Factors influencing low incidence of double brooding in the Great Reed Warbler

Alfréd Trnka[1] · Peter Samaš[2]

Abstract

Double brooding, the laying of a second clutch after successfully fledging young from a first nest in a season, is a common reproductive strategy among short-lived birds to increase annual breeding success. Nevertheless, there is widespread intra- and interspecific variation in the probability of producing a second clutch. Given that the frequency of double brooding could affect population growth rate, knowing what factors contribute to this phenomenon is also important in the conservation management of threatened facultative double-brooded species. Here, we examine the frequency of double brooding and the factors affecting the probability of this reproductive strategy in a population of the Great Reed Warbler, *Acrocephalus arundinaceus*, in south-western Slovakia. Results of a 15-year study (2008–2022) revealed low overall rate of double brooding in the Great Reed Warbler (5.6% per year, 0–15.4%). The length of breeding season, timing of the first clutch laying date and the size of the first broods were key factors influencing the female's decision to initiate a second clutch. On the other hand, successful brood parasitism did not affect second clutch initiation, which contrasts with our prediction. Given that only monogamous or primary females initiated a second clutch after successfully rearing a first one, we assume that producing two broods within the same season may be an alternative strategy for monogamous males to increase their annual reproductive output in this facultatively polygynous species. Therefore, due to relatively high rate of polygyny, we probably cannot expect higher rate of double broodings in the Great Reed Warbler in the future either.

Keywords Multiple brooding · Mating system · Brood parasitism · Great Reed Warbler · *Acrocephalus arundinaceus*

Zusammenfassung

Ursachen für die geringe Frequenz von Zweitbruten bei Drosselrohrsängern

Zweitbruten, d.h. erneutes Brüten nach erfolgreichem Ausfliegen der ersten Brut, ist eine nicht seltene Fortpflanzungsstrategie kurzlebiger Vögel mit dem Ziel, die Zahl ihrer Nachkommen zu steigern. Allerdings variiert die Wahrscheinlichkeit für Zweitbruten sowohl inter- als auch intraspezifisch beträchtlich. Falls die Häufigkeit von Zweitbruten das Populationswachstum beeinflusst, wäre es gerade bei Arten mit Bestandsrückgängen wichtig, die Einflussfaktoren für Zweitbruten zu analysieren. Dies wäre für wirkungsvolle Schutzkonzepte wichtig. Deshalb werden in der vorliegenden Studie die Frequenz von Zweitbruten und deren potentielle Einflussfaktoren bei Drosselrohrsängern *Acrocephalus arundinaceus* im SW der Slowakei untersucht. Die Ergebnisse dieser Langzeitstudie über 15 Jahre (2008–2022) zeigen, dass Zweitbruten eher selten gezeitigt werden (5,6% pro Jahr, Variationsbreite 0–15,4%). Länge der Brutsaison, Legebeginn und Größe der ersten Brut (Zahl der Nestlinge) waren die wichtigsten Faktoren für die Entscheidung individueller Weibchen zur Zweitbrut. Im Gegensatz zur Vorhersage hatte die erfolgreiche Aufzucht eines Kuckucks in der ersten Brut keinen Einfluss auf die Entscheidung für

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✉ Alfréd Trnka
  atrnka@truni.sk

1 Department of Biology, University of Trnava, Priemyselná 4, 91843 Trnava, Slovakia

2 Institute of Vertebrate Biology, Czech Academy of Sciences, Květná 8, 60365 Brno, Czech Republic

eine Zweitbrut. Nur Weibchen von monogamen Männchen und Erstweibchen von polygynen Männchen starteten nach erfolgreicher Erstbrut eine zweite Brut. Beim Paarungssystem des Drosselrohrsängers handelt es sich um fakultative Polygynie. Offensichtlich existieren zwei unterschiedliche Strategien der Männchen. Polygyne Männchen erhöhen die Zahl ihrer Nachkommen durch Paarbildung mit zwei oder drei Weibchen, monogamen Männchen gelingt dies über Zweitbruten. Da der Anteil polygyner Männchen in der Population hoch ist, bleibt die Rate von Zweitbruten gering.

