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Effect of reed burning and precipitation on the breeding success of Great Reed Warbler, *Acrocephalus arundinaceus*, on a mining pond

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Abstract: In this study, we present the effects of reed burning and precipitation on the breeding success of Great Reed Warblers on a mining pond (2008–2011). Breeding success, i.e. the probability that an egg would produce a fledgling, was 0.43. Clutch survival was lowest in 2010, due to the precipitation and high water level during the season. Breeding success was higher in the second half of the breeding season, although in 2008 and 2011 precipitation was also higher in the second half than in the first half of the breeding season. During the first half of the breeding season, daily egg and nestling survival did not differ. However, in the second half of the breeding season, daily egg survival was higher than daily chick survival. In years when reed was burned, breeding density varied between 7.7 and 12.3 pairs ha^{-1}, which was not significantly lower than in years when reed was not managed (average: 13.2 pairs ha^{-1}). Despite the availability of fresh reed in large areas, birds placed their nests mainly in mixed reed stands. Breeding success in fresh and mixed reed did not differ. Generally, breeding success and density were not affected by reed burning, but water level affected breeding success and density.

Key words: Daily survival rate, water level, breeding density, Mayfield's method, Kaplan–Meier survival curve, ecological trap

1. Introduction

Several studies have examined how anthropogenic and environmental factors affect the presence of passerines in reed beds (Báldi and Moskát, 1995; Báldi, 2001; Vadász et al., 2008; Moga et al., 2010). Báldi (2001) studied how inundation affected the local breeding passerines at the Kis-Balaton wetland. He collected observations in 3 groups (before, immediately after, and years after inundation) and quantified the changes in community structure parameters, community composition, differences between areas and periods, and species and abundances. Savi's Warbler, *Locustella luscinioides*, declined immediately after inundation, while Reed Bunting, *Emberiza schoeniclus*, and Sedge Warbler, *Acrocephalus schoenobaenus*, declined in the long term. However, the Great Reed Warbler (GRW), *Acrocephalus arundinaceus*, was the only species with a continuous increasing trend. Vadász et al. (2008) reported that the cutting of reed negatively influenced species richness and the abundance of reed passerines on Lake Kolon in Central Hungary. Savi's Warbler, Moustached Warbler *Acrocephalus melanopogon*, Sedge Warbler, and Reed Warbler *Acrocephalus scirpaceus* especially avoided cut areas, while GRW did not (Vadász et al., 2008). Báldi and Moskát (1995) and Moga et al. (2010) recorded the presence of GRW in unmanaged, burned, and mowed reed stands. Despite these sporadic observations, our knowledge about the effects of reed management and environmental factors on the breeding success of GRW is weak.

Nests of small open-nesting birds are often difficult to detect in the early stages of the breeding season (Mayfield, 1975). Due to the lack of information for the period before nests are found, estimates of mortality, survival, and breeding success can be severely biased. Mayfield (1975) developed a method for estimating breeding success that reduced potential sources of error. The proposed Mayfield estimator has been further recognized as a maximum likelihood estimator (MLE). The asymptotic distribution of the MLE has been calculated, which provides a measure of asymptotic variance (Hensler and Nichols, 1981). MLE and variance can be used to test the significance of daily survival (Hensler and Nichols, 1981). Lloyd and

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Tewksbury (2007) compared the performance of the Mayfield method to that of the more recently proposed logistic exposure method and found negligible differences between the results obtained by using the 2 methods. The Mayfield method can also be used effectively in studying the breeding biology of GRW. For example, Batáry and Báldi (2005) estimated the breeding success of GRW by using the Mayfield method, while Petro et al. (1998) calculated the percentages of failed and successful broods.

The breeding habits of GRW have already been discussed in several papers in the past 3 decades (Beier, 1981; Dyrcz, 1981; Woithon and Schmieder, 2004; Batáry and Báldi, 2005; Uzun et al., 2014). This species is a common breeder in the middle latitudes of the western Palearctic; it usually inhabits the tall, dense, and strong reed *Phragmites australis* (Cramp, 1998). Studies on the breeding biology of GRW have been mainly carried out on large ponds (Petro et al., 1998), fishponds (Prokešová and Kocian, 2004), lakes (Fisher, 1994; Woithon and Schmieder, 2004; Batáry and Báldi, 2005), or canals (Mérő and Žuljević, 2009), but not on mining ponds. The first aim of this study was to explore the effects of reed burning, precipitation, and water level changes on breeding success and clutch and chick survival of GRW on a mining pond. The second aim of this paper was to present differences in breeding success in the early and late periods of the breeding season.

