RESEARCH ARTICLE

Wing size-related reed habitat selection by Great Reed Warbler (*Acrocephalus arundinaceus*) males

Thomas Oliver Mérő,[1,3]* Antun Žuljević,[1] Katalin Varga,[2] and Szabolcs Lengyel[3]

[1] Nature Protection and Study Society - NATURA, Sombor, Serbia
[2] Institute of Biosciences, Technische Universität Bergakademie Freiberg, Freiberg, Germany
[3] Department of Tisza Research, Danube Research Institute, Centre for Ecological Research, Hungarian Academy of Sciences, Debrecen, Hungary
* Corresponding author: thomas.oliver.mero@gmail.com

ABSTRACT
In this study we explored the linkage between wing size of Great Reed Warbler males (*Acrocephalus arundinaceus*) and their habitat selection and relate these linkages to differences in reed habitat quality. We measured the wing sizes of males nesting in 6 different reed habitats. To explain reed habitat selection, we modeled male wing size as a function of 7 predictor variables describing reedbeds: proportion of managed reed; densities of mixed, old, and fresh reed; reed stem diameter; water depth; and fluctuation of water level. Mean wing size was greatest for males at large canals, intermediate at mining ponds and smaller canals, and lowest at marshes and very small canals. The proportion of managed reed and fluctuation of water level were negatively related to wing size, and water depth was positively related to wing size, which suggests that males with larger wings preferred reed habitats with little management in deep water with little fluctuation in water level. We concluded that the availability of stable, deep water and lack of management are primarily important in attracting larger-winged (presumably dominant) males.

Keywords: wing size, reed management, water depth, fluctuation of water level, male, habitat selection, *Acrocephalus arundinaceus*

Selección de hábitat de carrizo con relación al tamaño del ala de machos de *Acrocephalus arundinaceus*

RESUMEN
En este estudio exploramos el vínculo entre el tamaño del ala de los machos de *Acrocephalus arundinaceus* y su selección de hábitat, y relacionamos estos vínculos con diferencias en la calidad del hábitat de carrizo. Medimos el tamaño del ala de machos anidando en seis hábitat diferentes de carrizo. Para explicar la selección del hábitat de carrizo, modelamos el tamaño del ala de los machos como una función de siete variables predictivas de los carrizales: proporción de carrizales con manejo, densidad de carrizo mixto, viejo o nuevo, diámetro del tallo del carrizo, profundidad del agua y fluctuación del nivel del agua. El tamaño medio del ala de los machos fue mayor en los canales grandes, intermedio en los estanques cavados y en los canales más pequeños, y menor en los pantanos y en los canales muy chicos. La proporción de los carrizales con manejo y la fluctuación del nivel del agua estuvieron negativamente relacionadas al tamaño del ala, y la profundidad del agua estuvo positivamente relacionada al tamaño del ala, lo que sugiere que los machos con alas más grandes prefirieron hábitats de carrizo con poco manejo en aguas profundas y con poca fluctuación del nivel del agua. Concluimos que la disponibilidad de agua estable y profunda y la falta de manejo son principalmente importantes para atraer a los machos (presumiblemente dominantes) con alas más grandes.

Palabras clave: *Acrocephalus arundinaceus*, fluctuación del nivel del agua, macho, manejo del carrizo, profundidad del agua, selección de hábitat, tamaño del ala

INTRODUCTION

In birds, wing length is a fundamental body size variable that has various consequences on survival, habitat selection, and breeding success. Wing length was found to be associated with migration distances in long-distant migratory birds (Tarka et al. 2010), which may indicate its importance in flight ability and survival. Wing size is also a signal for dominance among males in reed passerines (Nowakowski 2000, Forstmeier et al. 2001), which can thus be used as a correlate of the quality of the breeding habitats (Johnson 2007). Furthermore, Alatalo et al. (1985) and Rayner (1988) suggested that habitat structure can have selective effects on wing sizes at microevolu-

tionary time scales. Studying the variability in wing size can thus help us understand both evolutionary processes acting on avian flight (Dial et al. 2008) and ecological processes related to habitat choice (Block and Brennan 1993).