Introduction

Life history theory predicts that short-lived species should invest more in their current breeding attempt as they may have no further possibility to reproduce (Drent and Daan 1980). Therefore, a good strategy to maximize their fitness is producing two or even more clutches within the same breeding season (Verhulst et al. 1997; Nagy and Holmes 2005a; Naef-Daenzer et al. 2011). Such multiple brooding has been documented in a variety of birds, mainly passerines (Jacobs et al. 2013; Cornel and Wiliams 2016). In many species, however, not all individuals have more than one brood in a season, and the proportion of multi-brooded pairs often varies between years (Verboven and Verhulst 1996; Carro et al. 2014). Given that frequency of multiple brooding potentially could have important effects on population dynamics, knowing what and how it contributes to this phenomenon may be important in the conservation management of many threatened facultative multiple-brooded species (Husby et al. 2009; Jackson and Cresswell 2017). Despite this, factors that determine the decision of females to initiate multiple-breeding attempts per season still remain poorly understood.

Previous studies have reported several factors potentially influencing the likelihood of multiple brooding in birds, but there is little consensus as to which of them is most important for the evolution and maintenance of this life history trait. The timing of the first brood is considered one of these factors (O'Brien and Dawson 2013; Zając et al. 2015; Jackson and Cresswell 2017; but see Nagy and Holmes 2005a; Cornell and Williams 2016; Nomi et al. 2018). This is because early-breeding females have more time to rear a second brood that can still be synchronous with the seasonal peak in food supply (Verboven and Verhulst 1996; Husby et al. 2009). However, the fact that a significant number of females laying their first eggs early did not have a second clutch suggests that other factors may interact with the timing of breeding. Such factors include body condition, age and breeding experience of the parents (quality hypothesis, O'Brien and Dawson 2013, Hoffman et al. 2015, but see Odgen and Stutchbury 1996; Nagy and Holmes 2005a), size of the first clutch (Tinbergen and Dann 1990; Verboven and Verhulst 1996; Parejo and Danchin 2006; but see Jacobs et al. 2013), male provisioning behaviour (Grüebler and Naef-Daenzer 2008; Nomi et al. 2018) and food availability (Verboven et al. 2001; Nagy and Holmes 2005b).

Multiple-brooded species may also benefit from the long-term warming associated with global climate change (Halupka et al. 2008; Dunn and Møller 2014; Halupka and Halupka 2017). However, some species did not respond to increasing temperatures with an increased frequency of extra broods (Husby et al. 2009). For example, Halupka et al. (2021) found that facultatively double-brooded Reed Warbler (*Acrocephalus scirpaceus*) females significantly increased the proportion of second broods over the 30-year period. However, in the closely related Great Reed Warbler (*Acrocephalus arundinaceus*) that nested in the same habitat and over the same time period, despite shifting laying dates (Dyrcz and Czyż 2018), the double brooding probably remained rare (Dyrcz and Halupka 2009; Dyrcz and Czyż 2018). Uncovering the causes of this phenomenon can therefore help better understand the determinants of multiple brooding in long-distance migratory passerines.

Here we analyzed breeding data collected over 15 years (2008–2022) in a colour-marked population of the Great Reed Warbler in south-western Slovakia to examine the frequency of double brooding, defined as the initiation of a second clutch after successfully rearing a first one (Jacobs et al. 2013), and the factors affecting the probability of such behavior in this species. Specifically, we tested for an effect of local spring temperature, spring total precipitation, laying date, clutch size and number of young fledged from the first clutch, brood parasitism and nest failure rates, length of the breeding season and female body condition. In addition, we also looked at how females that produced second broods differ in tested variables from single-brooded females. We predicted that double-brooded females should nest earlier and be in better condition but produce smaller clutches and fewer fledglings from their first nests than single-brooded females (Tinbergen and Daan 1990; Nagy and Holmes 2005a). As the Great Reed Warbler is a frequently parasitized host of the Common Cuckoo (*Cuculus canorus*), which entails high costs to parents in terms of time and energy expenditures (Davies 2000; but see Samaš et al. 2018), and has a facultatively polygynous mating system in which females of polygynous males receive significantly less male assistance with parental duties than monogamous females (Sejberg et al. 2000; Trnka and Prokop 2010; Požgayová et al. 2013), we also predicted that double-brooded females should be monogamous and were not successfully parasitized (i.e.

successfully reared the Common Cuckoo young) in their first nesting attempt.