2. Materials and methods

The study was conducted on Bager Pond (UTM CR 57 22; 45.788056°N, 19.098333°E) in the suburban area of the town of Sombor, Vojvodina, northern Serbia. Sombor is a typical lowland area (89 m a.s.l. on average) with a semidry continental climate, with mean annual precipitation of 590 mm (range: 400–900 mm). The mean annual temperature is 10.7° C: it is warmest in July (mean monthly temperature of 21.1 °C) and coldest in January (mean monthly temperature of 0.8 °C) (Tomić, 1996). The complex of 2 ponds (total area: 1.3 ha) was established in the 1960s at the location where clay was dug for the local brickyard. The water level in the pond depends on both the precipitation in autumn, winter, and early spring, and the level of groundwater. Water level mainly decreases throughout the summer and early autumn due to the evapotranspiration of reed. In 2009 about 85% and in 2010 about 50% of the reed was burned at the end of winter, while in 2008 and 2011 the reed was not managed. The pond is surrounded by meadows and cornfields (Table 1).

Fieldwork was conducted during the breeding seasons from 2008 to 2011, i.e. from 25 May to 10 July 2008, from 23 May to 30 July 2009, from 20 May to 12 August 2010, and from 17 May to 31 July 2011. The whole area of the pond was completely surveyed for GRW nests. The nests were checked regularly at 6-day intervals in 2008 and 5-day intervals in 2009, 2010, and 2011. During nest checks, the following data were collected: number of eggs, number of nestlings, number of lost eggs, number of lost nestlings, and number of fledglings; water depth was measured under nests. In cases when remains of eggs were found or nestlings had disappeared, we concluded that the nest had been predated. In all other cases, we recorded nest fate as "perished".

Breeding success was estimated by the Mayfield method (Mayfield, 1975), where data on egg-days and nestling-days were used. In this study, we define "breeding success" as the probability that an egg produces a fledgling. Two of Mayfield's statistics, daily survival rate of eggs and of nestlings, were compared using J-tests (Johnson, 1979; Hensler and Nichols, 1981). Nest survival was estimated by the Kaplan–Meier survival test. We used one-way ANOVA to compare mean clutch size and number of fledglings among the years. In this study, the breeding season is defined as the period between the finding of the first and last nests. The differences in survival among breeding seasons were tested with a log-rank (Mantel–Cox) test. Mean clutch size, mean number of nestlings, and hatchability of eggs (Mayfield, 1975) were also calculated. The correlation between precipitation and breeding success was estimated for the entire breeding season by Spearman rank correlations. The proportion of lost broods due to bad weather circumstances or predation was tested

Table 1. Characteristics and dominant vegetation of Bager Pond. Data on precipitation were provided by the water management company Zapadna Bačka, Sombor.

Year	Proportion of open water (%)	Mean water depth at breeding site (cm ± SD)	Vegetation		Precipitation in breeding season (mm)
			Phragmites australis (%)	*Typha* sp. (%)	
2008	10	59.4 ± 29.24	85	5	104.0
2009	8	6.8 ± 17.23	89	3	168.8
2010	7	108.2 ± 37.20	92	1	457.5
2011	8	77.5 ± 26.91	91	1	146.4

with chi-square tests. The breeding season lasted 28 days in 2008, 40 in 2009, 64 in 2010, and 60 in 2011. We grouped all nests into 2 categories based on whether they were first found in the first half (Early group; usually the second half of May and the first half of June) or the second half (Late group; the second half of June and the first half of July) of the breeding season.

We applied the J-test to compare overall (2008–2012) and yearly egg and nestling daily survival rates between the Early and Late groups. Furthermore, the J-test was also used to compare daily survival of eggs and nestlings between the Early and Late groups considering burned (2009 and 2010) and unburned years (2008 and 2011). Finally, we recorded the condition of the reed around the nest either as fresh reed that had grown up after burning or as mixed, unburned reed that consisted of both old and new reed. We estimated the number of breeding pairs by the number of nests found in managed or in unmanaged reed. This was possible because every individual was ringed with aluminum or colored rings (a few females were ringed only with aluminum rings) and could be linked to a nest (each was either recaptured at the nest or identified based on their colored ring code with binoculars or camera). Polygyny was also recorded, but in such cases we considered that each breeding female was one breeding pair. Statistical analyses were calculated in the R statistical environment software package (version 2.13.0, R Development Core Team, 2011) or with SPSS. Maps were drawn in ArcGIS (version 9.x), while the figures were formatted in CorelDraw X3 (version 13.0.0) software.

3. Results

3.1. General breeding success: egg and nestling survival

We found a total of 87 GRW nests in Bager Pond during 2008–2011. Mayfield breeding success for the 4 years averaged 0.43 (0.48 in 2008, 0.67 in 2009, 0.17 in 2010, and 0.69 in 2011). The maximum number of females per polygynous male was 2. The daily survival of nestlings and eggs did not differ (J-test, z = 1.29, P = 0.198). Although some nests were destroyed by predators (Little Bittern, *Ixobrychus minutus*; Grass Snake, *Natrix natrix*), most of the eggs and nestlings were lost due to cold, windy, and rainy weather (χ^2 = 3.86, P = 0.0495). Kaplan–Meier curves showed that nest survival was highest in 2011 (log-rank test, χ^2 = 30.23, P < 0.0001; Figure 1) and lowest in 2010, with 2010 differing significantly from the other 3 years (log-rank tests; vs. 2008: χ^2 = 5.88, P = 0.0153; vs. 2009: χ^2 = 10.78, P = 0.0048; vs. 2011: χ^2 = 23.61, P < 0.0001; Figure 1).