The Great Reed Warbler (*Acrocephalus arundinaceus*) is a long-distant migrant in which larger-winged males arrive earlier to the breeding ground and occupy the presumably most attractive territories (Hasselquist 1998). These early males are highly preferred by females, and females can gain direct benefits through the increased production of fledglings in high-quality habitats (Hasselquist 1998). The attractiveness of territories is often estimated by an occupancy rank, calculated from the date when the territory was first defended by a male during the season. The identification of the habitats attractive to these early males with larger wings is thus important not only for understanding the spatial variation of the population but also for the conservation of these high-productivity habitats to ensure high breeding success.

Several properties of reedbeds and water level are known to influence habitat selection of the Great Reed Warbler. For nesting, the species primarily prefers reedbeds containing both old and fresh reed stems with intermediate density of reed stems (Graveland 1998, Batáry and Báldi 2005, Mérő and Žuljević 2014). The effect of reed management is closely linked to water depth. Breeding density is low when water level is low (average 7 cm), whereas nesting density is higher at high water level (average 108 cm; Mérő et al. 2014). This relationship with water level was similar in years with fire management (burns in the early spring) and in years with no fire management (Mérő et al. 2014). High water levels, however, present risks of flooding the nests (Graveland 1998, Mérő et al. 2014), and some studies found most nests in water depths of 20 to 40 cm (Dyrcz 1981, Petro et al. 1998). In addition, large fluctuations in water level typically lead to reeds dying, which causes habitat loss, and to increased nest predation rates (Graveland 1998, Mérő et al. 2014). These previous studies suggest that the Great Reed Warbler may prefer little-managed reed habitats with intermediate reed density and intermediate water depth with minor fluctuations.

The aim of this study was to test whether male wing size as a signal of individual quality varies across reedbeds of different types and whether the variation in male wing size is explained by variation in reedbed properties (habitat structure). We hypothesized that reed habitats with intermediate reed density and with slightly fluctuating intermediate water depth are selected by larger-winged (presumably dominant) males. To test this hypothesis, we measured wing sizes of Great Reed Warbler males nesting in 6 different reed habitats across the region of Sombor (northwest Serbia): mining ponds, marshes, large canals, and 3 size classes of small canals (see Methods). We also measured 7 variables describing reed habitat quality (proportion of managed reed, reed stem diameter, mixed reed density, old and fresh reed densities, water depth, and fluctuation of water level) to test if males of different wing sizes select different habitats.

METHODS

Study Area

Our study sites were 6 reed habitats in the landscape of Sombor (1,178 km^2, central coordinate: 45°N, 19°E), Serbia: mining ponds, marshes, large canals, and 3 size classes of small canals. The 4 mining ponds were established between the 1900s and 1960s by clay excavation for the local brickyards. Their surface area varied from 0.7 to 4.5 ha, and they contained patchy or fragmented reedbeds (Appendix Figure 3). The water level depended exclusively on the amount of precipitation in autumn, winter, and early spring; the level fell throughout the summer and early autumn period due to evapotranspiration. In March 2014, the reed bed was almost completely burned at 2 of 4 mining ponds. The marshes (n = 5 sites) were established through regulation of sluggish and meandering Mostonga and Kígyós rivers and were characterized by closed reed stands formed in long, continuous succession.

The size of marshes varied between 2 and 13.5 ha (Appendix Figure 4). The water generally disappeared by early summer (June). Two small marshes were burned in February 2014, and the remaining 3 marshes were not managed either by mowing or burning in either study year.

Large canals (n = 3) varied in width from 15 to 35 m, and their total length was 114 km in the municipality. The banks of the large canals were covered with 2–6 m wide belts of reed, occasionally interspersed with *Typha* spp., *Carex* spp., or *Salix* spp. (Appendix Figure 5). The water originates from the Danube River through sluice systems, and the water level has only minor fluctuations. The reedbeds were partially burned on sections of 2 of the 3 large canals in March of both study years.

