Reed management influences philopatry to reed habitats in the Great Reed Warbler (*Acrocephalus arundinaceus*)

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RESEARCH ARTICLE

Reed management influences philopatry to reed habitats in the Great Reed Warbler (*Acrocephalus arundinaceus*)

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ABSTRACT

Management of reed beds primarily includes controlling water levels and removing vegetation by mowing, burning, or grazing. Although recent studies have demonstrated increased diversity and abundance of wetland specialists after reed bed management, documenting demographic benefits to individual species would add additional support to the advantages of appropriate management. Here, we explore the effects of reed management on the philopatry of Great Reed Warblers (*Acrocephalus arundinaceus*) over 7 yr. Reed beds were managed in the winter by occasional burning at mining ponds and large canals, infrequent burning in marshes, and frequent mowing of small canals. Based on resightings and recaptures of 1,243 adult and 1,428 nestlings individually marked at 57 sites in 6 different reed habitats, we built Cormack-Jolly-Seber models to estimate the apparent annual survival and encounter probabilities of birds banded as nestlings or as adults. Apparent survival varied in time for both age groups and both sexes, suggesting annual fluctuations in survival, whereas encounter probability remained constant across years. The encounter probability of birds banded as juveniles was higher in reed beds with shallower water. The encounter probability of birds banded as adults was higher in reed beds with deeper water for females, and strongly increased with variation in reed management and less strongly with variation in water depth for males. We also found that the few returning juveniles displayed strong philopatry to the reed habitat occupied in their first breeding season. Our study provides evidence that reed management influences the return rates of juveniles and adult males and females in different ways. Spatially variable reed management by mowing or burning should be applied and water of varying depths should be maintained to maximize return rates of Great Reed Warblers.

Keywords: ecosystem management, habitat use, indicator species, nest site selection, *Phragmites australis*, reed management, site fidelity, water depth

El manejo del carrizal influencia la filopatría a los hábitats de carrizal en *Acrocephalus arundinaceus*

RESUMEN

El manejo de los lechos de carrizal incluye principalmente el control del nivel del agua y la remoción de la vegetación mediante segado, quema o pastaje. Aunque estudios recientes demostraron un aumento en la diversidad y la abundancia de los especialistas de humedal luego del manejo del carrizal, los beneficios demográficos a las especies individuales agregarían apoyo adicional a los beneficios del manejo apropiado. Aquí exploramos los efectos del manejo del carrizal en la filopatría de *Acrocephalus arundinaceus* a lo largo de siete años. El carrizal fue manejado anualmente o una vez cada pocos años en primavera mediante quema ocasional en los estanques mineros y los canales grandes, quema infrecuente en los pantanos y segado frecuente en los canales pequeños. Basados en avistamientos repetidos y recapturas de 1,243 adultos y 1,428 polluelos marcados individualmente en 57 sitios en seis hábitats diferentes de carrizal, construimos modelos de Cormack-Jolly-Seber para estimar la supervivencia anual aparente y la probabilidad de encuentro de las aves anilladas como polluelos o como adultos. La supervivencia aparente varió a lo largo del tiempo para ambos grupos de edad y para ambos sexos, sugiriendo fluctuaciones anuales en la supervivencia, mientras que la probabilidad de encuentro permaneció constante a lo largo de los años. La probabilidad de encuentro de aves anilladas como juveniles fue más alta en los lechos de carrizal con aguas más someras. La mayor probabilidad de encuentro de aves anilladas como adultas en los bancos de carrizal con aguas más profundas se registró para las hembras, y aumentó fuertemente con la variación en el manejo del carrizal y menos fuertemente con la variación en la profundidad del agua para los machos. También encontramos que los pocos juveniles que retornaron mostraron fuerte filopatría al hábitat de carrizal ocupado durante su primera estación reproductiva. Nuestro estudio brinda evidencia de que el manejo del carrizal influencia las tasas de retorno de los machos y las hembras juveniles y adultos de modos diferentes. Debería aplicarse un manejo del carrizal generando

variación espacial mediante segado/quema y debería mantenerse una profundidad de agua variable para maximizar las tasas de retorno en *Acrocephalus arundinaceus*.

Palabras clave: especie indicadora, fidelidad al sitio, manejo del carrizal, manejo del ecosistema, *Phragmites australis*, profundidad del agua, selección del sitio de anidación, uso de hábitat

INTRODUCTION

Ecosystem or habitat management typically aims to provide the most favorable conditions for the survival and reproduction of species of conservation importance. An underlying but rarely tested assumption in such interventions is that management affects, and hopefully benefits, the survival and reproduction of target species. There have been a number of studies on how ecosystem or habitat management has influenced the population size of individual species or the abundance of species in species groups (Baines 1996, Dale et al. 1997, Berkeley et al. 2007, Perkins et al. 2011). However, studies on how management influences population parameters (survival, reproduction, or recruitment) are scarce for nongame species (Hartmann et al. 2015). Although habitat management is increasingly conducted to benefit species assemblages or communities (Mérő et al. 2015a, Lehikoinen et al. 2017, Maphisa et al. 2017), management for single species is typically limited to flagship species of exceptional conservation concern, for example, the Northern Spotted Owl (*Strix occidentalis caurina*; Noon and McKelvey 1996) or Bearded Vulture (*Gypaetus barbatus*; Oro et al. 2008). Similarly, links between management and population parameters of game bird species have been made (e.g., Sandercock et al. 2011). We know much less about how management influences nonthreatened species, despite the importance of these species for assessing the outcomes of habitat management.

