

Fitness consequences of longer breeding seasons of a migratory passerine under changing climatic conditions

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Abstract

1. Numerous studies have shown that climate change affects the timing of migration and bird laying dates, but the resulting changes in the duration of breeding seasons and their fitness consequences remain largely unknown.
2. We compared breeding parameters of 343 individually marked female Eurasian reed warblers, a multi-brooded migratory passerine, studied in the same area in 1980–1983 and 2005–2012. The latter period was warmer, with mean temperatures during the breeding season higher by 1.5°C on average. As, in recent years, birds arrive earlier from wintering areas and the breeding season of the population is longer, we hypothesized it should result in the increased re-nesting opportunities of individual females.
3. We found that breeding periods of individual females (from building of the first nest till the end of caring for last fledglings/last nest failure) in the current century have extended by 2 weeks compared to the 1980s. In the 2000s, females produced 75% more fledglings annually than females in the 1980s (2.8 vs. 1.6, respectively). The proportion of females raising second broods increased from 2.7% to 23.6% between the first and the second study period while the share of females that did not produce any young annually decreased from 48.1% to 15.5%. The higher offspring production in recent years was related to more successfully fledged broods and an earlier start of breeding, which secured more time to re-nest.
4. Higher female parental effort in recent years was not manifested in the reduction of the female apparent survival: it was almost identical in the two study periods (0.30 vs. 0.31).
5. We conclude that prolonged reproductive seasons might be beneficial for some species. Identifying causes and consequences of changes in the duration of breeding seasons may be essential to predict demography of populations under changing climatic conditions.

KEYWORDS

Acrocephalus scirpaceus, climate change, duration of breeding season, Eurasian reed warbler, fitness consequences, offspring production, second broods, survival

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1 | INTRODUCTION

During the past few decades, the Earth's climate has been rapidly changing, as manifested by the increase in ambient temperatures, changes in rainfall patterns, the occurrence of extreme weather events and other phenomena (Houghton, 2015). Rising temperatures result in shifts of climatic zones (Jylhä et al., 2010) and hence they alter conditions animals experience at their breeding grounds. Numerous research has provided evidence that various organisms, including birds, respond to rising temperatures (Crick & Sparks, 1999; Halupka, Czyż, et al., 2020; Radchuk et al., 2019; Usui et al., 2017).

So far, most avian studies regarding climate-driven changes in breeding biology have focused on changes in arrival and laying dates (Ambrosini et al., 2019; Dunn & Winkler, 2010; Usui et al., 2017). After two decades of research, it is clear that arrival from the wintering grounds and laying dates have advanced in many species, and greater advances in laying are usually associated with larger increases in temperatures (Dunn & Møller, 2014; Radchuk et al., 2019). Climatic factors may also affect the earliest and latest laying dates (marking the start and cessation of breeding) and hence the duration of avian breeding seasons (Hällfors et al., 2020; Møller et al., 2010), but opposite patterns have been detected for single- and multi-brooded species (reviewed by Halupka & Halupka, 2017). Single-brooded species were found to have shorter seasons while multi-brooded species were found to have longer seasons in response to climate change (Halupka & Halupka, 2017). Lengthening of the breeding season in multi-brooded species increases re-nesting potential and leads to higher young production, as in multi-brooded species the number of breeding attempts in a year is a major determinant of an individual's fecundity (Nagy & Holmes, 2005; Townsend et al., 2013). However, studies investigating relationships between climate-driven changes in breeding season duration (start and cessation dates) and productivity are extremely rare. One of these research revealed that long-tailed tits significantly advanced egg-laying termination dates, which resulted in the reduction of breeding season duration (Gullet et al., 2013). The authors estimated this should result in a substantial loss of reproductive opportunity. Another study has found that barn swallows increased fledging success across time, which was linked to a longer inter-clutch interval (Møller, 2007). A few other long-term studies investigated links between the initiation/cessation of laying dates and fecundity, although the temperatures and/or phenology of the studied bird species have not changed over time. Thus, black-throated blue warblers started nesting earlier in warmer years, and early breeders were more likely to attempt a second brood (Townsend et al., 2013). The authors, however, did not detect any trend in temperature or mean first laying dates across years. In a population of song sparrows, the duration of breeding period strongly affected female annual fecundity, but no consistent temporal pattern in laying dates and the duration of breeding season has been found (Tarwater & Arcese, 2018). Likewise, in Australian fairy-wrens earlier laying dates were associated with a higher number of young produced in a season by successful females but the authors did not find temporal trends in phenology or climate during