Methods

Study site and study species

The Great Reed Warbler is a medium size (31 g) insectivorous passerine, one of the largest species in the family Acrocephalidae, breeding throughout mainland Europe and the west Palearctic and wintering in Sub-Saharan Africa (Cramp 1992; Leisler and Schulze-Hagen 2011). Birds arrive on their breeding grounds in mid-April—early May, males typically earlier than females, and start laying eggs in May, continuing until late July. It is a facultatively polygynous species, the rates of social polygyny (i.e., percentage of polygynous males) ranges between 8 and 56% (Catchpole et al. 1985; Hasselquist 1998; Leisler and Wink 2000). Only the female builds the nest and incubates the clutch, however, both female and male contribute to raising the brood (Požgayová et al. 2009; Trnka and Grim 2013). Females breed usually once a year, double brooding has so far been documented only rarely in Poland, Switzerland, Slovakia and the Czech Republic (3–8%, Trnka 2011). In Central Europe, the Great Reed Warbler is one of the most widespread cuckoo hosts, with parasitism rate (the percentage of nests in which cuckoo eggs were laid) ranging from 0 to 68% (Moskát et al. 2008; Trnka et al. 2012).

The study was conducted over 15 years (2008–2022) in a fishpond system near Štúrovo, south-western Slovakia (47°51′ N 18°36′ E, 114–116 m a.s.l.). The overall study area was ca. 45 ha. For a detailed description of the study site see, e.g. Trnka and Prokop (2010). Great Reed Warblers breed there in relatively narrow (approximately 3–10 m wide) strips of the Common Reed (*Phragmites australis*) that border the ponds. During the study period, Great Reed Warbler population comprised 18–56 pairs (i.e. breeding females). The rate of polygyny varied from 21 to 43%, and the rate of brood parasitism from 0 to 49%. The rate of successful parasitism (the percentage of nests that successfully fledged the cuckoo) averaged 16.7% and the percentage of nest failures (predated or destroyed nests) ranged between 10 and 44%. The Great Reed Warbler is the only breeding species of the genus *Acrocephalus* in the studied locality. Other reed-nesting passerines included the Reed Bunting (*Emberiza schoeniclus*) and Savi's Warbler (*Locustella luscinioides*).

General field procedures

Each year, we mist-netted adult birds during the territory establishment (males) or captured them at or near their nests during the nest-building or egg-laying stages (females). We marked all captured birds with one aluminium ring and a unique combination of two or three coloured plastic rings for visual identification. We also measured their body mass using an electronic balance (accuracy: 0.1 g) and tarsus length (minimal) using a digital calliper to the nearest 0.01 mm. We then calculated the body condition index as residuals from the regression of mass on tarsus length to estimate female quality. To locate Great Reed Warbler nests, we systematically searched the reed beds at 4–5 day intervals from May to late July. Each found nest was then checked at 1–2 day intervals to determine the day of clutch completion, the final clutch size and to detect the presence of a cuckoo egg (for details see Trnka et al. 2012). Since we found almost all nests during nest building or egg-laying, the onset of laying was assessed directly, in exceptional cases, it was recalculated according to the date of hatching. For each nest, we recorded the brood size when the nestlings were 10 days old. Annual productivity was calculated as the total number of young fledged across all nesting attempts made by a given female. The social mating status of each female and her mate was determined based on their captures at the nests during the nest building or egg-laying stages and confirmed it repeatedly throughout a season by direct observations of colour-ringed birds defending their nests or feeding their young. We defined a female as double-brooded if it produced at least one fledgling during its first breeding attempt and initiated egg laying in a second nest in the same breeding season (see also Husby et al. 2009; Grüebler and Naef-Daenzer 2010; Jacobs et al. 2013; Carro et al. 2014). We then calculated the rate of double brooding as the proportion of double-brooded females per all individually marked females that attempted to nest for each study year. The length of the breeding period we defined for all first broods as time interval between the first egg laid to last young fledged or last nest failure (see also Halupka et al. 2021).