Finally we classified small canals into 3 size classes, following the categorization of the local water management authority, based on their width, drainage capacity, and size of water catchment basin. The width of small canals I varied from 4 to 6 m (total length in the municipality: 205 km). Average water depth was 100 cm, and water level showed minor fluctuations with occasional larger fluctuations due to extreme drought or high precipitation. The reedbeds were located in patches on

one or both banks (Appendix Figure 6). At most small canal I sites, reed was mowed in late summer, and only a few sections were nonmanaged. The width of small canals II varied from 2 to 4 m (total length in the municipality: 364 km). Average water depth was 60 cm, and water level showed large seasonal and annual fluctuations due to precipitation. Reed grew over the entire width of the canal and exhibited a patchy structure (Appendix Figure 7). The reed was irregularly managed, more often by burning than by mowing. Finally, the width of small canals III varied from 1 to 2 m (total length in the municipality: 175 km). Average water depth was 20 cm, and water level depended on precipitation. Water was typically present from the winter until the end of May or the beginning of June, although in drier springs water may be absent. The reedbeds were patchy and often sparse (Appendix Figure 8) and occasionally mown.

Sampling

Fieldwork was conducted from April 13 to July 27, 2013, and from April 22 to June 29, 2014. We captured only territorial males, defined as a bird holding a territory based on the presence of any of 3 behavioral clues: singing, defending a nest, or defending a female mate. Males on migration (not tied to territories), females, and juveniles were not taken into account. We individually color banded Great Reed Warblers on 4 mining ponds, 5 marshes, and on 9.3 km of large canals, 28.8 km of small canals I, 68.1 km of small canals II, and 19.1 km of small canals III (Figure 1). Birds were attracted with a play-back male song and captured with mist nets near nests or territories. For every captured male, we recorded the total wing length and the length of the third primary as a control measurement (Berthold and Friedrich 1979) by using a 150 mm wing rule (Svensson 1992). Wing lengths were measured exclusively by one of the authors (T.O.M.) to avoid potential differences in measurements by other authors.

Males were assigned to a specific habitat type only if they were found to be actively breeding in a specific habitat. We inferred breeding either by the presence of color-banded males in the breeding habitats early in June or by color banding and observing marked birds on territories in June because migratory individuals have moved through the area by this time. If first identified in July, when the autumn migration period typically starts, birds were only considered on territory if identified as associated with an active nest (male do not sit on the nests).

We used 7 variables to characterize the structure of reed habitats: proportion of managed reed; reed stem diameter; densities of old, fresh, and mixed reed; water depth; and fluctuation of water level. To determine the size of managed and nonmanaged parts of the reedbeds, we took waypoints with a GPS device (Asus MyPal A639) while walking around the border of managed and nonmanaged parts. Data on reed and water variables were collected at 10 nests per reed bed. In reedbeds with <10 nests, all nests were considered. In mining ponds, we surveyed the entire reed bed for nests, whereas in marshes we surveyed only selected parts (i.e. where mist-netting was possible). Along canals, selected sections were systematically surveyed for nests by walking on both sides. Data on reed variables were collected both in the egg and the nestling stages at the nest for both nest-supporting reed stems and for stems in the surroundings. The diameter of stems was measured at nest height with calipers. We determined reed density by counting stems and recording their age as old, new, or mixed (i.e. having both old and new growth) in a 50 cm diameter circle and then extrapolating to 1 m^2. Then we estimated the density of old, new, and mixed stems in 6 reed habitats (Table 1). Water depth was measured with a measuring stick (accuracy: 5 cm), and the fluctuation in water level near nests was quantified by repeated measurements until the fledglings left the nest. Water depth at individual nests was taken as the maximum measured depth. We then calculated the mean water depth for each reed habitat (Table 1) as well as the water level fluctuation, calculated as the difference between the maximum and minimum measured water depths during the breeding season.

Statistical Analysis

We used one-way ANOVA to test differences in mean wing length among reed habitats and compared group means by Tukey's HSD test. A general linear model (GLM) was constructed to model the relationship between wing length (response variable) and the proportion of managed reed, reed density (old, fresh, and mixed reed stems), reed stem diameter, water level, and water level fluctuation. Wing length measures originating from recaptures, which were consistent apart from occasional minor fluctuations (Pearson correlation, $r = 0.90$, $n = 15$, $p < 0.01$), were not included in the GLM.