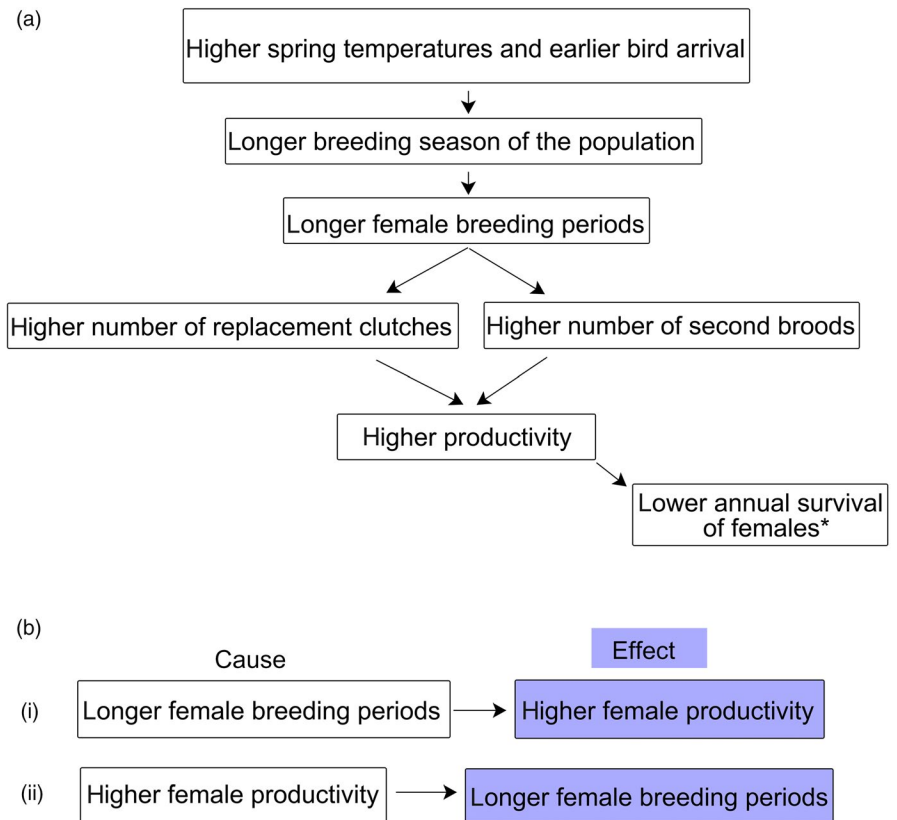
their study period (Lv et al., 2019). Female prothonotary warblers increased the proportion of second broods across time, but it was not related to changes in laying dates (Bulluck et al., 2013). All these studies demonstrated that an earlier start of breeding and/or longer breeding season were associated with higher production of young by breeding females, but they did not find consistent changes in spring temperatures across years. Therefore, the fecundity effects of changing breeding season duration remain still unknown from the areas where climatic conditions have changed.