The mean clutch size was 4.1 ± 0.17, range = 1–7 (2008–2011), while the mean number of fledglings was 2.0 ± 1.04, range = 1–5 (2008–2011). Mean clutch size did not vary among years (one-way ANOVA, $F_{3,70}$ = 0.387, P = 0.7625), whereas the mean number of fledglings differed among years, as it was very low in 2010 ($F_{3,70}$ = 9.666, P < 0.0001; Figure 2). The mean hatching rate of the 4 breeding seasons was 0.93, indicating that 7% of eggs did not hatch (0.85 in 2008, 0.91 in 2009, 0.95 in 2009, 0.97 in 2011).

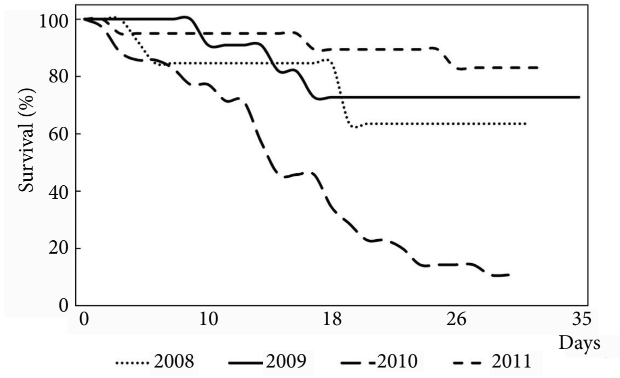

Figure 1. Kaplan–Meier survival curves of GRW nests in breeding seasons 2008–2011.

3.2. Breeding success in the Early and Late groups

Although most nests were found in the Early group (χ^2_3 = 14.78, P < 0.01), breeding success was higher in the Late group for the entire study time (χ^2_3 = 33.89, P < 0.0001; Table 2), probably because of significantly lower precipitation amounts for the Late group (χ^2_1 = 7.71, P < 0.01). Mayfield statistics suggested that daily egg survival was higher than daily nestling survival in the Late group in 2008 and 2010. However, differences in egg and nestling survival in the Early group were found only in 2011 (Table 2). In other groups, there was no difference between egg and nestling daily survival (Table 2). The overall daily survival of eggs differed between the Early and Late groups (z = 4.92, P < 0.0001; daily survival rate (DSR) of Early group: 0.96; DSR of Late group: 0.99), but not in nestlings (z = 1.55, P = 0.1208; DSR of Early group: 0.96; DSR of Late group: 0.98). Furthermore, we found that both daily

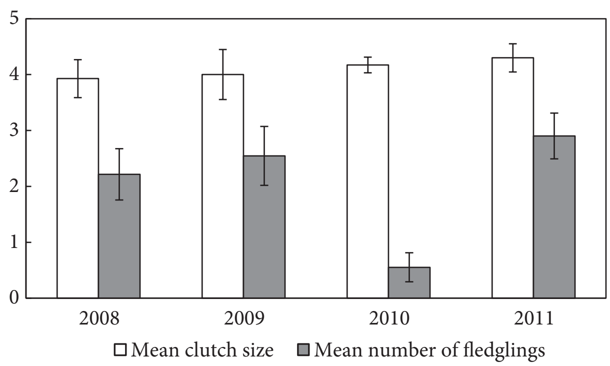

Figure 2. Mean (±SE error bars) clutch size and number of fledglings at Bager Pond, 2008–2011.

Table 2. Breeding success of Early and Late groups at Bager Pond (2008–2011; z*-value is the result of J-test; level of significance: *P < 0.05, **P < 0.01).

Group	Year	Value given for each group						
		Precipitation amount (mm)	Daily survival rate		z*-value	P-value	Hatching rate	Breeding success (%)
			Egg	Nestling				
Early	2008	91	0.96	0.98	0.41	0.681	0.85	43.3
	2009	154	0.98	0.99	1.33	0.186	0.90	61.2
	2010	416	0.91	0.79	1.64	0.101	1.00	1.9
	2011	42	0.99	0.98	2.48	0.013*	0.98	70.4
Late	2008	104	0.99	0.95	2.82	0.005**	0.83	41.7
	2009	76	1.00	1.00	0.00	1.000	0.93	100.0
	2010	173	0.98	0.95	2.18	0.029*	0.94	39.4
	2011	125	0.98	0.98	0.29	0.765	0.95	60.6

egg and nestling survival rates were significantly greater in the Late group than in the Early group in 2009 (extremely low water depth; Table 1) and 2010 (extremely high water depth; Tables 1 and 3). In years with average water depth, daily survival of eggs and nestling did not differ between the groups (Table 3).