The meteorological data (mean temperature and total precipitation during the months of April – July) were obtained from the nearest national climate station (the city Hurbanovo) located 28 km west of the study site.

We included in the analysis the data on 459 breeding events by 355 individually colour-ringed females, of which 63 (17.8%) females were recorded breeding in two seasons, 26 (7.3%) in three seasons, 7 (1.9%) in four seasons, 4 (1.1%) in five seasons and 4 (1.1%) in six seasons.

Table 1 Output of full and final general linear model with binomial distribution testing effect of breeding and environmental variables on the probability of double brooding in the Great Reed Warbler during 15 breeding seasons (2008–2022)

Model	Parameter	Estimate ± SE	Chi-square	P
Full				
	Intercept	-27.51 ± 131.6	0.04	0.834
	Year	0.01 ± 0.06	0.02	0.879
	First egg laid	0.07 ± 0.07	0.93	0.335
	Length of breeding season	0.06 ± 0.05	1.50	0.220
	Nest failure rate	-0.01 ± 0.04	0.09	0.768
	Parasitism rate	0.003 ± 0.03	0.02	0.898
	Temperature	0.07 ± 0.50	0.02	0.890
	Precipitation	-0.004 ± 0.005	0.57	0.451
Final				
	Intercept	-6.93 ± 1.57	19.564	<0.001
	Length of breeding season	0.08 ± 0.03	7.610	0.006

Statistical analysis

At the season level, we used a generalized linear model with binomial distribution to test the effects of breeding and environmental variables on the probability of double breeding. Predictors included year, median of the first egg laid in the breeding season (1 = 1st May), length of breeding season (in days), annual nest failure rate, annual parasitism rate, average temperature (°C) and total precipitation (mm) during the months of April–July.

Marginal means estimated by a linear model were calculated using the R package emmeans v. 1.7.5 (Lenth 2022). We presented outputs of full and final models. Final model was the one with the lowest AIC_c. Potential collinearity among the covariates was low, variance inflation factors were < 2.5 in all cases (Zuur et al. 2010). We performed model residual diagnostics with R package DHARMa v. 0.3.3.0 (Hartig 2020).

At the individual level, we used the non-parametric Mann–Whitney U test due to the unequal sample sizes of the tested variables. Egg laying date, clutch size, brood size, time between initiation dates of first and second clutches, body condition index and annual productivity are presented as mean ± SD unless stated otherwise. All statistical analyses were conducted in R v. 4.1.3 (R Core Team 2020).

Results

Over the 15 years of study, we recorded only 26 cases of double brooding in the Great Reed Warbler population, which represents 5.6% of 459 breeding histories observed in the study site. Two females produced two broods in the same season in two consecutive years. Double-brooded females usually re-nested with the same mate (23/26), only 3 females changed their mates for the second brood in the

same breeding season. Rates of double brooding ranged from 0 to 15.4% (Table 1, Fig. 1).