If individuals stay longer at their breeding grounds and allocate more resources towards reproduction, their increased reproductive effort may lead to a fitness cost manifested by reduced survival and/or a decreased future reproductive output (Williams, 1966). This hypothesis has been tested in many experimental studies, but their results were equivocal (reviewed by Bleu et al., 2016; Santos & Nakagawa, 2012). It has been argued that the lack of the expected relationships might result from fluctuations in resource availability, individual quality or age (van Noordwijk & de Jong, 1986; Santos & Nakagawa, 2012). Furthermore, it seems that characteristics related to body size (and hence life span, age at maturity and fecundity) may play a role (Bleu et al., 2016; Hamel et al., 2010). Bleu et al. (2016) found that bird species showing survival costs of high reproductive effort had on average shorter life span than species suffering from fecundity costs of reproduction.

In our previous paper (Halupka et al., 2008), we provided evidence that Eurasian reed warblers *Acrocephalus scirpaceus* from our study population started arriving earlier from wintering areas and advanced the initiation of breeding, which corresponded with the considerable increases in ambient temperatures. Because the timing of cessation of laying remained unchanged across years, this resulted in the extension of breeding seasons of the whole population. We suggested that it should increase re-nesting opportunities and hence the population productivity.

The aim of this study was to verify whether the extension of breeding season observed at the level of population across the last several decades has affected breeding parameters of reed warbler females studied in two study periods: the 1980s and the current century. We predicted that longer breeding seasons, observed in our population during the second study period, will result in (a) lengthening of breeding periods of individual females, (b) the increase in the annual number of breeding attempts as well as 'true' second broods (raised after successful fledging of the first brood) and (c) the increase in the number of young produced by breeding females during the breeding season. We also predicted that (d) the increased reproductive effort of breeding females would result in a lower female apparent survival; Figure 1a. Furthermore, because our preliminary data suggested that breeding success was higher in the second study period, we wanted to test two hypotheses explaining the relationships between the duration of female breeding periods (the annual number of days a female devoted to parental care) and female productivity: (a) an earlier initiation of breeding resulted in the extension of female breeding periods, increasing the chances for re-nesting, (b) longer female breeding periods were a by-product of

FIGURE 1 (a) Main hypotheses explaining fitness consequences of longer breeding seasons of reed warblers in the 2000s compared to the 1980s. We predicted that longer season of the population (a result of earlier bird arrival and initiation of nesting but unchanged cessation of breeding in the 2000s) is associated with longer breeding periods of individual females, causing higher re-nesting potential and higher female productivity, and their lower apparent survival (*survival costs of high reproductive effort are expected mainly in small-bodied species with fast pace of life); (b) Proximate hypotheses explaining a positive correlation between the duration of female breeding period and the annual number of offspring produced by a female



higher nesting success and higher productivity (a successful breeding attempt lasts longer than unsuccessful one, and hence raising successful broods may extend the breeding season); Figure 1b.

2 | MATERIALS AND METHODS

2.1 | Study species

The Eurasian reed warbler is a small passerine (c. 12 g), with a relatively long reproductive season (May–August in most studied populations), breeding in Palearctic reedbeds (Cramp, 1992). The species is a long-distance migrant wintering in sub-Saharan Africa. European populations of the species are stable or increasing (Inger et al., 2015). The arrival of both sexes to the breeding grounds is asynchronous and lasts for more than a month. Reed warblers reach very high breeding densities (that may exceed 200 pairs per 10 ha), hold small territories and move short distances within a breeding season (Cramp, 1992; Halupka, Halupka, et al., 2014; Wierucka et al., 2016). After arrival to the breeding area, males settle in territories and commence singing, whereas females find mates in a short time and start nest-building. Male singing activity ceases after pairing and males begin mate-guarding their females as they build the nest. The small, cup-shaped nests are attached to reed stems and usually contain 3–5 eggs (median = 4, exceptionally 2 or 6). The species suffers relatively high nest losses (55.1% on average in Europe, and 53.4% in our study population; Halupka, Halupka, et al., 2014; Schulze-Hagen et al., 1996) and frequently re-nests after nest failure, laying up

to five clutches per season. Most pairs remain together throughout the whole breeding season, however within-seasonal split-ups occur infrequently (Halupka, Sztwiertnia, et al., 2014). Both parents are engaged in incubation and feeding of the young (Cramp, 1992; Klimczuk et al., 2015). They care for fledglings for about 2 weeks, and then some pairs start preparations for their second broods.