Capture–mark–recapture techniques allow the quantification of return rates (natal and breeding philopatry) and encounter probabilities of individuals and estimation of survival, as opposed to the dispersal and mortality of individuals (Sandercock 2006). Survival analyses for bird populations conducted in relation to environmental factors (e.g., predation, food supply, or weather) are of major importance for understanding the vital rates, such as philopatry, survival, and dispersal, that determine population dynamics (Newton 1998, Ryan et al. 2016). For migratory passerines, breeding dispersal is often more restricted than natal dispersal, resulting in higher breeding philopatry than natal philopatry, and this is often related to the age distribution of individuals or habitat structure and availability (Hansson et al. 2002, Cline et al. 2013). Low natal philopatry of passerines is suspected to be related more to ecological factors than to the avoidance of inbreeding in a population (Weatherhead and Forbes 1994). Philopatry is also related to individual quality; for example, philopatric individuals are often regarded to be of

higher quality than immigrant individuals (Bensch et al. 1998). Breeding philopatry in passerines is also related to nest success; for example, parents that raised a parasitic nestling or produced fewer fledglings are less likely to return to their breeding site than parents that produced more fledglings (Koleček et al. 2015). The survival of passerines between breeding seasons depends on factors such as postbreeding dispersal, conditions at migratory stopover sites and wintering areas, and age and body condition (Seward et al. 2013, Miholcsa et al. 2016, Rockwell et al. 2017). In general, the survival of adult, experienced individuals is higher than the survival of younger birds during the nonbreeding season (e.g., Gardali et al. 2003). These findings suggest that philopatry, dispersal, and survival are key factors in the dynamics of passerine populations, and that these parameters may depend on environmental factors such as habitat structure and availability. Therefore, detailed information on marked and tracked individuals can provide valuable information on how populations respond to habitat structure and management actions.

Reed beds, that is wetlands dominated by the common reed (*Phragmites australis*), host an array of species of conservation importance, and occur in both natural conditions (e.g., floodplains, estuaries, marshes, and swamps) and artificial settings (e.g., canals, environmental remediation areas, and sewage treatment ponds). The management of reed habitats is mostly done by the regulation of water levels (inundation), or by harvesting, burning, grazing, or mowing (Valkama et al. 2008). Management is usually considered necessary to maintain reed beds (Lougheed et al. 2008). However, the effects of management depend on the type, temporal frequency, spatial extent, and local intensity of manipulations (McCabe and Gotelli 2000). For example, late-summer burning leads to the disappearance of reeds by the next spring (Mester et al. 2015), resulting in increased species richness and abundance of all birds (Mérő et al. 2015b). However, the potential food sources of reed specialists, including passerines and invertebrates, are usually negatively affected by reed management (Valkama et al. 2008). The abundance of reed-specialist passerines decreases in mowed, grazed, and burned parts of reed beds, and some warblers in the genus *Acrocephalus* avoid mowed areas entirely (Vadász et al. 2008, Mérő et al. 2015b). In years in which a reed bed is burned, Great Reed Warblers (*Acrocephalus arundinaceus*) build nests in unburned parts of the reed bed, and dominant males occupy reed

habitats that experience little management (Mérő et al. 2014, 2015c, 2016). However, reed management can also lead to rejuvenation of reed beds; for example, reed regrowth is stronger in burned areas than in unmanaged or grazed areas (Mester et al. 2015). In addition, inappropriate management may lead to reed dieback (Graveland 1998). The size of reed beds is also important, as *Acrocephalus* species respond to changes in the area and configuration of reed beds (Benassi et al. 2009, Mortelliti et al. 2012). Despite this understanding of habitat associations, it is currently not known how reed management influences the population parameters of reed-nesting songbirds. The Great Reed Warbler is often considered a flagship species for the conservation of reed beds and, based on its strong dependence on reed bed quality, can be an indicator of habitat quality for other components of biodiversity (e.g., waterfowl, rails, coots, and grebes) in declining wetland ecosystems (Mérő et al. 2015b, Horns et al. 2016). An understanding of the population-level responses of this species to management can thus also inform management for other reed bed species of conservation concern.

The Great Reed Warbler is a widespread reed bed specialist that can be used to evaluate the relationship between reed management and bird survival. Here, we use data collected in 6 different reed habitats over a period of 7 yr in northwestern Serbia to determine how reed management by mowing, burning, and inundation influences the apparent survival and encounter probability of Great Reed Warblers. We analyze return rates, natal and breeding philopatry, and dispersal distances for both juveniles and adults, as influenced by reed habitat type, management, and water depth.

METHODS

Study Species
The Great Reed Warbler inhabits various reed habitats in the western Palaearctic (Cramp 1998, Báldi and Kisbenedek 1999). A large-scale declining trend of this species was reported in Europe in the 1970s and 1980s (Hagemeijer and Blair 1997), although the species is currently listed as Least Concern (IUCN 2016). Previous studies have suggested that the selection of breeding habitats and nest sites is strongly influenced by habitat quality, e.g., reed density and diameter, availability of old reeds, reed management, and water depth (Graveland 1998, Poulin et al. 2002, Mérő and Žuljević 2014, Mérő et al. 2014, 2016). Old and experienced, often dominant, males are the first to arrive on the breeding grounds and to establish territories, often on or near reed bed edges (Hasselquist 1998), usually in reed beds that are rich in old (previous-year) reeds and have deep water (Mérő et al. 2016). Males usually show high natal and breeding philopatry, depend-

ing on the quality of the reed habitat (Hansson et al. 2002, Mátrai et al. 2011, 2012). Great Reed Warblers strongly prefer the edges of reed beds and particularly avoid closed and homogeneous reed beds (Báldi 1999, Báldi and Kisbenedek 1999). Shortly after females arrive back from the wintering grounds, they choose among territory-occupying males and build their nests, generally in the second half of May before water levels drop (Mérő et al. 2014). Both reed and water management have previously been found to influence habitat occupancy (Graveland 1998, Mérő et al. 2016) and breeding success (Mérő et al. 2014). Water levels are important as deep water can keep mammalian predators away, although avian predators or snakes may still depredate nests. In unmanaged marshes, Great Reed Warblers rely on their ability to hide nests in dense reeds (Mérő and Žuljević 2017a). The presence or absence of water significantly affects nestling survival (Mérő et al. 2015c), and inappropriate water management and reed dieback can result in a rapid decline of Great Reed Warbler breeding populations (Graveland 1998).