There was a significant negative relationship between breeding success and amount of precipitation (Spearman's rho = –0.76, P = 0.0368; Figure 3). The negative effect was mainly because of 2010, when total rainfall reached as high as 457.5 mm during the entire breeding season (Table 1). The rate of water level increase in the pond was so rapid in rainy periods that some nests were submerged in both the egg and nestling stages.

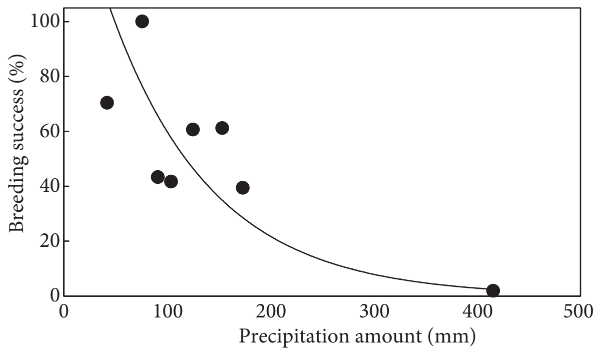

Figure 3. Correlation between amount of precipitation and breeding success at Bager Pond, 2008–2011. Data points are Early and Late groups in 4 years.

3.3. Effect of reed burning on breeding density and success

GRW rarely preferred fresh reed for breeding, as most pairs built their nests in mixed reed (χ^2_1 = 30.18, P < 0.0001; Figure 4). In 2008 and 2011, the reed was not burned, so all nests were in mixed reed. In 2009 and 2010, the proportion of nests in fresh reed was 27.3% and 12.8%, respectively (Figure 4).

Table 3. Overview of egg and nestling survival between Early and Late groups (2008–2011; z*-value is the result of J-test; level of significance: *P < 0.05, **P < 0.01, ***P < 0.001).

Years	Egg		Nestling	
	z*-value	P-value	z*-value	P-value
2008	1.234	0.2171	1.326	0.1847
2009	3.196	0.0013**	2.010	0.0444*
2010	6.077	<0.0001***	2.193	0.0283*
2011	1.418	0.1561	0.483	0.6285