2.2 | Study population and data collection

We studied a colour-ringed population of Reed Warblers nesting on the fish-pond Słoneczny in the Stawy Milickie (Milicz fish-ponds) nature reserve (SW Poland, centre of the study plot: 51.5386 N, 17.3398 E) in 1980–1983 and 2005–2012. The study plot of c. 3 ha comprised of an extensive reedbed (up to 150 m wide) with a system of bays and channels within. The dominant plant species of the reedbed was common reed *Phragmites communis*, accompanied by scattered patches of bittersweets *Solanum dulcamara*, and cattails *Typha angustifolia*.

Each year the study site was monitored from the time of arrival of the first individuals (late April/early May) until the fledging of the last young (mid-August) for 5–7 days a week and 8–10 hr a day. We mist-netted and individually marked birds (combinations of three colour and one metal ring), mapped singing males every 1–2 days, and started looking for a pair when a male ceased singing. We searched for nests primarily by observing nest-building behaviour, which starts soon after pair formation. Due to frequent mapping of singing males, we were able to identify males that stopped singing

after attracting of a female. Then we tried to spot a patch with a nest from 6-m high wooden towers and/or a 3-m high portable aluminium ladders. Additionally, we found some nests by systematic searches through the reedbed. Nests were visited every 2–4 days. If a nest check revealed that the nest had been lost (among failed nests, 77% were predated and the remaining ones parasitized by the common cuckoo, deserted or nestling died during heavy rainfall; Halupka, Halupka, et al., 2014), we immediately started searching for a new nest of the pair, which was usually located nearby (on average at a distance of 18 m, Halupka, Halupka, et al., 2014). Likewise, we started looking for a second brood of a pair about 2 weeks after successful fledging of the young from the first nest. We assumed that a nest containing 10-day-old young was successful (Halupka, Halupka, et al., 2014). Since we found most nests (c. 85%) as they were being built, their first-egg dates were accurately measured. When a nest with a complete clutch was found, we monitored the nest until hatching day and then backdated to estimate clutch initiation date, assuming one egg laid per day and an incubation period of 11 days. If the nest had nestlings when found, we estimated the age of the young (following Halupka et al., 2018) and then backdated the laying dates.

Throughout the breeding season, we made every effort to identify singing males and parental birds in their territories (by observation and/or video-recording at the nests using digital camera JVC Everio GZ330) to be able to monitor breeding effort of the pairs across the breeding season. However, not all pairs were traced throughout the breeding season for various reasons (e.g. too late mist-netting of a female, failure of a nest on the day of laying of the first egg). Furthermore, because some pairs split during the breeding season (c.f. Halupka, Sztwiertnia, et al., 2014), we decided to calculate breeding statistics only for females.

For the purpose of this paper, we included in the analysis only females monitored throughout the whole breeding season, for which we were able to assess the total number of breeding attempts during the breeding season and the annual number of fledged young. The necessary conditions for these females were as follows: (a) settlement of their mates and pairing events were observed, (b) females were individually marked already at their first breeding attempt in a season and (c) all their nests in a season were found. We assumed (based on the timing of ringing recoveries from autumn migration) that all breeding pairs are rearing young at least until early July.

We included into analysis the data on 343 individually marked females (305 females observed only in one season, 30 females in two seasons, seven in three seasons and one in four seasons), and a total of 390 female annual observations. Across 12 breeding seasons, we followed fates of 759 nests; on average, we observed 33 females (range 23–49) at 63 nests annually (see Table S1 for annual numbers).