In the double-brooded females, the mean laying date of the first breeding attempts was 12 May (mean ± SD = 11.73 ± 6.74, range: 27 April–29 May), mean laying date of the second breeding attempts was 26 June (mean ± SD = 56.77 ± 6.44, range: 8 June–6 July). The mean time between laying date of first and second clutches was 45 days (mean ± SD = 45.05 ± 7.56, range: 32–66). Clutch size in the first breeding attempt (mean ± SD = 4.89 ± 0.65, range: 4–7) of double-brooders was significantly larger than in the second breeding attempt (mean ± SD = 4.04 ± 0.60, range: 3–5; Welch's t-test: $t_{25} = 4.7$, $p < 0.001$), and this difference might be even bigger due to cuckoo egg rejection. Brood size in the first breeding attempt (mean ± SD = 2.92 ± 1.90, range: 0–5) had a non-significant tendency to be higher than in the second breeding attempt (mean ± SD = 2.19 ± 1.74, range: 0–5; Welch's t-test: $t_{25} = 1.78$, $p = 0.09$). Double-brooded females fledged the Common Cuckoo with similar rates in their first (6 out of 26 nests) and second nests (2 out of 26 nests; Fisher's exact
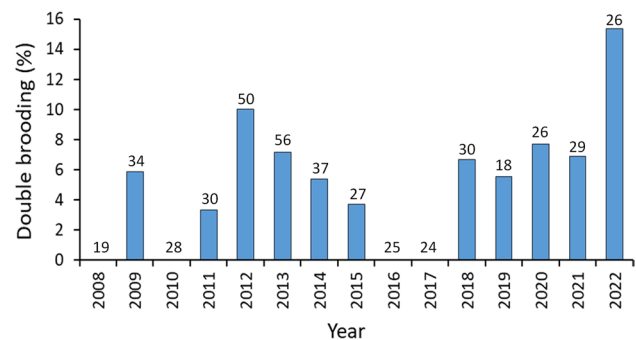

Fig. 1 The percentage of breeding Great Reed Warbler females that initiated a second clutch after successfully raising a first clutch for each year from 2008 to 2022. Numbers at the top of the bars indicate sample size (total number of females)

Table 2 Selected breeding and individual parameters of Great Reed Warbler females and Mann–Whitney test outputs on difference in these parameters between single-brooded females that succeeded with their first breeding attempt and double-brooded females

Parameter	Single-brooder		Double-brooder		Test	
	N	mean ± SD	N	mean ± SD	W	P
Egg laying date	331	22.49 ± 8.94	24	11.12 ± 6.49*	1039	< 0.001
Clutch size*	306	4.84 ± 0.53	24	4.88 ± 0.68	3649	0.95
Brood size*	237	4.19 ± 0.85	24	3.29 ± 1.43	1858	0.003
Body condition index	188	0.06 ± 1.83	24	−0.48 ± 1.94	1926	0.25
Annual productivity	206	3.21 ± 0.89	24	5.46 ± 2.50	3760	< 0.001

*May nests (or first nests in double-brooded females) only

test: $p = 0.25$), in one case both the first nest and the second nest of the same female were successfully parasitized. The rate of successful brood parasitism did not differ between first nests of double-brooded females and the nests of single-brooded females (23.1% vs 16.9%, respectively, $\chi^2 = 0.65$, df = 1, $p = 0.42$). Out of 26 first nests, 20 were nests of monogamous females and 6 of primary females, all second nests were monogamous. No secondary female initiated a second clutch in the same breeding season. The proportion of females mated with polygynous males in their first nesting attempt differs significantly between double-brooded and single-brooded females (23.1% vs 47.4%, respectively, $\chi^2 = 5.83$, df = 1, $p < 0.05$).

GLM showed that only length of breeding season was important in predicting double brooding in the Great Reed Warblers. Other environmental and breeding parameters had no effect on the probability of being a double-brooder (Table 1).

Comparisons of parameters between first breeding attempts in single-brooded and double-brooded females (Table 2) showed that double-brooded females did not differ from single-brooders neither in the clutch size nor in the body condition index. However, double-brooded females started breeding approximately 10 days earlier in the season and had significantly lower brood size at fledging from their first nests compared to nests of single-brooded females. For the potential effect of the brood size on the probability of double brooding see also Fig. 2. Their mean annual productivity was almost twice as high as for all single-brooded females.

Discussion

Results of our long-term study revealed a relatively low rate of double brooding in the local Great Reed Warbler population in Slovakia, which is, however, comparable to that found in the other populations of this species in earlier years (1970–1976, Dyrcz 1981). This finding is in contrast to the significant increase of second broods (from 2.7 to 23.6% between 1980s and the current century) in a closely related species breeding in the same habitat, the Reed Warbler.

