, hc0.3–1, hc>3, Npsp. One hundred and thirty-eight nest sites (of them 37 great reed warbler's and 101 reed warbler's nests) were tested in DFA. DFA was successful, the resulting discriminant function being significant ($P < 0.001$, Tab. 4a). The percentage of correct resubstitution (backward tabling of samples to groups = species) was high (Tab. 4b). The important variables for separation of their nest sites (the highest values of classification coefficients) were: height of reed, number of plant species around the nest, diameter of new stems and horizontal coverage of vegetation in layer 0–0.3 m. The height of reed was the most important one. The great reed warblers nested in narrow beds very near to open water sur-

Table. 4. DFA between *A. arundinaceus* and *A. scirpaceus*.
4a. Classification coefficients of variables, their average and standard deviations.

Factor	Classification coefficient	$\bar{x} \pm$ S.D.	
		A. arundinaceus	*A. scirpaceus*
PaH	**0.405**	**3.29 ± 0.55**	**2.53 ± 0.38**
PaD_1	0.104	0.35 ± 0.48	0.19 ± 0.39
PaD_3	−0.253	0.27 ± 0.45	0.52 ± 0.50
DnstPa	**0.360**	**6.80 ± 1.17**	**5.13 ± 0.99**
DostPa	0.258	6.57 ± 1.23	5.02 ± 1.08
Hc0-0.3	**−0.372**	**0.23 ± 0.18**	**0.41 ± 0.22**
Hc0.31-1	−0.035	0.71 ± 0.20	0.80 ± 0.18
Hc>3	−0.023	0.25 ± 0.33	0.03 ± 0.13
Npsp	**−0.354**	**1.24 ± 0.83**	**1.97 ± 1.17**
Eigenvalue	1.107		
Wilks – Lambda	0.475		
Sig. Level	**0.00000 ($P \ll 0.001$)**		

4b. Resubstitution of samples.

Species	*A. arundinaceus*	*A. scirpaceus*	Number of nests
A. arundinaceus	31 nests (**83.78%**)	6 nests (16.22%)	37 nests (100%)
A. scirpaceus	9 nests (8.91%)	92 nests (**91.09%**)	101 nests (100%)

face (Prokešová & Kocian, in press) where the reed was the highest (3.29 ± 0.551 m). However, reed warblers were also breeding in coherent reed beds at a distance of more than 20 m from open water surface (Prokešová & Kocian, in press) where the reed was lower (2.53 ± 0.385 m). However, around the nests of reed warbler other plant species were also growing (especially *Carex* sp., *Urtica dioica*, *Humulus lupulus*, *Calystegia sepium* and *Galium* sp.). It was caused by a low water level beneath the nests, the proximity of the shore, and breeding more often in terrestrial reed. The diameter of new stems of reed was also important for separation. Near the nests of the great reed warbler the stems were thicker (6.8 ± 1.17 mm on the average) compared to the stems near the reed warbler's nests (5.1 ± 0.99 mm on the average). Different values were also found in horizontal coverage of vegetation in layer 0–0.3 m. The greatest values were detected around reed warbler's nests. There were not more stems of reed around reed warbler's nests compared with great reed warbler's nests (*A. arundinaceus* vs. *A. scirpaceus*: 240 ± 88 stems/m^2 vs. 256 ± 124 stems/m^2, Kruskal–Wallis test, $t = 0.177$, $P > 0.05$). Also, no significant difference was found between the coverage of reed near their nests. The different values of hc0–0.3 could be caused by a higher water level under the nests of the great reed warbler, which makes it impossible for the other plant species to grow there. Also on higher reed stems the first leaves were higher up on the stems.

Comparison between great reed warbler nest sites
Although two variables, PaH and PaD_3, were significant and were used in DFA, the analysis did not reveal any differences between nest sites of these species on the study areas. However, one discriminant function was significant ($P < 0.01$, Tab. 5a), namely the second one, which is necessary for distinction of three groups, was not. The percentages of resubstitution were low (Tab. 5b). The failure of DFA can be explained by this species' preference of very similar nest sites on all study areas, which differed neither in plant structure nor in plant composition.