We defined the duration of female breeding period as the annual period of parental care of a female, covering days from the beginning of building of her first nest until the end of caring for last fledglings or a failure of last nest. In all analyses, we use 'the date of breeding period initiation' as the date of laying of the first egg in a season

by a female, as it was more accurate that the date of beginning of nest-building.

2.3 | Climatic data

Data on mean monthly temperatures and total monthly precipitation for the months corresponding with the species breeding season (April–August) were obtained from the regional meteorological station in Wrocław.

2.4 | Statistical analysis

The analysis was performed in R environment (ver. 3.6.3; R Core Team, 2020), using the package `LME4` (Bates et al., 2015) for GLMMs. For count data (number of fledglings, number of nests), we used GLMMs with Poisson error structure and log-links, Boolean data (nesting success, occurrence of second brood) were modelled using GLMMs with binomial error and logit link, and phenological variables (Julian date of the breeding season initiation and duration of female breeding period) were analysed in LMMs with Gaussian error distribution.

There were 12 years and 343 unique females, which in sum produced 390 observations. In all models, year and identity of a female were entered as random intercepts. However, in some models, the variance explained by one or even both random terms was estimated as zero. We followed recommendations by Bolker et al. (2009) and Barr et al. (2013) and dropped such random terms from the model. In particular, female ID was removed in the model of seasonal reproductive output (Table 3). This model was crucial for interpretation of the study; thus, it was resampled with 5,000 random sets of unique females, to cross-check its results.

We checked residual plots to ensure that model fits were good (Hartig, 2020). Additionally, for Poisson GLMMs, we calculated overdispersion parameters (ratio of sum of squared residuals to residual degrees of freedom), to check for zero-inflation. They varied between 0.84 and 1.17, which is an acceptable range (McCullagh & Nelder, 1989). Statistical inferences were based on 95% confidence intervals around estimates of parameters in question. R output for models in Tables 2 and 3 is listed in Halupka, Borowiec, et al. (2020).

2.5 | Estimation of apparent survival

Individual encounter histories included both recaptures and resightings (hereafter re-encounters) of all females ringed in the two periods, thus more females than included in the analysis of breeding performance. To estimate apparent survival of female reed warblers in the two periods, we fitted two separate survival models, one for each of the two periods (1980–1985 and 2005–2013), fully covering periods with reproduction data. Since survival rate is estimated for (and refers to) intervals between years, to get an estimate between,

for example, 1983 and 1984 (for females nesting in 1983), data for the latter year must be included, even though the reproduction has not been studied in 1984. However, due to low re-encounter rates in 1983–1984, we prolonged data analysed for the first period with an additional year (1985), which provided two females ringed prior to 1984, not re-encountered in 1984 but recaptured in 1985, and allowed for a better estimation of the survival parameter for 1980s. The analysis covered 291 females in 1980–1985 and 342 females in 2005–2013. Because we were interested in comparing (a) mean survival between both periods and (b) temporal variance of the survival process, we used Bayesian formulation of the model, in which both these quantities, along with estimates for separate years, are available (Kéry & Schaub, 2012). In this formulation, survival estimates for successive time (year-to-year) periods are random effects: time-specific deviations ('temporal residuals') from the mean survival over the whole period and are assumed to come from a common, normal distribution:

$$\text{Logit}(\phi_{it}) = \mu + \varepsilon_t,$$

$$\varepsilon_t \sim \text{Normal}(0, \sigma^2),$$

where σ^2 is the temporal variance on the logit scale $\sigma_\phi^2 = \frac{\exp(\mu)}{\exp(1+\mu)}$ (Kéry & Schaub, 2012). Re-encounter parameter p was treated as a fixed, time-specific effect, since initial analyses indicated large variation in this parameter. We carried out a Bayesian analysis using WinBUGS (Lunn et al., 2000) run using R (R Core Team, 2020) with the R2WinBUGS library (Sturtz et al., 2005). We used uniform (0, 1) priors for both ϕ and p , and a wide uniform distribution (0, 5) for σ^2 . We ran three Markov chain Monte Carlo (MCMC) simulations, each with 550,000 iterations, first 50,000 discarded as a 'burn-in' and a thinning rate of 1,000 to get a posterior sample of 500 for all parameters from each simulation. Chain convergence was monitored visually by assessing chain behaviour and by Brooks–Gelman–Rubin statistics (\hat{R} , Gelman & Hill, 2007), reported by WinBUGS and no issues were detected. \hat{R} were in almost all cases < 1.01 . Parameters are summarized using means of posterior distributions and 95% confidence intervals