Study Area and Reed Management
Our study sites ($n = 57$) were located in 6 different reed habitats (mining ponds, marshes, large canals, and 3 size classes of small canals) in the region of Sombor, northwestern Serbia (1,178 km^2; 45°N, 19°E). We categorized reed habitats based on their origin (artificial or seminatural), type of water body (stagnant or flowing), and size (large canals and small canals; Table 1).

Mining ponds ($n = 5$ sites) were established in the 1900s or 1960s for clay or sand excavation. These ponds (surface area: 0.7–2.0 ha) contained either patchy and fragmented or closed and homogeneous reed beds, occasionally interspersed with cattails (*Typha* spp.; Supplemental Material Figures S1A, S1B). Water levels in the breeding period depended on precipitation in autumn, winter, and early spring and on the groundwater table. Water levels typically decreased from spring throughout the summer and into early autumn. Local people burned parts of the reed beds at the end of winter in all years except 2015 (Supplemental Material Figures S2A–S2G).

Marshes ($n = 8$; surface area between 2.0 and 13.5 ha) were remnants of slow-flowing and meandering lowland rivers and were characterized by closed and often homogeneous stands of reeds (Supplemental Material Figures S1C, S1D). Water level in the breeding period depended exclusively on precipitation from late autumn until early spring, and water generally disappeared from the marshes by June due to evapotranspiration. No management occurred in the marshes, except that one marsh was burned in the winter of 2014.

Large canals ($n = 7$; total length surveyed = 13.3 km) varied between 15 m and 35 m in width and their banks were covered by 2- to 6-m wide belts of reeds occasionally

TABLE 1. Mean values of the proportion of managed (mown and burned) reed areas, mean water depth during the breeding season, and number of banded adults and hatch-year Great Reed Warblers in the 6 reed habitats studied for 7 yr (2009–2015) in Sombor, Serbia.

Reed habitat (number of sites)	Total reed area (ha)	Management variables (mean ± SD)		Number of banded individuals	
		Porportion (%) of managed reed area	Water depth (cm)	Adults	Hatch-year birds
Mining pond (5)	3.5	20 ± 31	67.3 ± 27.6	295	437
Marsh (8)	11.3	1 ± 10	23.9 ± 29.9	43	27
Large canal (7)	3.3	30 ± 24	97.5 ± 26.8	138	421
Small canal I (11) [a]	4.3	59 ± 42	65.0 ± 11.5	309	200
Small canal II (19) [a]	7.3	30 ± 42	49.9 ± 22.5	358	224
Small canal III (7) [a]	0.7	26 ± 42	21.2 ± 11.0	100	119

[a] Small canals were divided into 3 size classes based on their width, drainage capacity, and catchment basin.

interspersed with *Typha*, *Carex*, or *Salix* species (Supplemental Material Figures S1E, S1F). Water levels were regulated by the water management authority through a sluice system using water from the Danube River, and thus were stable during the breeding season. Reeds were managed by mowing in autumn and by burning at the end of winter in smaller sections in several study years, resulting in alternating managed and unmanaged sections.

Small canals, which served drainage and irrigation purposes, were classified into 3 size classes according to the categorization of the water management authority based on width, drainage capacity, and catchment area. Small canals I (width: 4–6 m, $n = 11$, total length surveyed = 35.4 km) were relatively deep and water levels were regulated using sluices, resulting in little variation in water levels except in years of drought (e.g., 2012). Reed belts (width = 1–3 m) were located on one or both banks and were regularly mowed in late summer and autumn by the water management authority according to a predefined schedule (Supplemental Material Figures S1G, S1H). Small canals II ($n = 19$, total length surveyed = 68.1 km) varied from 2 to 4 m in width, and patchy reed beds occupied their entire widths (Supplemental Material Figures S1I, S1J). Water levels depended primarily on precipitation and catchment area, and water depth was intermediate and decreased from the breeding season onward. Reeds were typically mowed on both sides in the autumn and burned at the end of winter. Finally, small canals III ($n = 7$, total length surveyed = 19.1 km) were narrow (1–3 m wide) and shallow depressions containing patchy stands of reeds (Supplemental Material Figures S1K, S1L). Water levels depended on precipitation, and the canals usually dried out by late May or early June. Reeds were rarely mowed in the autumn and some sections were never managed, resulting in reed stands of different ages.

Management intensity thus varied among the reed habitats from little or no management (marshes, small canals III) through intermediate (mining ponds, small canals II) to intensive management (large canals, small canals I). Mowing at small canals II and III depended on the working plan and annual budget of the water management authority, and mowing of these canals was thus irregular. All mowing was carried out by the local water management authority, whereas all burning was initiated illegally by local people.

The water depth of mining ponds and marshes was largely dependent on precipitation (Mérő et al. 2014), whereas water levels of canals were more stable due to control measures by the local water management authority as per their protocols. In wet years, water levels increased in mining ponds, marshes, and small canals, but not in large canals, where water levels were highly regulated.

We used 2 variables to characterize reed management: the proportion of managed (mowed or burned) reed area, and water depth. To determine the area of managed and unmanaged parts of the reed beds, we mapped managed areas with a GPS device (Garmin eTrex 10, Garmin International, Olathe, Kansas, USA; accuracy of 5–8 m). Water depth was measured at 10 randomly chosen Great Reed Warbler nests in each reed bed. Water depth was measured with a stick (accuracy of 5 cm) several times at each nest until the fledglings left the nest, and the maximum depth was considered to be the water depth at each individual nest. We then calculated the mean water depth for each reed habitat from the 10 maximum depth measurements. Both the proportion of managed reed beds and water depth varied considerably among the study sites (Table 1).