Comparison between reed warbler nest sites
Nine variables were significant and were used in DFA: PaH, PaD_1, PaD_3, NnstPa, DostPa, hc0.31–1, hc1.1–3, hc>3, Npsp. From 101 samples (nest sites of reed warbler), 51 were from Jakubovské rybníky fishponds, 9 from Jakubovské štrkovisko gravel pit and 41 from Vojenské rybníky fishponds. DFA was successful in separating the nest sites of this species between the study areas. Two dis-

Table 5. DFA of *A. arundinaceus*.
5a. Classification coefficients of variables, their average and standard deviation.

Factor	1. *df*	2. *df*	$\bar{x}$ ± S.D.		
			JRF	JŠGP	VRF
PaH	0.798	0.642	2.92 ± 0.36	3.83 ± 0.24	3.31 ± 0.57
PaD_3	−0.454	0.918	0.54 ± 0.52	0	0.21 ± 0.42
Eigenvalue	0.590	0.014			
Wilks – Lambda	0.621	0.987			
Sig. Level	**0.00304**	**0.50031**			

5b. Resubstitution of samples.

Site	JRF	JŠGP	VRF	Number of nests
JRF	7 nests (**63.64%**)	0 nests (0.00%)	4 nests (36.36%)	11 nests (100%)
JŠGP	0 nests (0%)	5 nests (**71.43%**)	2 nests (28.57%)	7 nests (100%)
VRF	7 nests (36.84%)	7 nests (36.84%)	5 nests (**26.32%**)	19 nests (100%)

Table 6. DFA of *A. scirpaceus*.
6a. Classification coefficients of variables, their average and standard deviation.

Factor	1. *df*	2. *df*	$\bar{x}$ ± S.D.		
			JRF	JŠGP	VRF
PaH	**−0.181**	**−0.540**	**2.47 ± 0.34**	**3.08 ± 0.47**	**2.47 ± 0.33**
PaD_1	**0.273**	**−0.424**	**0.16 ± 0.37**	**0.56 ± 0.53**	**0.15 ± 0.36**
PaD_3	**0.683**	**−0.544**	**0.33 ± 0.48**	**0.22 ± 0.44**	**0.81 ± 0.40**
NnstPa	**−0.459**	**0.256**	**38.22 ± 16.49**	**24.90 ± 8.09**	**31.51 ± 18.02**
DostPa	−0.088	0.146	5.05 ± 1.27	5.61 ± 0.74	4.84 ± 0.83
Hc0.31-1	**−0.357**	**−0.340**	**0.80 ± 0.18**	**0.94 ± 0.09**	**0.76 ± 0.19**
Hc1.1-3	0.291	−0.190	0.82 ± 0.17	0.97 ± 0.05	0.87 ± 0.19
Hc>3	**−0.377**	**−0.376**	**0.02 ± 0.09**	**0.24 ± 0.35**	**0.00 ± 0.02**
Npsp	**−0.601**	**0.025**	**2.35 ± 1.26**	**2.33 ± 1.32**	**1.42 ± 0.74**
Eigenvalue	0.786	0.518			
Wilks – Lambda	0.369	0.659			
Sig. Level	**0.00000**	**0.00000 ($P_1 \ll 0.001$; $P_2 \ll 0.001$)**			

6b. Resubstitution of samples.