However, this should be taken with caution considering species-specific differences between the two species in their body size and life history traits with different migration strategies. For example, the other closely related *Acrocephalus* species, the Marsh Warbler (*Acrocephalus palustris*) as the furthest migrant with the shortest stay in the breeding area is almost exclusively a single-brooded. In any case, the pattern observed in the Reed Warbler is supposed to be a result of the extension of the breeding season due to global climate change (Halupka et al. 2021). Similarly, GLM model showed that the length of breeding season was the most important factor affecting the probability of producing a second brood by the Great Reed Warbler females as well. However, our study was carried out only in the period of the last 15 years, during which no significant changes in the mean temperature and total precipitation were detected (results not shown). Therefore, we cannot confirm that our findings are the result of global warming. On the other hand, Halupka and Halupka (2017) in their meta-analysis revealed that changes in the duration of the breeding season are not directly related to changes in mean laying dates but rather they are affected by local climatic variables. Thus, the length of the breeding
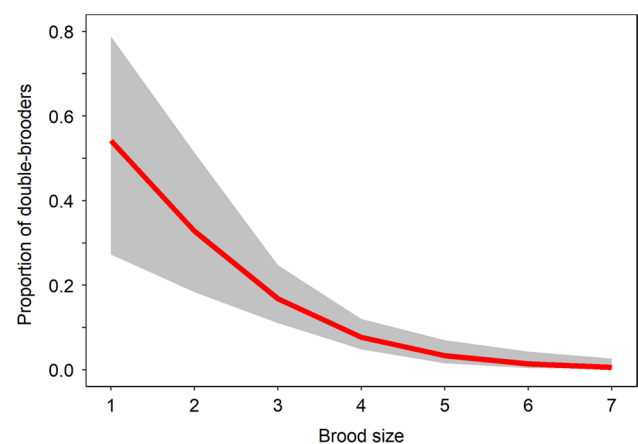

Fig. 2 The effect of brood size (the number of 10-day-old nestlings per nest) in the first breeding attempt on the probability of double brooding in the Great Reed Warbler. Predicted line with 95% confidence bands are estimated from a generalized linear model with binomial distribution

season and the weather during that period could influence whether or not a female attempts a second brood. Given that we used only rough-scaled meteorological data in our study, additional more detailed studies are needed to support this claim. In the Great Reed Warbler, the situation is further complicated by the fact that most of the nests are initiated in a very short period of time at the beginning of the season, thereby compressing the main breeding season and potentially masking the effect of the weather during the entire breeding season on the double brooding (see also Schaefer et al. 2006; Dyrcz and Halupka 2009).

Nevertheless, a comparison of selected breeding and individual parameters between double-brooded and single-brooded females indicated that early timing of the initiation of the first clutch may also play a significant role in double brooding, which is in accordance with our predictions. It seems reasonable to assume that early breeding allows females to extend the length of their breeding season and, consequently, to have more time to raise second broods.

The second important finding is that double-brooded females had significantly lower brood size at fledging from their first nests than single-brooded females. The reasons for this are unknown and further research is needed to reveal them. However, given that clutch sizes of single- and double-brooders were almost identical, this may be caused by partial egg losses due to cuckoo egg rejection, increased number of sterile eggs, etc. This finding suggests that not clutch size, as stated in the other literature (Verboven and Verhulst 1996; Nagy and Holmes 2005a), but final brood size seems to be a more significant predictor of the occurrence of double brooding in the study Great Reed Warbler population, which could also depend on the energetic reserves of individual females. Hence, females seem not to make decisions to double brood already when laying their first clutches. That likelihood of double brooding decreased as the number of fledglings from the first nest increased has also been experimentally shown in the other bird species (Parejo and Danchin 2006; Siefferman and Hill 2008). Successful brood parasitism, on the other hand, did not affect second clutch initiation since almost a quarter of females that attempted additional brood successfully fledged a parasitic chick in their first nest. This, as well as the fact that the Great Reed Warblers successfully fledged a cuckoo nestling in the nest twice in one nesting season also suggests that the cuckoo parasitism is not as costly to this host species as previously thought (see also Samaš et al. 2019 for the Reed Warbler). However, considering that raising more young in the first nesting attempt is usually associated with higher costs in terms of time and energy, we suggest that the trade-off between fecundity and energy allocated to reproduction in order to achieve the highest possible production of young in a given season may have influenced the decision of females to initiate another brood. On the other hand, double brooding may be associated with higher costs in terms of the reduced survival of double brooding females, delaying migration and the acquisition of a winter territory, reduced body condition of fledglings from the first or second broods and their lowered recruitment probabilities (Verhulst 1998; Siefferman and Hill 2008; Hoffman et al. 2015). However, given that other studies have revealed no (Ogden and Stutchbury 1996; Carro et al. 2014) or even positive relationship (Hoffman et al. 2015) between the number of young in the first clutch and the probability of double brooding, additional studies are needed to support the suggestion mentioned above.