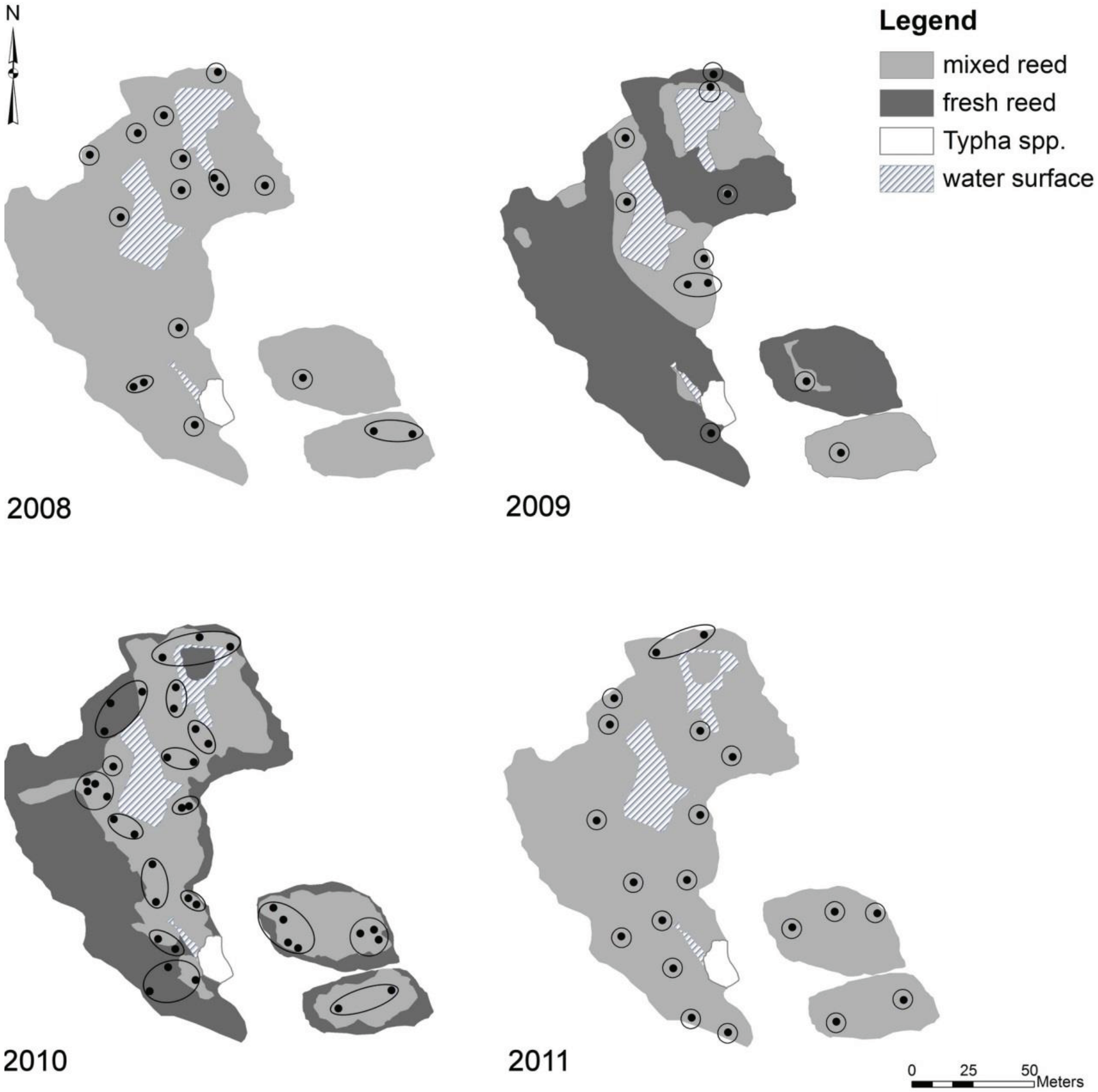

Figure 4. Spatial distribution of GRW nests and actual pairs on Bager Pond. Black dots represent GRW nests and ellipsoids indicate actual breeding pairs. Ellipsoids contain both successful and perished nests (dots) belonging to the same female. Ellipsoids containing 2 (1 original and 1 replacement clutch) or more dots show that 1 female raised 1 or more replacement clutches.

Mean (female) breeding density for the 4 years was 11.9 ± 2.97 pairs ha^{-1}. Breeding density varied over the 4 years and was lowest in 2009: 10.8 pairs ha^{-1} (number of ellipsoids on map, Figure 4) in 2008 (13.1 nests ha^{-1}, number of dots on map, Figure 4), 7.7 pairs ha^{-1} in 2009 (8.5 nests ha^{-1}), 12.3 pairs ha^{-1} in 2010 (30.0 nests ha^{-1}), and 14.6 pairs ha^{-1} in 2011 (15.4 nests ha^{-1}). Breeding density correlated positively with the water level in the pond in spring (rho = 0.75, P = 0.0368). For instance, in 2009 and 2010 the difference in breeding density was great despite the fact that the reed was burned in both years. The difference in water depth near nests was also great (15.0 ± 26.55 cm in 2009 and 91.3 ± 37.77 cm in 2010; Figure 4). The spatial distribution of GRW nests showed aggregation in the first 3 years, while in 2011 a more even distribution of nests was recorded (Figure 4).

In 2009 and in 2010, breeding success was similar in fresh and mixed reed (fresh reed: 0.37; mixed reed: 0.32). Daily survival did not differ between eggs and nestlings in nests built in fresh reed (z = 0.73, P = 0.463; DSR for eggs: 0.96; DSR for nestlings: 0.97), whereas nestlings survived better than eggs in mixed reed (z = 2.64, P = 0.008; DSR for eggs: 0.94; DSR for nestlings: 0.97). In burned years (2009 and 2010), we found that egg and nestling daily survival was significantly higher in the Late group (z = 4.06, P < 0.0001; DSR for eggs and nestlings in the Early group: 0.94; DSR for eggs and nestlings in the Late group: 0.97), while in unburned years there was no difference in egg and nestling survival between the groups (z = 1.35, P = 0.1781; DSR for eggs and nestlings in the Early group: 0.99; DSR for eggs and nestlings in the Late group: 0.98).

4. Discussion

Total breeding success for the 4 studied years (0.431) of GRW on Bager Pond did not differ significantly from that reported in other studies (Petro et al., 1998; Mérő and Žuljević, 2009). At the Heřmanický fishpond (Czech Republic), breeding success was 0.468 (Petro et al., 1998), and on large and small canals in northern Serbia, the average breeding success was 0.420 (Mérő and Žuljević, 2009). Hatching rate (0.927) was higher in our study than that of Heřmanický fishpond (0.653; Petro et al., 1998), but was similar to that of a fishpond in Poland (0.887; Dyrcz, 1981) and to that of canals (0.940; Mérő and Žuljević, 2009). According to Petro et al. (1998), eggs failed to hatch because some of them were not fertilized or the embryos died. Petro et al. (1998) also reported that 7% of the eggs vanished, and a similar proportion was predated or deserted. Our Kaplan–Meier survival curves showed that survival of nests was better in the 3 drier years (2008, 2009, and 2011). Most nest failure occurred in our study due to bad weather conditions, mainly in 2010. The effect of weather may have been both direct (cooling and hypothermia of eggs/nestlings) and indirect (more time spent away by parents to search for food and/or higher activity by predators, resulting in higher nest predation rates). We presume that GRW clutches and nestlings are probably more important sources of food to predators in adverse weather when food is hard to find, e.g., when cold temperatures and rainy weather are present for several days. GRW nestlings are most sensitive to cold and wet weather, followed by low temperatures (Beier, 1981; Fischer, 1994), so if the female parent is away from the nest for a longer time, the body temperature of the chicks will fall and the probability of mortality is higher. In cold and wet weather, the parents need more time to find food and to feed nestlings. Petro et al. (1998) identified 3 sources of nestling mortality: predation (4.3% of all nestlings), desertion (10.4% of all nestlings), and perishing (20.0% of all nestlings). The relatively high percentage of perished nestlings in Petro et al.'s (1998) study refers to chicks that died when the weather was bad during the nestling period.