presented as 2.5% and 97.5% percentiles of posterior distributions (Bayesian credible intervals, BCI).

3 | RESULTS

3.1 | Changes in meteorological variables

Between 1980 and 2012, there was an increase in mean temperatures in April–August, the period corresponding with the species breeding season ($r_s = 0.713$, CI: 0.49–0.85, $n = 33$). The first study period (1980–1983) was colder (mean = 14.64°C) than the second period (2005–2012; mean = 16.19°C). Temporal trends for each month of the breeding season, as well as monthly values for each period, are shown in Table S2.

Total precipitation in April–August did not change throughout the study period ($r_s = 0.036$, CI: -0.31 to 0.37, $n = 33$), and was similar in the first and the second study period (respective means of 338 and 348 mm; see Table S3 for monthly values).

3.2 | Changes in breeding parameters

Timing of breeding of individual females changed between the two study periods. In the 2000s, females started nest-building on average 7 days earlier, laid the first egg of the season about 6 days earlier and they finished parental care a week later than in the 1980s (Table 1). Overall, the duration of female breeding period, defined as a period of parental care (i.e. from the beginning of building of her first nest until the end of caring for last fledglings or a failure of last nest) was extended by 13.5 days (Table 1).

Mean clutch size of the first breeding attempt and the total number of eggs laid within the season by a breeding female were very similar in the 1980s and 2000s (Table 1). However, breeding success was higher in the 2000s, and an average female raised approximately 0.5 broods (successful nests) more than

TABLE 1 Model-adjusted mean values (with 95% confidence intervals) of breeding parameters of reed warbler females in the two study periods and beta coefficients referring to differences between them (those with 95% confidence intervals not covering a value of zero, are in bold). In all models, year and female IDs were entered as random intercepts and, if their variances were estimated as zero, they were dropped. Total numbers of observations were 106 (including 97 unique birds) in the 1980s and 284 (246) in the 2000s, except for the comparison of the first clutch size: 94 (87) and 255 (226), respectively

Breeding parameter (model type)	The 1980s	The 2000s	β
Number of fledglings (GLMM, Poisson)	1.61 (1.34; 1.94)	2.81 (2.53; 3.12)	0.556 (0.347; 0.780)
Number of eggs (GLMM, Poisson)	6.89 (6.35; 7.46)	7.46 (7.10; 7.77)	0.076 (-0.013; 0.165)
Clutch size of the first nest (GLM, Poisson)	4.10 (3.71; 4.53)	4.35 (4.10; 4.62)	0.064 (-0.051; 0.181)
Number of nests (GLM, Poisson)	1.95 (1.70; 2.24)	1.95 (1.79; 2.12)	-0.001 (-0.158; 0.161)
Number of successful nests (GLM, Poisson)	0.52 (0.40; 0.68)	0.96 (0.85; 1.08)	0.617 (0.336; 0.916)
Julian date of start of nest-building (LMM, Gaussian) 1 = 1 May	32.3 (30.0; 34.5)	25.5 (24.0; 27.0)	-6.778 (-9.284; -4.295)
Julian date of breeding period initiation (LMM, Gaussian)	38.4 (36.1; 40.7)	32.4 (30.8; 33.9)	-6.021 (-8.565; -3.497)
Julian date of breeding period end (LMM, Gaussian)	81.1 (77.3; 84.9)	88.2 (85.6; 90.8)	7.077 (3.036; 11.122)
Duration of female breeding period in days (LMM, Gaussian)	50.1 (47.2; 53.1)	63.7 (61.9; 65.5)	13.522 (10.085; 16.960)

in the earlier study period (Table 1). The seasonal reproductive output was also higher in the 2000s by 75% (Figure 2), when an average female produced 1.2 more fledglings per season than in the 1980s.