Bird Sampling

Fieldwork was conducted in the breeding season (April to August) in 7 yr (2009–2015). We studied Great Reed Warblers at 5 mining ponds and 8 marshes, and along 13.3 km of large canals, 35.4 km of small canals I, 68.1 km of small canals II, and 19.1 km of small canals III (Figure 1). We searched for Great Reed Warbler nests exhaustively in each study site. Breeding adults were captured and marked only if they were known to hold a territory or nest based
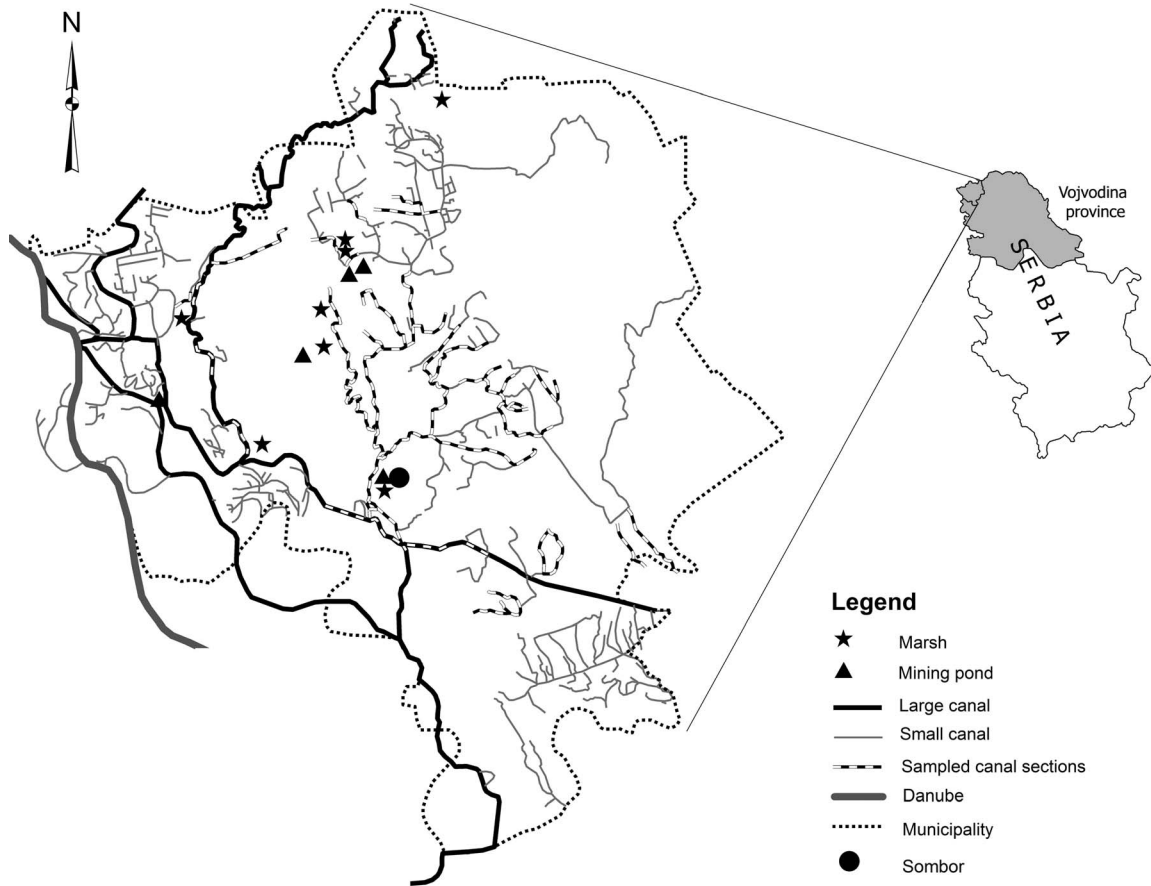
FIGURE 1. The canal network of the municipality of Sombor, Serbia, where we studied the effects of reed management on the philopatry of Great Reed Warblers.

on behavioral clues (singing, and nest or territory or mate defense for males; incubation, nest defense, or feeding of young for females; Valkama et al. 2011). Individuals that could not be tied to a territory or nest were excluded from the study. Adult Great Reed Warblers were captured with mist nets near their nests or in their territories and individually marked with aluminum and color bands. Birds marked as nestlings are referred to as hatch-year birds (HYB). These birds were designated as HYB throughout the study, regardless of the number of recaptures in later years.

Data on recaptures came from resightings or recaptures of marked birds in years after their initial marking. We searched intensively for marked individuals in all study sites. In addition, once an adult was linked to a territory or nest, we attempted to catch the bird. The number of visits was similar across all study sites, but the duration of every visit was adjusted to cover the entire area of each study site. We considered all marked birds as resighted if they were visually observed, or as recaptured if they were caught by mist netting after the year of marking. A returning adult was considered to be a

breeding individual if it was observed to hold a territory or an active nest.

Variables and Statistical Analysis

We defined natal philopatry to have occurred when a HYB was encountered as an adult within the same reed habitat in any subsequent year. Similarly, we defined breeding philopatry to have occurred when an individual marked as an adult was encountered within the same reed habitat in any subsequent year. Encounter probability was defined as the chance that an individual returned to a specific reed habitat for breeding. Finally, we defined apparent annual survival as the survival of an individual from one breeding season to the next (i.e. through autumn migration, the wintering period in Africa, and spring migration).

We first calculated the recapture rate of HYBs and adults as the number of recaptures divided by the total number of previously marked individuals. Second, we estimated the recapture rate of HYBs for the subsequent year. Third, we measured the distance between the sites of capture and recapture as the shortest distance between the 2 localities in Google Earth (Google, Mountain View,

California, USA; accuracy: ±50 m). We compared the median distances of natal vs. breeding dispersal using a Mann-Whitney U-test.