Mean clutch size was generally higher in similar Central European studies than in this study on Bager Pond or in a previous study of ours on canals in Sombor (Table 4). The mean number of fledglings, however, was similar in this study to that found in most other studies, with the exception of studies by Hudec (1975), Dyrcz (1981), and Mérő and Žuljević (2009) (Table 4).

Studies in the Czech Republic showed that the first eggs were laid in the first (2%), second (24%), and third (57%) 10-day periods of May and the first 10 days (17%) of June (Petro et al., 1998). In our study, breeding began almost 2 weeks later than the first 10-day period of May. One exception was a 4-egg nest in 2011, which was found on 10 May. On the Milicz fishponds (Poland), the mean dates of laying of the first eggs were between 19 and 25 May over 6 years, and this was similar (21–24 May) for those of Swiss lakes, as well (Dyrcz, 1981). The latter results are similar to those of our study, where 69% of nests were found in the Early group. However, our study is special in that egg-laying also occurred in later periods of June, and there were a few nests containing eggs even in July. None of the Central European studies mentioned above reported egg-laying so late in the season.

In this study, the overall survival of eggs differed between the Early and Late groups. However, eggs are better protected than nestlings from rainy and cold weather because the female does not leave the nest as often as in the chick-rearing period. We presume not only that the sensitivity of chicks to cold and rainy weather is

Table 4. Comparative overview of mean clutch sizes and number of fledglings of GRW in Central European studies.

Study area	Country	Clutch size	Number of fledglings	Source
S Moravian ponds	Czech Republic	4.4	3.1	Hudec (1975)
Milicz fishponds	Poland	4.8	2.2	Dyrcz (1981)
Swiss lakes	Switzerland	4.6	3.1	Dyrcz (1981)
Northern Bavaria	Germany	4.7	2.2	Beier (1981)
Heřmanický fishponds	Czech Republic	4.8	2.3	Petro et al. (1998)
Velence Lake	Hungary	4.9	1.7	Batáry and Báldi (2005)
Sombor (canals)	Serbia	3.9	1.0	Mérő and Žuljević (2009)
Bager Pond	Serbia	4.1	2.0	This work

responsible for mortality, but, as we mentioned before, that adverse weather circumstances can result in a food-supply deficit. If we consider the weather circumstances, the years 2009 and 2010 were extremes; 2009 was very dry and 2010 had much precipitation. Water level is an important factor in the breeding of GRW (Figure 3), which can be clearly seen in these 2 years (Figure 4). If there is not enough reed area covered with water, GRW density decreases, because the quality of the breeding site is poor, e.g., breeding density in 2009 was only 7.7 pairs ha^{-1}. In the 2 years (2008 and 2011) when the water depth varied between 60 and 80 cm at the breeding site (Table 1), the number of breeding pairs was much higher (Figure 4).

The low breeding performance in 2010 meant that Bager Pond functioned as an ecological trap in that year. Despite the high breeding density, breeding success was very low due to high precipitation and rapid water level increase. Nevertheless, although water rapidly submerged nests, GRWs did not leave the reed habitat; they even occasionally raised a fourth brood. In an Oregon study, Spotted Towhees, *Pipilo maculatus*, preferred edges for breeding, where fledgling mortality was high due to predation by domestic cats, *Felis catus*, creating a severe ecological trap (Shipley et al., 2013). Several studies have reported ecological traps established through anthropogenic habitat alteration or rapid environmental changes (Kokko and Sutherland, 2001; Battin, 2004; Lengyel, 2006; Robertson, 2012). In our study, GRW had low breeding success in 2010, which had no impact on breeding density and success in the next breeding season. However, there are cases where ecological traps lead to deterministic extinctions (Kokko and Sutherland, 2001).