In the 2000s, we observed both a higher success of first breeding attempts and a higher incidence of 'true' second broods (i.e. those commenced after successful fledging of the first brood). In the 1980s, 29.2% of 106 females fledged first broods, while in the 2000s as many as 51.1% ($n = 284$; binomial GLMM controlling for random seasonal variation and female identity: odds ratio = 2.57; 95% CI: 1.42–4.97). Similarly, only 2.8% of 106 females had 'true' second broods in the 1980s, but as many as 23.6% of 284 in the 2000s (binomial GLMM controlling for random seasonal variation and female identity: odds ratio = 11.14; 95% CI: 7.03–15.25). Overall, in the 2000s, some females fledged young from two nests annually and produced more than 5 young while this did not occur in the 1980s (Figure 2). Furthermore, the proportion of females that did not produce any young in the season decreased from

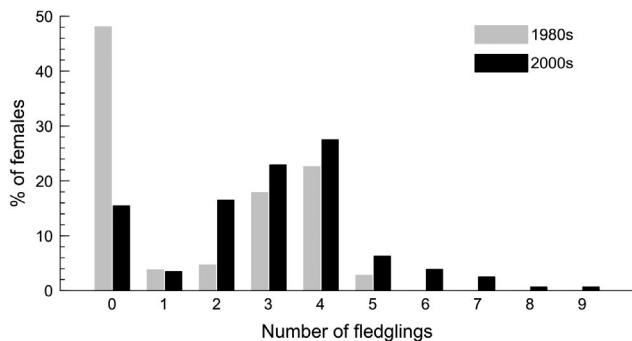


FIGURE 2 Proportion of females producing different number of young (0–9) annually in the 1980s and 2000s

48.1% to 15.5% between the two study periods (binomial GLMM controlling for female identity: odds ratio = 0.175; 95% CI: 0.081–0.377; Figure 2).

3.3 | Duration of the breeding season versus reproductive output

The first hypothesis predicted that an earlier initiation of breeding was positively correlated with the re-nesting potential (the probability of starting a replacement clutch and/or raising two broods; Figure 1b i). Re-nesting potential was analysed in a subsample of females that had failed in their all breeding attempts and eventually did not produce any fledglings. It appeared that an earlier initiation of breeding significantly extended the period in which re-nesting attempts occurred and this correlation worked in both study periods (Table 2, left column). An earlier initiation of the female breeding period also increased significantly the likelihood of having a second brood in females that successfully fledged the first brood. Once again, it appeared that this pattern hold across study periods (Table 2, middle column).

To test the second hypothesis, that longer female breeding periods in the 2000s were a by-product of a higher nesting success (Figure 1b ii), we constructed a model in which the duration of female breeding period was predicted by the number of fledglings (entered in the model both as a linear and quadratic term), Julian date of laying the first egg in the earliest clutch, and study period (Table 2 and Figure 3). The results showed that the time spent by birds in the breeding area was generally longer in the 2000s than in the 1980s. The duration of female breeding period increased with the number of fledglings, but not linearly: among females with a relatively low reproductive output, the breeding period slowly prolonged with the

TABLE 2 Models explaining variation in the duration of female breeding periods and occurrence of true second broods in female reed warblers across 12 years. Year and identity of female were entered as random factors and, if they explained a negligible amount of variance, were dropped in the final versions of models. Beta coefficients with 95% confidence intervals not covering a value of zero, are in bold