To estimate the apparent survival (ϕ) and encounter probability (p) of marked individuals, we built Cormack-Jolly-Seber (CJS) models (Lebreton et al. 1992, Sandercock 2006) in program MARK (Cooch and White 2016). In the MARK analysis, we included all HYBs and adults (Table 1) and specified 4 attribute groups: adults, HYBs, males, and females. The basic assumption of CJS models is that all individuals have the same chance of survival and the same chance of remaining in the population to be encountered (White and Burnham 1999). We tested whether our data fit this assumption by a goodness-of-fit test calculated for the null model $\phi(g \times t)$ $p(g)$, where g is the grouping variable (adult, HYB, male, female) and t is time (in years; Cooch and White 2016), in program RELEASE run from program MARK. Our data did not differ from the null model ($\chi^2_{47} =$ 53.8, $P = 0.23$), indicating that our data fit the assumption of the CJS model. The variance inflation factor, $\hat{c}$, was subsequently adjusted to 1.07, as recommended by Cooch and White (2016).

We studied the influence of reed management on encounter probability and apparent survival by incorporating the proportion of managed (mowed or burned) reed beds and water depth into models as covariates. To explore the effects of potential spatial and temporal variation in reed management, we also used the coefficient of variation (CV; i.e. the ratio of the standard deviation to the mean) of both the proportion of reed beds managed and water depth for each reed habitat as covariates. First, we ran all possible models without covariates and selected the model with the lowest Akaike's information criterion value corrected for small sample sizes (AIC$_c$) as the best model. Second, the best model was run with the 4 variables describing management (mean and CV of proportion of managed reed beds, and mean and CV of water depth) as covariates (Ryan et al. 2016). Because management and water depth could vary across years at each site, we added the 4 management variables as covariates to each year. We ran all possible combinations of the best model with the covariates. Models with a difference in AIC$_c$ value (ΔAIC$_c$) >2 were considered to have much less support from the data than those with a difference <2 (White and Burnham 1999). Because the distribution of variables did not differ from a normal distribution, we applied Student's t-test to test differences in apparent survival between HYBs and adults and between the 2 sexes. Nonlinear regression was then applied to test the relationship between the encounter probability of individuals and the mean or CV of the proportion of managed reed beds or the mean or CV of water depth. All statistical analyses were performed in SPSS for Windows 20.0 (IBM, Armonk, New York, USA).

TABLE 2. Number of Great Reed Warbler individuals that were marked and that returned to reed habitats in Sombor, Serbia, 2009–2015, and return rates in the 6 studied reed habitats ranked by return rate. See Table 1 for small canal habitat definitions.

Philopatry	Habitat type	Number of individuals Returned	Number of individuals Marked	Return rate
Natal	Marsh	3	27	0.11
	Small canal I	10	200	0.05
	Small canal II	11	224	0.05
	Mining pond	19	437	0.04
	Large canal	11	421	0.03
	Small canal III	2	119	0.02
	Total	56	1,428	0.04
Breeding, males	Small canal I	70	235	0.30
	Large canal	32	119	0.27
	Marsh	9	37	0.24
	Small canal II	63	293	0.21
	Mining pond	41	208	0.20
	Small canal III	9	76	0.12
	Total	224	968	0.23
Breeding, females	Marsh	2	6	0.33
	Mining pond	14	87	0.16
	Small canal I	6	74	0.08
	Small canal II	1	65	0.01
	Large canal	0	19	0.00
	Small canal III	0	24	0.00
	Total	23	275	0.09

RESULTS

Captures

In 7 nesting seasons (2009–2015), we banded a total of 2,671 Great Reed Warbler individuals. Of these birds, 1,243 were banded as adults (968 males and 275 females) and 1,428 were banded as HYBs.

Recapture Rates and Philopatry

We recaptured 303 of 2,671 individuals, resulting in an overall recapture rate of 11% (Table 2). The recapture rate of adults was higher (20%; $n = 1,243$) than that of HYBs (4%; $n = 1,428$). The majority of recaptured individuals that were banded as adults were males (224, or 91% of $n = 247$ total). Similarly, 46 (or 82%) of the recaptured HYBs ($n = 56$ total) were males.

Only 2% of the HYBs displayed natal philopatry immediately after the year of banding. For the entire study period, 89% of the recaptured birds banded as adults ($n = 247$) demonstrated breeding philopatry, whereas 66% of the recaptured HYBs ($n = 56$) showed natal philopatry in subsequent years. Of 40 individuals that were banded as adults and were encountered in ≥2 subsequent years, 95% showed breeding philopatry to the original reed habitat in which they were marked. Each HYB that was encountered in ≥2 subsequent years ($n = 12$) returned to breed in the

TABLE 3. The top 10 Cormack-Jolly-Seber (CJS) models estimating the apparent survival (ϕ) and encounter probability (p) of Great Reed Warblers in relation to the proportion of managed reed area (m = mean; m_{cv} = coefficient of variation) and water depth (w = mean; w_{cv} = coefficient of variation) in 6 reed habitat types in Sombor, Serbia, 2009–2015. Individuals were banded either as hatch-year birds (pull) or as adults (ad); g is the grouping variable (adult, hatch-year, male, female) and t is time (yr).