We tested for multicollinearity between independent variables by Pearson correlation analyses. We excluded old and fresh reed densities from the GLM because these variables exhibited significant correlation in all cases (Pearson correlation, $r > 0.93$, $n = 702$, $p < 0.01$). The final GLM contained the proportion of managed reed, water depth, water level fluctuation, mixed reed density, and reed stem diameter as main effects. We also included relevant 2- and 3-way interactions between (1) the proportion of managed reed and mixed reed density, (2) water depth and proportion of managed reed, (3) water depth and mixed reed density, and (4)
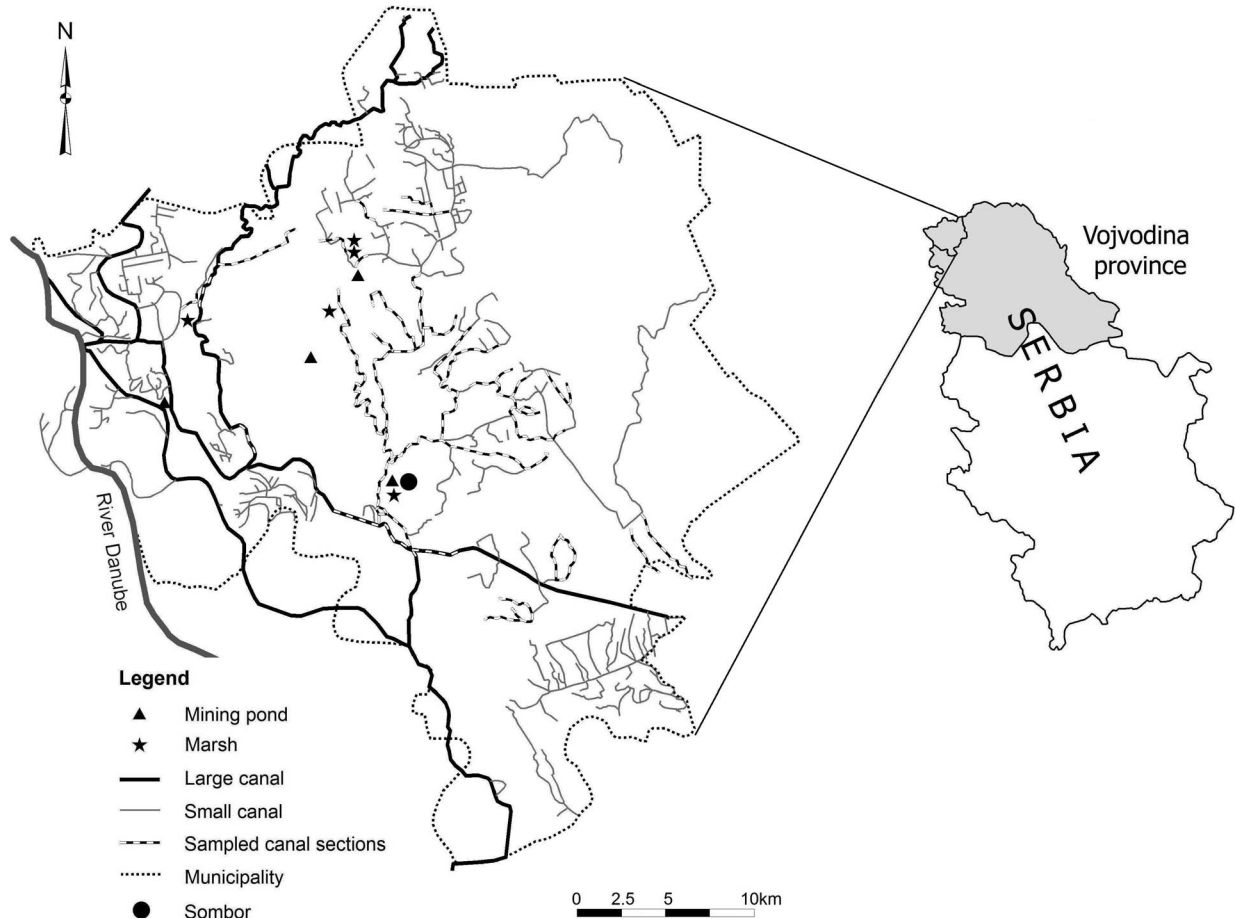
FIGURE 1. The canal network of the municipality of Sombor, Serbia, and the sampled marshes (stars), mining ponds (triangle). Sampled canal sections are striped.