Site	JRF	JŠGP	VRF	Number of nests
JRF	37 nests (**72.55%**)	3 nests (5.88%)	11 nests (21.57%)	51 nests (100%)
JŠGP	1 nest (11.11%)	6 nests (**66.67%**)	2 nests (22.22%)	9 nests (100%)
VRF	6 nests (14.63%)	2 nests (4.88%)	33 nests (**80.49%**)	41 nests (100%)

criminant functions were significant ($P < 0.001$, Tab. 6a). Nest sites differed in dispersion of reed, number of plant species around the nest, number of new reed stems and in height of reed. The reed where the reed warbler built its nests formed clusters on Jakubovské rybníky fishponds and also on Vojenské rybníky fishponds. In comparison, the reed on Jakubovské štrkovisko gravel pit was uniformly distributed. On Vojenské rybníky fishponds the reed warbler was breeding in homogenous reed without other plant species, while other plant species usually grew near the nests of this species on the Jakubovské rybníky fishponds and partly also on Jakubovské štrkovisko gravel pit. On Jakubovské štrkovisko gravel pit reed warblers built their nests in terrestrial reed where old stems were situated more abundantly, while at the other two sites the new stems prevailed near reed warbler's nests. The height of reed, where the nest was situated, also differed among the localities. Thus we found that the nest sites of reed warbler were not similar and this species bred in reed of different type and quality.

Discussion

Density of great reed warbler and reed warbler in the study areas

The knowledge of the density of species is important for the study of their ecological demands. Changes in ecological factors influencing the density of the species are the most important for their maintenance and protection. We carried out our research only on study plots and not on the whole area so the density assumption from the study plots could distort the density values. We tried only to estimate the relative values of density. To determine the exact number of breeding pairs it would be necessary to ring the birds or walk through the whole reed area. Even using this method there are still two problems which could distort the values: the verification of second breeding and polygamy of the great reed warbler. The applied method stating the density from study plots satisfied the requirements of our habitat selection study.

Comparison between great reed warbler and reed warbler nest sites

The number of studies investigating habitat selection of various bird species has increased over the past 30 years (Cody, 1985; Nilsson & Persson, 1986; Wiens, 1989; Ille & Hoi 1995). Detailed studies were also made on *Acrocephalus* warblers by Leisler (1981), Van der Hut (1986), Hoi et al. (1991, 1995), Graveland (1998), Medveďová (1999), Ivanitskii et al. (2002) and Poulin et al. (2002). These studies were not carried out using uniform methods so it is very difficult to compare them. Based on the results of these studies we know that the quality of nesting habitat and quality of individual nesting microhabitat are important for habitat selection. The body size of the great reed warbler is larger and for breeding and mobility it requires reed with thick, firm and stable stems. The great reed warbler is also adapted for this type of reed by its food morphology (Leisler, 1975). Higher and thicker reed stems are usually found in nest sites of the great reed warbler as compared with reed warbler nest sites. The importance of other variables, e.g. age of stems and stem density may change. Habitat selection can geographically change in different areas depending on acceptable plant structure and the presence of other competitive species (Van der Hut, 1986). We found that habitat selection on our study areas in Slovakia was similar to that in Western Europe found by Leisler (1981), Nilsson & Persson (1986), Van der Hut (1986) and Graveland (1998). The great reed warbler nested in the highest reed with thicker stems near open water surface compared to reed warbler. However we found that in some cases this species, like the reed warbler, was also able to build its nests in terrestrial reed (six nests on Jakubovské štrkovisko gravel pit). Unlike Leisler (1981) and Hoi et al. (1991, 1995), we did not find any prevalence of old reed stems in the vicinity of great reed warbler nests compared to reed warbler nest sites. Also, in contrast to Graveland (1998) and Leisler (1981), we did not detect a bigger density of reed in the vicinity of great reed warbler nests as compared to the vicinity of reed warbler nests. In contrast, Ivanitskii et al. (2002) indicated that the reed warbler nested in dense reed stands compared to the great reed warbler.

The great reed warbler is dominant in competition with reed warbler and does not tolerate it in its territory (Hoi et al., 1991; Honza et al., 1999). The absence of the reed warbler in some parts of the reed beds could be caused not by unsuitability of reed for building nests there but by the presence of the dominant great reed warbler. In our plots we observed that nests of reed warblers were usually farther from great reed warbler's nests and in some cases, when the nests were relatively near (like on Jakubovské štrkovisko gravel pit), reed warblers bred later (unpubl.).