Cormack-Jolly-Seber model	K [a]	ΔAIC_c [b]	w_i [b]	Deviance
1. $\phi(t \times g)$, p(pull(w)×ad($wm_{cv}w_{cv}$)×male($m_{cv}w_{cv}$)×female(w))	32	0.0 [c]	0.12	4,246.1
2. $\phi(t \times g)$, p(pull(ww_{cv})×ad($mwm_{cv}w_{cv}$)×male($wm_{cv}w_{cv}$)×female(w))	34	0.7	0.09	4,243.0
3. $\phi(t \times g)$, p(pull(ww_{cv})×ad($wm_{cv}w_{cv}$)×male($m_{cv}w_{cv}$)×female(w))	33	0.8	0.08	4,245.2
4. $\phi(t \times g)$, p(pull(ww_{cv})×ad($wm_{cv}w_{cv}$)×male($m_{cv}w_{cv}$)×female(w))	33	0.9	0.08	4,245.3
5. $\phi(t \times g)$, p(pull(ww_{cv})×ad($mwm_{cv}w_{cv}$)×male($wm_{cv}w_{cv}$)×female(m_{cv}))	34	1.1	0.07	4,243.4
6. $\phi(t \times g)$, p(pull(ww_{cv})×ad($mwm_{cv}w_{cv}$)×male($wm_{cv}w_{cv}$)×female(w_{cv}))	34	1.2	0.07	4,243.6
7. $\phi(t \times g)$, p(pull(ww_{cv})×ad($mwm_{cv}w_{cv}$)×male($wm_{cv}w_{cv}$)×female(m))	34	1.4	0.06	4,243.8
8. $\phi(t \times g)$, p(pull(ww_{cv})×ad($mwm_{cv}w_{cv}$)×male($wm_{cv}w_{cv}$)×female(wm_{cv}))	35	1.6	0.05	4,241.9
9. $\phi(t \times g)$, p(pull(wm_{cv})×ad($wm_{cv}w_{cv}$)×male($m_{cv}w_{cv}$)×female(w))	33	1.9	0.05	4,246.3
10. $\phi(t \times g)$, p(pull(wm)×ad($wm_{cv}w_{cv}$)×male($m_{cv}w_{cv}$)×female(w))	23	2.0	0.04	4,246.4

[a] K is the number of model parameters.
[b] Models were ranked based on the difference from the top model in adjusted Akaike's information criterion (ΔAIC_c) and Akaike model weight (w_i).
[c] The AIC_c value of the best model was 4,310.9.

reed habitat in which it first bred after its hatching year. Eight of these individuals (67%) had earlier also displayed natal philopatry. The median natal dispersal distance was greater (median = 7,700 m; quartile Q_1 = 4,000 m; quartile Q_3 = 9,500 m) than the median breeding dispersal distance (median = 1,900 m; Q_1 = 800 m; Q_3 = 6,275 m; Mann-Whitney U-test, U = 422, P = 0.001).

Encounter Probability and Apparent Survival

The $\phi(t \times g)$ $p(g)$ model had the smallest AIC_c value (4,371.7) and was thus selected as the best model. This model showed that encounter probability was constant through time for all 4 attribute groups (i.e. adults and HYBs, and males and females). Based on this result, we did not consider time-dependence of encounter probability in further models, but allowed apparent survival to vary with time.

In the final model that included each of the 4 groups and 4 covariates, the encounter probability of HYBs was influenced by water depth (Table 3, model 1), and the relationship was negative (Figure 2A; nonlinear regression, $F_{1,99}$ = 3,852.3, P < 0.001). In contrast, the encounter probability of adults was positively influenced by water depth (Table 3, Figure 2B; $F_{1,99}$ = 2,502.9, P < 0.001). In addition, the encounter probability of adults was positively related to the CV of reed management (Figure 2C; $F_{1,99}$ = 6,922.2, P < 0.001) and to the CV of water depth (Figure 2D; $F_{1,99}$ = 22,536,879.0, P < 0.001), mostly because of the influence on adult males (Table 3; reed management CV: Figure 2E, $F_{1,99}$ = 14,436.2, P < 0.001; water depth CV: Figure 2F, $F_{1,99}$ = 43,550,695.5, P < 0.001). Differences in the slopes suggested that these relationships were stronger for the CV of reed management than for the CV of water depth (Figure 2). Finally, the encounter probability of

females was positively related only to water depth (Table 3, Figure 2G; $F_{1,99}$ = 69,377.0, P < 0.001).

Encounter probability did not differ significantly between individuals banded as adults and those banded as HYBs (Table 4; Student's t-test, t_1 = 1.9, P = 0.31), nor between males and females (Table 4; t_1 = 5.4, P = 0.12).

Apparent annual survival varied with time (t) and among the 4 attribute groups (g; Table 3). The mean apparent survival of adults (0.47 ± 0.10 SE) did not differ from that of HYBs (0.34 ± 0.09; t_5 = 0.8, P = 0.44).