mixed reed density and water depth and water level fluctuation. All independent variables were treated as fixed factors, and nonsignificant interactions ($p > 0.1$) were removed from the GLM to obtain a minimum adequate model.

The normality of the variables was tested by the Shapiro-Wilk test, and the homogeneity of variances was checked by Bartlett tests. We applied a chi-square test to check whether the recaptured males changed their nesting territory among the reed habitats in 2014. Finally, we applied one-way ANOVA to explore the potential differences in mixed reed density and reed stem diameter among the 6 reed habitats. Statistical analyses were performed in SPSS for Windows (17.0).

TABLE 1. Mean ± SD values of the proportion of managed area, reed, and water variables for the 6 studied reed habitats, based on data combined from 2 years.

Reed habitat (n)	Mean values (mean ± SD)				
	Proportion of managed reed (%)	Mixed reed density (m^{-2})	Stem diameter (mm)	Water depth (cm)	Change in water level (decrease, cm)
Mining ponds (4)	12.1 ± 25.6	225.4 ± 51.8	6.3 ± 0.9	70.2 ± 10.7	56.9 ± 4.6
Marshes (5)	4.8 ± 19.8	360.5 ± 163.8	6.6 ± 2.1	32.8 ± 11.6	32.8 ± 11.6
Large canals (3)	20.0 ± 20.7	211.2 ± 69.3	8.1 ± 1.6	136.2 ± 12.1	2.5 ± 2.5
Small canals I (11)	68.4 ± 46.6	207.0 ± 68.0	6.2 ± 0.7	68.5 ± 13.4	12.3 ± 4.2
Small canals II (19)	30.0 ± 39.0	166.3 ± 42.9	7.0 ± 1.2	60.2 ± 27.5	32.5 ± 7.5
Small canals III (7)	23.4 ± 39.2	232.6 ± 70.7	6.8 ± 1.1	26.8 ± 16.5	26.8 ± 16.5
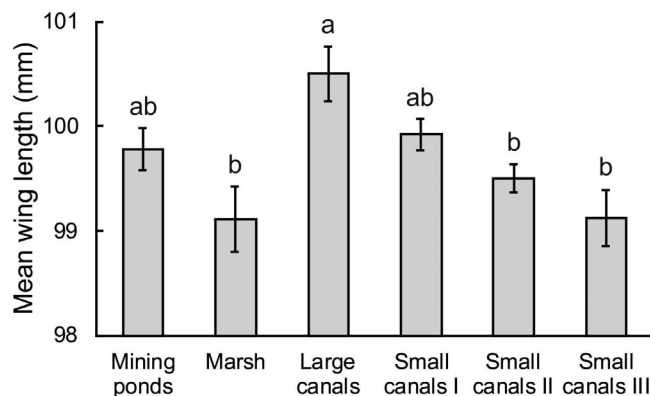
FIGURE 2. Mean wing length ± SE of the Great Reed Warbler males for the 6 different reed habitats. Reed habitats not sharing lowercase letters are significantly different (Tukey's HSD test, $p < 0.05$).

RESULTS

We captured 702 males (2013: $n = 357$; 2014: $n = 345$) and recaptured 45 in 2014. The mean wing length was 99.8 ± 2.1 mm (mean ± SD), range 94–106 mm (Appendix Figure 9). Mean wing length differed significantly among the 6 reed habitats (one-way ANOVA, $F = 5.1$, df = 5, $p < 0.001$; Figure 2). Males nesting along large canals had significantly longer wings than those nesting in marshes and small canals II and III, whereas wing length was intermediate for males nesting in mining ponds and small canals I (Figure 2).