Comparison between great reed warbler nest sites

Studies comparing habitat demands of the great reed warbler (or reed warbler) in different sites are absent in literature. It is only this kind of study that could prove or disprove the influence of individual differences of any particular sites on the character of habitat selection. The great reed warbler was breeding in very similar nest sites on all of our study areas (DFA did not separate them according to measured variables). The great reed warbler bred in homogenous reed of equal or unequal dispersion, and only rarely in clusters. This reed was usually the highest on the study area and was at least 3 m high. The great reed warbler usually bred in narrow beds near the surface of open water (Dyrcz, 1980; Beier, 1981; Honza et al., 1993; Ivanitskii et al., 2002; Prokešová

& KOCIAN, in press), where the stems were thicker and with prevalence of new ones. Other plant species were unable to grow there. In this type of reed the nests were at a height of 78 ± 22.4 cm (PROKEŠOVÁ & KOCIAN, in press). The reed of this quality grew mainly on Jakubovské štrkovisko gravel pit where we detected the highest number of breeding pairs of this species. A similar situation can also probably be encountered on other gravel pits on Záhorská nížina lowland. KALIVODOVÁ & FERIANCOVÁ–MASÁROVÁ (1998) described this species as eudominant or dominant on 14 gravel pits there. The fact that this endangered species was so abundant in this type of man-made habitats increases their importance for the great reed warbler's survival. The nesting niche of the great reed warbler was more specialised than that of the reed warbler. This could be caused by polygamy. The females choose the males on the basis of the quality of its habitat and not on its body quality (ILLE et al., 1996). Thus each male is trying to occupy the best habitat after arrival and to mate with one or more females. Further research is required to confirm or reject this theory.

Comparison between reed warbler nest sites

When we compared the results of LEISLER (1981), HOI et al. (1991, 1995) and GRAVELAND (1998), it was evident that the demands of this species differed according to site. This was evident also from our study. DFA separated microhabitats of this species among sites. This species bred in reed with bigger or lower density at different distances from the surface of open water (PROKEŠOVÁ & KOCIAN, in press). Usually, the reed was lower compared to that where the great reed warbler was nesting. There could be predominant old or new stems. Even though the reed warbler preferred reed clusters, it also bred in homogenous or patchy reed. The reed growing from low water deep and terrestrial reed was not homogenous. There were also other plant species growing. These plants can sometimes also be used as structures supporting the nest (GLUTZ VON BLOTZHEIM & BAUER, 1991). The reed warbler was nesting in narrow beds as well as in extensive continuous reed contrary to IVANITSKII et al. (2002). In this author's study the reed warbler did not ever breed in narrow reed beds. The nesting niche of this species was wider than that of the great reed warbler. The female chooses the male according to its body quality, not according to the quality of its habitat (ILLE et al., 1996). It is a monogamous species and the male participates in looking after the nestlings. It is the female that selects the nest site (BOROWIEC, 1992). Also the expressive influence of the great reed warbler on the breeding of the reed warbler could not be ignored. HOI et al. (1991) and HONZA et al. (1999) found that the great reed warbler can destroy reed warbler's nests and does not tolerate it in its territory. If we compared these two species, the reed warbler is subdominant. It could be forced by some males of the great reed warbler to build its nests in reed of worse quality. However, this reed occurs at a high density in many potential breeding habitats. Monogamy and the influence of the great reed warbler could cause wider ecological valence in habitat selection of this species. The strict distribution of the great reed warbler only to a given type of nest site of high quality, which has declined in many sites due to eutrophication, could be the cause of the decline of great reed warbler populations. In contrast, flexibility in habitat selection of the reed warbler along with the decline of the great reed warbler's breeding pairs could explain its increasing density in many areas. Further research is required to confirm these statements.

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