DISCUSSION

Encounter Probability

Our first key result was that water depth influenced the encounter probabilities of hatch-year birds (HYBs), all adults, and adult females, whereas the coefficient of variation (CV) of reed management and CV of water depth influenced the encounter probability of adult males. Both the effects of the CV of reed management and the CV of water depth were positive, indicating a higher encounter probability for adult males in spatially more heterogeneous reed beds. In addition, the steeper slope for the effect of the CV of reed management indicated that this had a more profound effect on the encounter probability of adult males than the CV of water depth. For example, return rates of adult males were highest on small canals I, followed by large canals and small canals II, where the proportions of managed reed beds were usually high ($\geq$30%). A likely explanation is that spatially variable management by mowing and burning and more fluctuating water levels lead to heterogeneous reed beds with a higher proportion of reed bed edges, which are preferred by male Great Reed Warblers for establishing territories
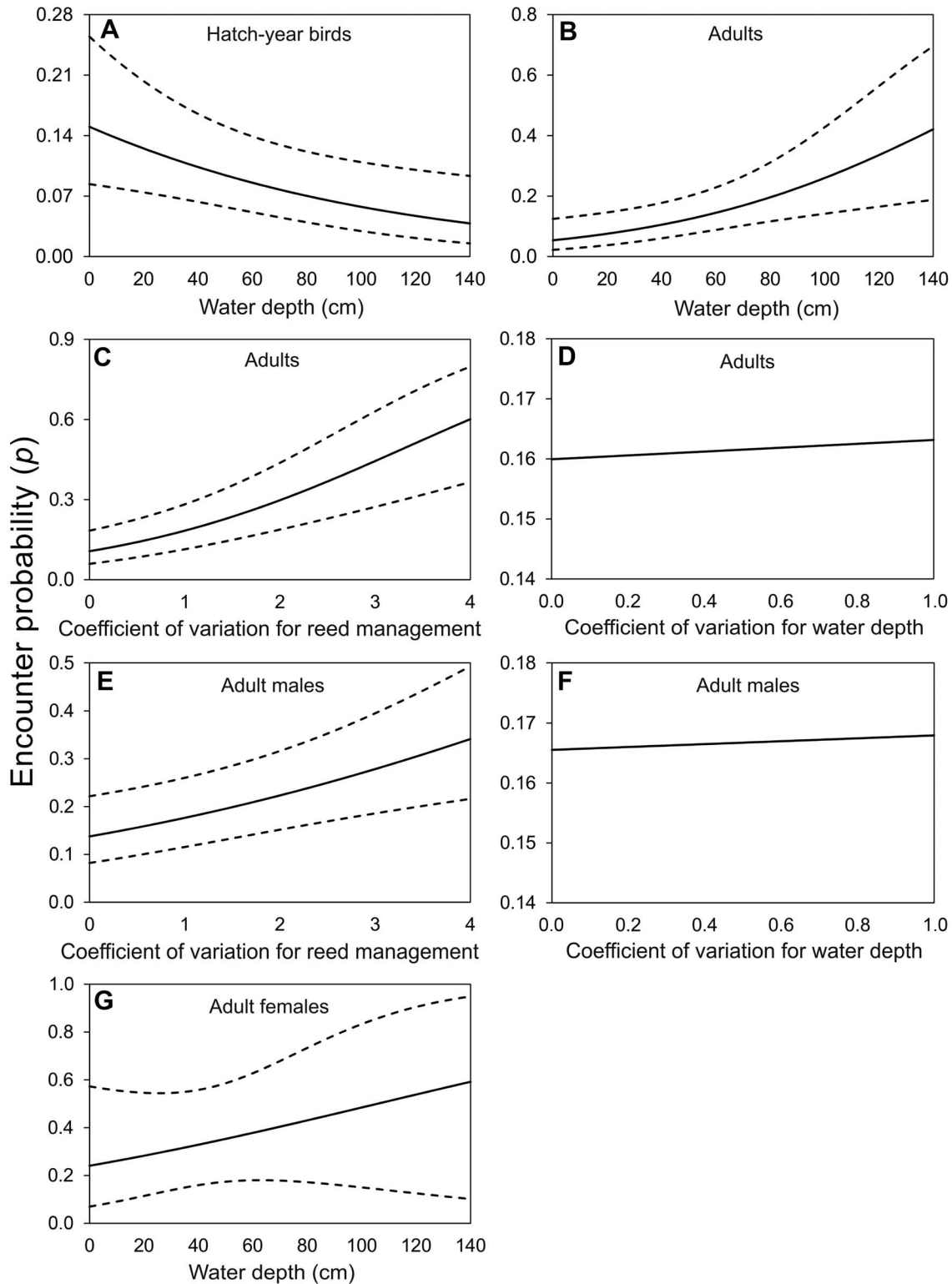
FIGURE 2. Regressions of encounter probability of (**A**) hatch-year birds, (**B**, **C**, **D**) all adults, (**E**, **F**) adult males, and (**G**) adult females of Great Reed Warblers as a function of the mean and coefficient of variation (CV) for water depth and the CV for the proportion of reeds managed by mowing and burning in Sombor, Serbia, 2009–2015. Dashed lines indicate 95% confidence intervals (omitted from **D** and **F** for clarity). Note the different scaling of the *y* axes. Parameter estimates were obtained from model 1 (Table 3).

TABLE 4. Apparent annual survival (φ) and encounter probability (*p*) of hatch-year, adult, male, and female Great Reed Warblers in Sombor, Serbia, 2009–2015. Parameters were estimated in program MARK (Cooch and White 2016) based on model 1 (Table 3).

Parameter	Year interval (no. of banded birds)	Hatch-year birds	Adults	Males	Females
φ (± SE)	2009–2010 (*n* = 89)	0.00 ± 0.00	0.93 ± 0.01	0.92 ± 0.04	0.00 ± 0.00
	2010–2011 (*n* = 291)	0.25 ± 0.10	0.15 ± 0.05	0.24 ± 0.07	0.74 ± 0.03
	2011–2012 (*n* = 754)	0.20 ± 0.05	0.33 ± 0.05	0.54 ± 0.07	0.25 ± 0.10
	2012–2013 (*n* = 523)	0.52 ± 0.12	0.56 ± 0.07	0.70 ± 0.07	0.22 ± 0.08
	2013–2014 (*n* = 546)	0.42 ± 0.11	0.47 ± 0.05	0.52 ± 0.05	0.41 ± 0.13
	2014–2015 (*n* = 468)	0.67 ± 0.20	0.44 ± 0.05	0.51 ± 0.05	0.28 ± 0.11
p (± SE)	2009–2015 (*n* = 2,671)	0.10 ± 0.02	0.38 ± 0.04	0.39 ± 0.03	0.34 ± 0.11

and building nests (Báldi 1999, Báldi and Kisbenedek 1999). For example, large canals are typically occupied by large-winged, dominant males, and are thus suspected to be high-quality breeding habitat (Mérő et al. 2016). Interestingly, nest success remained extremely low on large canals due to high rates of brood parasitism by Common Cuckoos (*Cuculus canorus*) and nest abandonment (Mérő et al. 2015c). These results suggest that large canals may function as ecological traps (Kokko and Sutherland 2001, Battin 2004). Nevertheless, our results underline the importance of management to maintaining reed beds for territory establishment and nest building by Great Reed Warblers.