The GLM indicated that wing length correlated negatively with the proportion of managed reed and water level fluctuation but was positively related to water depth. The interaction between the proportion of managed reed and water depth was also significantly positive (Table 2) because the proportion of managed reed had a larger effect on wing size when water depth was small than when it was large. Other reed variables were not related to wing size (Table 2). In the case of recaptured males, we did not observe differences in reed habitat preference during the 2 years ($\chi^2 = 0.15$, df = 4, $p = 0.99$). Finally, reed stem diameter varied significantly among reed habitats ($F = 1.6$,

df = 5, $p < 0.001$), whereas mixed reed density did not ($F = 10.8$, df = 5, $p < 0.16$).

DISCUSSION

The positive correlation between wing size and water depth, and the interaction between the proportion of managed reed and water depth, indicated that males nesting on large canals had larger wings than males nesting on very small canals and in marshes (Tables 1 and 2). The negative correlations between wing size and proportion of managed reed and between wing size and fluctuation in water level indicated that little-managed reed habitats with minor fluctuation in water level (large canals; Table 2) were preferred by larger-winged males. Although the proportion of managed reed was similar in small canals III to those in large canals, small canals III hosted smaller-winged males, possibly due to the low and largely fluctuating water levels (Table 1). Thus our results suggest that large canals (i.e. reed habitats with little management and deep water and little fluctuation in water level) are preferred by larger-winged males (Figure 2). Other reed habitats were probably of lower quality. For example, marshes, which had almost no management and low and largely fluctuating water levels, seemed to be poor habitats because they hosted males with smaller wings (Figure 2). Strongly mowed small canals I were also less preferred by larger-winged males (Figure 2). Males showed high breeding fidelity to reed habitat types; we did not find evidence of changes between habitat types. Our results thus supported the hypothesis that little management and deep water with little fluctuations in water level (large canals) are important factors in the habitat selection of Great Reed Warbler males. In contrast, reed properties were found to be less important in habitat selection.

Our findings provide evidence that differences in wing size can result in considerable differences in habitat selection within a species, such as in flycatchers (Alatalo et al. 1985) and tits (Lemel 1989). In other *Acrocephalus* warblers, large-winged males were reported to select different habitats than small-winged ones, also supporting a link between wing size and habitat selection (Shennan

TABLE 2. Results of a general linear model testing the main effects and interactions of the proportion of managed reed, water, and reed variables on wing size of Great Reed Warbler males. Significant effects are in bold.

Independent variables		Estimate ± SE	F	df	p value
Main effects	**Proportion of managed reed**	**−3.3 ± 1.1**	**2.4**	**8, 702**	**0.01**
	Water depth	**3.8 ± 1.2**	**1.7**	**15, 702**	**0.04**
	Fluctuation of water level	**−1.9 ± 0.8**	**2.6**	**8, 702**	**<0.01**
	Mixed reed density	0.2 ± 0.7	1.2	1, 702	0.28
	Reed stem diameter	0.7 ± 0.3	3.1	1, 702	0.08
Interactions	**Proportion of managed reed * Water depth**	**5.7 ± 2.1**	**3.7**	**3, 630**	**0.02**
	Mixed reed density * Water depth * Water level fluctuation	2.1 ± 1.2	1.3	8, 630	0.06

1985, Nowakowski 2000). Small-winged individuals, however, seem to play an important role in the capability to inhabit empty parts of certain habitats, described as suboptimal habitats by Nowakowski (2000). Tarka et al. (2010) suggested there is a trade-off within local Great Reed Warbler populations between longer wings adequate for long-distance migration and shorter wings optimized for maneuverability in nesting habitats, which may explain why smaller-winged individuals can persist in the population. Several mechanisms can explain wing size-related habitat selection, for example, food availability (Schluter 1982, Poulin et al. 2002), adaptation of body morphology to vegetation structure (Leisler et al. 1989), or availability of nest construction material (Kluyver 1955). Videler (2005) suggested that "cluttered" habitats are generally occupied by small-winged individuals while "looser" habitats host larger-winged individuals. This distinction supports our finding that larger-winged Great Reed Warbler males preferred large canals containing partially managed patches, which thus represented "looser" habitat, providing better opportunities for maneuverability and territorial defense (Vanhooydonck et al. 2009, Tarka et al. 2010). Such habitat choice was found to be closely linked to wing size and maneuverability (Kaboli et al. 2007). Moreover, Kaboli et al. (2007) reported that shorter and rounder wings enhance maneuverability in cluttered habitats, suggesting that cluttered habitats are not necessarily poorer habitats.