Mean breeding density was higher in this study than in previous studies. Although reed was burned in 2009 and 2010, the mean breeding density was still relatively high (approximately 10.0 pairs ha^{-1} combined). In 2008 and 2011, when reed was not burned, density was about 4 pairs ha^{-1} higher (13.9 pairs ha^{-1} combined). Nest densities varied between 0.5 and 0.8 nests ha^{-1} at the Heřmanický fishpond between 1975 and 1979 (Petro et al., 1998), between 1.5 and 3.1 pairs ha^{-1} in Poland, and between 0.4 and 2.3 pairs ha^{-1} in Switzerland (Dyrcz, 1981). It seems that breeding density shows fluctuations even in native, unmanaged reed beds; however, we presume that these densities also depend on reed quality. Furthermore, these studies were done on large reed habitats such as lakes and fishponds (Dyrcz, 1981; Petro et al., 1998), where densities differ greatly from canals (12.0 pairs ha^{-1}; Mérő and Žuljević, 2009) and the reed habitat in this study. In our present study, the differences in breeding density are not only caused by reed burning but also by water level fluctuations. When reed is burned, male GRWs arriving back from migration compete for reed patches that remain standing after the burning. New reed gets strong enough for breeding only in mid-June. This difference in available breeding sites could be a reason why most nests were in mixed reed stands (Figure 4). In 2010, nest density was extremely high (30 nests ha^{-1}) because nests were destroyed by windy and rainy weather or were submerged because of rapid water level increase, and many nests were rebuilt close to the failed ones. In contrast, there were no quality breeding sites in 2009 because only small reed patches remained after the burn at the start of the breeding season, and water level was also low. Although we did not find differences in breeding success between fresh (burned areas) or mixed reed, other studies reported that mixed reed is denser and provides easier access for mammal predators (Dyrcz, 1981). Recorded GRW nest predators were the American Mink *Mustella vison* (Bensch, 1993), Marsh Harrier *Circus aeruginosus*, and Little Bittern (Dyrcz, 1981). Disease or loss of one or both parents also can lead to nest failure (Beier, 1981; Fischer, 1994). We found that new reed stems were not yet sturdy enough to hold the nests in the Early group, especially under rainy and windy conditions (personal observation). Our observations agree with previous ones in that GRW predominantly uses microhabitats where thick reed stems grow (Dyrcz, 1981; Graveland, 1998). Dyrcz (1981) also concluded that GRW mainly requires mixed reed for breeding. Other studies also confirm the importance of mixed reed; e.g., the presence of reed passerines was lower in cut reed with much growth of new reed than in uncut mixed reed stands (Báldi and Moskát, 1995; Vadász et al., 2008). However, according to Moga et al. (2010), GRW preferred both burned and unburned reed areas.

Another interesting finding of this study is that clutches laid in the second half of the breeding season were more likely to survive. Our observations suggest that this may be because the weather was more stable and dry for the Late group than for the Early group. A few studies report that earlier clutches in several species are larger and their breeding performance is better (Pied Flycatcher *Ficedula hypoleuca*, Järvinen, 1989; first brood of Barn Swallow *Hirundo rustica*, Møller, 2002), but some species show opposite trends, e.g., Collared Flycatcher *Ficedula albicollis* (Sheldon et al., 2003), Great Tit *Parus major*, and Blue Tit *Parus caeruleus* (Winkel and Hudde, 1997). Studies done on the breeding biology of Lark Bunting, *Calamospiza melanocorys*, concluded that variability of climatic changes (e.g., daily or seasonal precipitation and temperature) affects breeding success during the breeding season (Skagen and Adams, 2012).

Although reed burning probably also affected breeding density, we conclude that water level is primarily responsible for the variable breeding density. Although reed burning did not affect breeding success, nestling survival was generally higher than egg survival in mixed, unmanaged reed. Despite the fact that there were 2 years with more precipitation in the Late than in the Early period (Table 2), breeding success was higher in the Late than in the Early group. In general, precipitation affected breeding success negatively, e.g., through the cooling and hypothermia of eggs and nestlings or the flooding of the nests. Nowadays, reed management and its consequences on the breeding avifauna in reed habitats are important issues in conservation biology. Our results, which fill a gap in the knowledge of the breeding habits of the Great Reed Warbler, thus have high conservation relevance.

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References

Báldi A, Moskát C (1995). Effect of reed burning and cutting on breeding birds. In: Bissonette JA, Krausman PR, editors. Integrating People and Wildlife for a Sustainable Future. Proceedings of the First International Wildlife Management Congress. Bethesda, MD, USA: The Wildlife Society, pp. 637–642.

Báldi A (2001). Factors influencing passerine bird communities breeding in a changing marshland. In: Hoi H, editor. The Ecology of Reedbirds. Vienna, Austria: Austrian Academy of Sciences, pp. 11–25.

Batáry P, Báldi A (2005). Factors affecting the survival of real and artificial Great Reed Warbler's nests. Biologia 60: 215–219.

Battin J (2004). When good animals love bad habitats: ecological traps and the conservation of animal populations. Conserv Biol 18: 1482–1491.

Beier J (1981). Untersuchungen an Drossel- und Teichrohrsanger (*Acrocephalus arundinaceus, A. scirpaceus*): Bestandsentwicklung, Brutbiologie, Ökologie. J Ornithol 122: 209–230 (in German).

Bensch S (1993). Costs, benefits and strategies for females in a polygynous mating system: a study on the Great Reed Warbler. PhD, Department of Ecology, Animal Ecology, Lund University, Lund, Sweden.