Still, as double-brooded Great Reed Warbler females were found to produce almost twice as many chicks as females that bred only once per breeding season in our study population, it could be expected that double brooding would be a more common strategy in this species, as was also found in the other bird species (Hoffmann et al. 2015; Cornell and Williams 2016). We can therefore speculate, for example, that only the highest-quality females may produce two broods within the same season as they may be better able to sustain the energetic investment entailed by double brooding (O'Brien and Dawson 2013; Hoffmann et al. 2015). Nevertheless, we found no significant difference in individual quality between females who produced two broods and those raising only one brood within the same breeding season, although there may be other parameters of body condition such as endoparasite load (e.g. blood haemosporidian parasites, Asghar et al. 2015) that could influence the likelihood of double brooding in this species.

However, based on a comparison of the breeding and mating strategies in the Great Reed Warbler and the closely related Reed Warbler that markedly increased the rate of double brooding in the current century, we hypothesize that different sex-specific parental care strategies and polygynous mating system may be major limiting constraints on the double brooding rate in the Great Reed Warbler. While Central European populations of the Reed Warbler are almost exclusively monogamous (Halupka et al. 2014), with both sexes incubating eggs and feeding the young (Cramp 1992; Klimczuk et al. 2015), the Great Reed Warbler is a facultatively polygynous species in which the male never incubates the eggs and contributes less also to other aspects of parental care, in particular nestling provisioning (Sejberg et al. 2000; Požgayová et al. 2013). Thus, given that Great Reed Warbler females receive less male assistance in parental care than Reed Warbler females, they are also less likely to be double-brooded. The rationale is that male contribution to parental care may reduce the reproductive effort of females and allow them to allocate more energy to additional broods (Nomi et al. 2018). Thus, only females mated with monogamous males that typically provide more parental care to their mates than polygynous males may be capable of double brooding, as we also found in our study population. Which

strategy is more successful for males, i.e. monogamous male with double-brooded female or polygynous male with two single-brooded females, is a challenge for further research.

In conclusion, Great Reed Warblers exhibited low rates of double brooding compared to other double-brooded passerines. Since females initiated a second brood in almost all cases with the same male, double brooding may be an alternative strategy for monogamous males to increase their annual reproductive success. This can primarily be explained by reduced male contribution to parental care due to the different interests of both sexes (Clutton-Brock 1991), but other factors such as the length of breeding season and the small brood size of first nest may influence whether a female will produce two broods in one breeding season. However, we could not evaluate differences in survival rates between double-brooded and single-brooded females and their offspring due to low return rates of adult females and fledglings to our study area (23–24% and 3%, respectively, Trnka and Trnka 2014, this study). Therefore, additional studies assessing the fitness consequences of double brooding in this species are necessary. Moreover, as the incidence and rate of double brooding may also vary considerably between populations of double-brooded species (Bukor et al. 2022), no definite conclusion can be made without more studies conducted on the other Great Reed Warbler populations in various environmental conditions. So far, however, it seems that producing two broods within the same season is still costly for the Great Reed Warbler females, and therefore, we probably cannot expect a higher rate of double broodings in this species in the future either.

Declarations

Conflict of interest The authors declare that they have no competing interests.

Ethical approval The study was conducted in compliance with the law of Slovakia. The licences and permissions to handle and ring the birds were issued by the Ministry of Environment of the Slovak Republic (number 3320/2019–6.3).

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