In general, reed habitats with little management, deep water, and minor fluctuation in water level seem to benefit early arriving (larger winged) males, and therefore regulation of water can increase the attractiveness of these habitats for such males. Our observations that larger-winged Great Reed Warbler males arrive earlier at breeding sites at large canals than at other sites suggests that this reed habitat contained territories that were most attractive to males (Hasselquist 1998). In some extreme cases males hold their territories even when fresh reed is not sufficiently developed to support nests, during which time they sing on shrubs or trees or on the remaining old reed stems.

Furthermore, because females moisten nest material during nest construction (Kluyver 1955), a constant source of water is needed during nest-building, conditions found in reed habitats with high and stable water level such as large canals. By contrast, water disappeared in marshes and small canals III by mid-June in both years, thereby ruling out the possibility of re-nesting. In some other habitats, such as small canals II and mining ponds, high fluctuation of water level also represents risks of flooding the nests (Mérő et al. 2014).

Despite the suggested links between wing size and vegetation structure (Graveland 1998, Mérő and Žuljević 2014), our results indicated that wing size was not related to reed variables. These previous studies reported that the Great Reed Warbler positively preferred sparse reedbeds and thicker reeds for nesting. In our study, the lack of differences in reed density between reed habitats may potentially explain the lack of effect of reed variables on wing size, suggesting that reed variables were less relevant at a broader scale (among reed habitats in the landscape) than they are locally at the reedbed level (Mérő and Žuljević 2014).

In conclusion, our results suggest that larger-winged males chose reed habitats with little-managed reed and deep water with minor fluctuations (large canals). Reed habitats with low and/or highly fluctuating water level were occupied by smaller-winged males. Our results indicate that reed habitats where the water level can be regulated, such as canals and ponds, should provide a stable and high water level during the nesting season (spring and summer) and should be only little managed (e.g., by mowing reed on only one side of the canals) in the nonbreeding period to increase reed habitat quality and attractiveness to larger-winged males.

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APPENDIX FIGURE 3. Mining pond in Sombor municipality near Gakovo (1.4 ha), Serbia.

APPENDIX FIGURE 4. Marsh in Sombor municipality, Serbia; the meander of the former river Severna Mostonga (∼13.5 ha) is completely dried out.

APPENDIX FIGURE 5. Large canal (~30 m) in Sombor, Serbia.
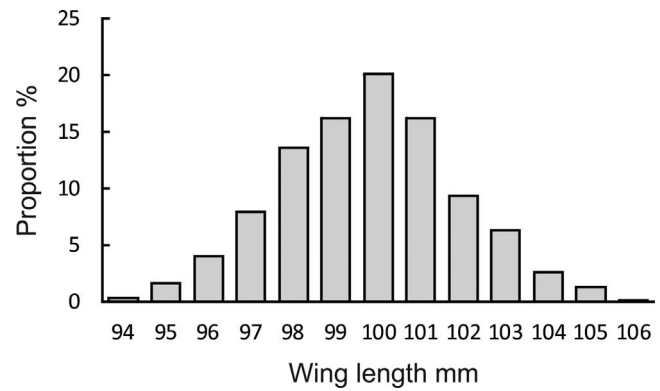

APPENDIX FIGURE 8. Small canal of third order (average width: 1 m) in Sombor municipality, Serbia, that is completely dried out.

APPENDIX FIGURE 6. Small canal of first order (average width: 5 m) in Sombor, Serbia.

APPENDIX FIGURE 9. Proportion of Great Reed Warbler males with different wing length.

APPENDIX FIGURE 7. Small canal of second order (average width: 3 m) in Sombor municipality, Serbia.