Cramp S (1998). The Birds of the Western Palearctic. Oxford, UK: Oxford University Press, CD-ROM.

Dyrcz A (1981). Breeding ecology of Great Reed Warbler *Acrocephalus arundinaceus* and reed warbler *Acrocephalus scirpaceus* at fishponds in SW Poland and lakes in NW Switzerland. Acta Ornithol 18: 307–334.

Fischer S (1994). Einfluss der Witterung auf den Bruterfolg des Drosselrohrsängers *Acrocephalus arundinaceus* am Berliner Miiggelsee. Vogelwelt 115: 287–292 (in German).

Graveland J (1998). Reed die-back, water level management and the decline of the great reed warbler *Acrocephalus arundinaceus* in the Netherlands. Ardea 86: 187–201.

Hensler GL, Nichols JD (1981). The Mayfield method for estimating nesting success: a model, estimators and simulation results. Wilson Bull 93: 42–53.

Hudec K (1975). Density and breeding of birds in the reed swamps of southern Moravian ponds. Acta Sci Nat Brno 9: 1–40.

Järvinen A (1989). Pattern and causes of long-term variation in reproductive traits of the pied flycatcher *Ficedula hypoleuca* in Finnish Lapland. Ornis Fennica 66: 24–31.

Johnson DH (1979). Estimating nest success: the Mayfield method and an alternative. Auk 96: 651–661.

Kokko H, Sutherland WJ (2001). Ecological traps in changing environments: Ecological and evolutionary consequences of a behaviourally mediated Allee effect. Evol Ecol Res 3: 537–551.

Lengyel S (2006). Spatial differences in breeding success in the Pied Avocet (*Recurvirostra avosetta*): effects of habitat on hatching success and chick survival. J Avian Biol 37: 381–395.

Lloyd JD, Tewksbury JJ (2007). Analyzing avian nest survival in forest and grasslands: a comparison of the Mayfield and logistic-exposure methods. Stud Avian Biol 34: 96–104.

Mayfield H (1975). Suggestions for calculating nest success. Wilson Bull 87: 456–466.

Mérő TO, Žuljević A (2009). Breeding density and breeding success of the Great Reed Warbler *Acrocephalus arundinaceus* in Sombor municipality. Ciconia 18: 91–98.

Moga CI, Öllerer K, Hartel T (2010). The effect of reed burn on the habitat occupancy of passerine species. North-West J Zool 6: 90–94.

Møller AP (2002). North Atlantic Oscillation (NAO) effects of climate on the relative importance of first and second clutches in a migratory passerine bird. J Anim Ecol 71: 201–210.

Petro R, Literak I, Honza M (1998). Breeding biology and migration of the Great Reed Warbler *Acrocephalus arundinaceus* in the Czech Silesia. Biologia 53: 685–694.

Prokešová J, Kocian Ľ (2004). Habitat selection of two *Acrocephalus* warblers breeding in reed beds near Malacky (Western Slovakia). Biologia 59: 637–644.

R Development Core Team (2011). A Language and Environment for Statistical Computing. Vienna, Austria: R Foundation for Statistical Computing.

Robertson BA (2012). Investigating targets of avian habitat management to eliminate an ecological trap. Avian Cons Ecol 7: 2.

Sheldon BC, Kruuk LE, Merilä J (2003). Natural selection and inheritance of breeding time and clutch size in the collared flycatcher. Evolution 57: 406–420.

Shipley AA, Murphy MT, Elzinga AH (2013). Residential edges as ecological traps: postfledging survival of a ground-nesting passerine in a forested urban park. The Auk 130: 501–511.

Skagen SK, Adams AAY (2012). Weather effects on avian breeding performance and implication of climate change. Ecol Appl 22: 1131–1145.

Tomić P (1996). Klima. In: Đuričić J, editor. Opština Sombor. Novi Sad, Serbia: Prirodno - matematički fakultet, Institut za geografiju & Prosveta, pp. 16–21 (in Serbian).

Uzun A, Ayyıldız Z, Yılmaz F, Uzun B, Sağıroğlu M (2014). Breeding ecology and behavior of the Great Reed Warbler, *Acrocephalus arundinaceus*, in Poyrazlar Lake, Turkey. Turk J Zool 38: 55–60.

Vadász C, Német Á, Biró C, Csörgő T (2008). The effect of reed cutting on the abundance and diversity of breeding passerines. Acta Zool Hung 54: 177–188.

Winkel W, Hudde H (1997). Long-term trends in reproductive traits of tits (*Parus major*, *Parus caeruleus*) and pied flycatchers *Ficedula hypoleuca*. J Avian Biol 28: 187–190.

Woithon A, Schmieder K (2004). Bruthabitatmodellierung für den Drosselrohrsänger (*Acrocephalus arundinaceus* L.) als Bestandteil eines integrativen Managementsystems für Seeufer. Limnologica 34: 132–139 (in German).