Our second key result was that water depth had the opposite effect on the encounter probabilities of adults (primarily females) and HYBs. Although the return rate of females was highest in marshes, their encounter probability was highest in reed habitats with deep water. The positive effect of water depth on the encounter probability of females may be explained by the attraction of female birds to territories of higher quality, such as those with abundant reed bed edges along large canals. Such edges are probably more frequent in deeper water (e.g., toward the open water surface) than in shallower water (e.g., toward the shore or near the bank). In addition, nests located on thick reed stalks in deeper water (Poulin et al. 2002) may experience lower predation pressure by small or medium-sized mammals than nests built on reeds in shallower water (Jobin and Picman 1997, Hoover 2006). Finally, Great Reed Warbler females moisten the plant materials used for nest building (Kluyver 1955); therefore, reed bed edges in deep water with a constant water supply during arrival on the breeding grounds and throughout the breeding season may provide better opportunities for nest building or renesting than edges in shallower water that may become dry as the season progresses (Mérő et al. 2016).

The negative effect of water depth on the encounter probability of HYBs was probably related to age-related differences in nest site selection by the Great Reed Warbler. HYBs presumably have little breeding experience, and such birds usually arrive back from the wintering grounds later and occupy poorer reed habitats than older birds with more experience (Hasselquist 1998). In our study, unmanaged marshes and mining ponds, and little-managed small canals III, were such habitats, and were also characterized by shallower water, and these habitats were where the encounter probabilities of HYBs were highest. Marshes and small canals III have previously been found to be low-quality breeding habitats that are typically occupied by small-winged, probably younger, males (Mérő et al. 2016). Taken together, these observations may explain the negative relationship between water depth and the encounter probability of HYBs.

Natal and Breeding Philopatry
Although HYBs displayed low natal philopatry in the year immediately after banding, HYBs recaptured ≥2 times in subsequent years displayed strong philopatry to the reed habitats that they occupied in their first breeding season. This finding was in line with the large number of adult Great Reed Warblers observed to show philopatry to their nesting reed habitat. Generally, we found that natal dispersal was higher than adult dispersal, which conforms to the general pattern found in Great Reed Warblers and other migratory passerines (e.g., Procházka and Reif 2000, Hansson et al. 2002, Craig et al. 2015). Hansson et al. (2002) reported that both breeding philopatry (92%) and natal philopatry (69%) were relatively high for Great Reed Warblers nesting on lakes. Although a direct comparison is difficult because we calculated philopatry to reed habitats and not to nesting lakes, our values are similar to these previously reported values. However, the dispersal distances of adults and HYBs were considerably smaller in our study than in previous studies. This is likely related to differences in the densities of suitable breeding habitats, which are much lower in Sweden (the location of Hansson et al.'s (2002) study) and the Czech Republic and Slovakia (the location of Procházka and Reif's (2000) study; BirdLife International 2004) than in our study region (northern Serbia), where suitable Great Reed Warbler habitats are closer to each other (Mérő and Žuljević 2017b). Furthermore, Mérő et al. (2015c) demonstrated that habitat use depended primarily on the availability of reed bed edges

and the quality of stands of reeds, not on the size of available reed habitats. In fragmented marshlands, Great Reed Warbler abundance increased with fragment area probably because larger marsh fragments contained more suitable edges (Báldi and Kisbenedek 1999, Benassi et al. 2009). In summary, this comparison of philopatry suggests that natal and breeding philopatry may show similar patterns in the various regions of the breeding range of the Great Reed Warbler, but that dispersal distances may vary depending on the density of suitable habitats in the landscape.

Survival

We found that apparent survival showed strong temporal variation across years. Such variation is not surprising if we consider that the Great Reed Warbler is a long-distance, trans-Saharan migrant and that the survival of individuals is largely determined by the difficulties of migration through the Mediterranean region and the deserts of the Sahara and by the environmental conditions on the wintering grounds in sub-Saharan Africa (Horns et al. 2016). The higher mortality and lower return rates of inexperienced, young HYBs (Table 2) is likely due to their more frequent exhaustion due to the energetic costs of autumn migration and to their overwintering in poorer wintering habitats (Sillett and Holmes 2002).

Conclusions

Wetland-specialist migratory passerines are highly vulnerable and more than two-thirds are threatened with extinction (Horns et al. 2016, IUCN 2016). Many of these birds are rare or difficult to observe, with little information on their abundance, reproductive success, survival, and return rate. In contrast, Great Reed Warblers are large, reed-specialist passerines that are relatively easy to mark, observe, and monitor by resighting or recapture, and, as our study has shown, are sensitive to habitat management. For these reasons, Great Reed Warblers are potentially good candidates as an indicator species for other components of biodiversity of reed beds.

Our study showed that reed management can influence the encounter probability of Great Reed Warbler individuals and that reed bed management can thus be related to natal and breeding philopatry in the Great Reed Warbler. The encounter probability of adults increased and that of HYBs decreased with water depth. The encounter probability of adult males increased with variability in the proportion of mowed or burned areas and in water depth, although the effect of the CV of reed management was greater than that of the CV of water depth. These findings imply that the spatial heterogeneity of reed habitats is important for Great Reed Warblers. To increase the availability of reed bed edges, which are preferred by Great Reed Warblers for nesting, limited management by

mowing or burning, which increases heterogeneity but does not lead to the destruction of the reed bed, as well as deep water that is allowed to fluctuate within and between years, should be maintained. Our results suggest that spatial heterogeneity is necessary to provide habitat both for early-returning adult males and for later-arriving females and young birds to occupy territories and initiate nests and thus to maximize the return rates of Great Reed Warblers. Because the Great Reed Warbler is sensitive to reed bed quality, knowledge from this study can also be used to design and implement conservation measures for other wetland-specialist birds.

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