Term	Response variable and observation selection criteria		
	Log(duration of breeding period) Females without fledglings	Second brood (1 = yes) Females with successful 1st brood	Log(duration of breeding period)
Intercept	3.844 (3.777; 3.912)	-2.709 (-5.550; -1.046)	3.869 (3.814; 3.924)
No. fledglings			-0.021 (-0.053; 0.011)
(No. fledglings) ²			0.016 (0.007; 0.026)
Initiation of female breeding period (Julian date, standardized)	-0.133 (-0.197; -0.069)	-2.870 (-7.848; -0.523)	-0.109 (-0.132; -0.087)
Study period (1 = 2000s)	0.233 (0.141; 0.325)	1.963 (0.110; 4.824)	0.214 (0.140; 0.288)
Fledglings ² : Study period			-0.009 (-0.016; -0.003)
Initiation : Study period	0.020 (-0.070; 0.110)	1.262 (-1.190; 6.252)	
ID female (random intercepts)	<10 ⁻⁵	<10 ⁻⁵	0.041 (0.000; 0.117)
Year (random intercepts)	<10 ⁻⁵	0.286 (0.000; 1.454)	<10 ⁻⁵
No. observations (unique females)	95 (93)	176 (166)	390 (343)

number of fledglings and then, among better-performing individuals, the curve accelerated, with a higher rate in the 1980s than in the 2000s (Figure 3).

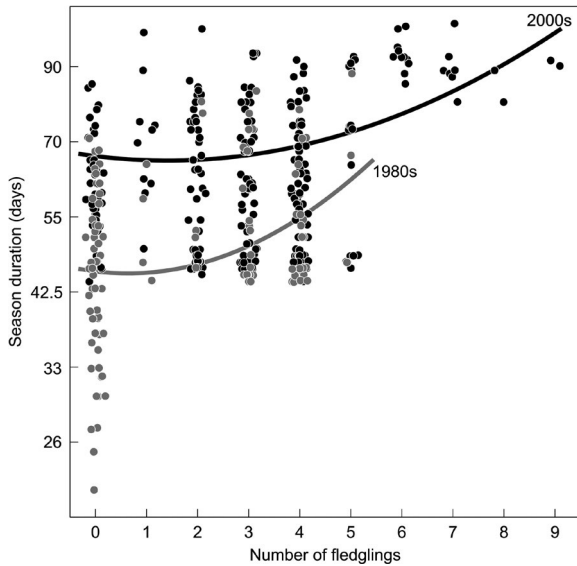


FIGURE 3 Relationships between females' seasonal fledgling production and duration of their breeding periods (log scale) in the 1980s (grey dots) and the 2000s (black dots). Points, each representing observation of one female, were 'jittered', to avoid over-plotting. Regression lines are drawn using coefficients of the model listed in Table 2 (left column)

3.4 | Final model of seasonal reproductive output

The results may suggest that an increase in seasonal reproductive output in the 2000s was due to greater nesting success and earlier arrival on the breeding area, which provided an increased opportunity to re-nest. The final model explaining the variation in fledgling production included three explanatory variables—study period, date of initiation of breeding (the first-egg laying date in the first annual clutch), and success of the first nest, along with their interactions. We expected that females successful in their first breeding attempt would lay another clutch, provided that they have had enough time to raise their offspring. This should favour early females and result in steeper relationships between the fledgling production and initiation of breeding in the 2000s, compared to the 1980s (Figure 4).

The model (Table 3) showed that the date of breeding initiation was strongly correlated with reproductive output in females that failed in their first breeding attempts. Such individuals still had a relatively high likelihood of raising some offspring in replacement broods, provided that they had begun reproduction early in the season (i.e. had enough time to re-nest). Success in the first breeding attempt to some extent cancelled out the importance of the date of breeding initiation: early females still did better than late ones, but the difference was not dramatic (Figure 5, top panel). This pattern was similar in both study periods and it appeared that a relatively higher average reproductive output in

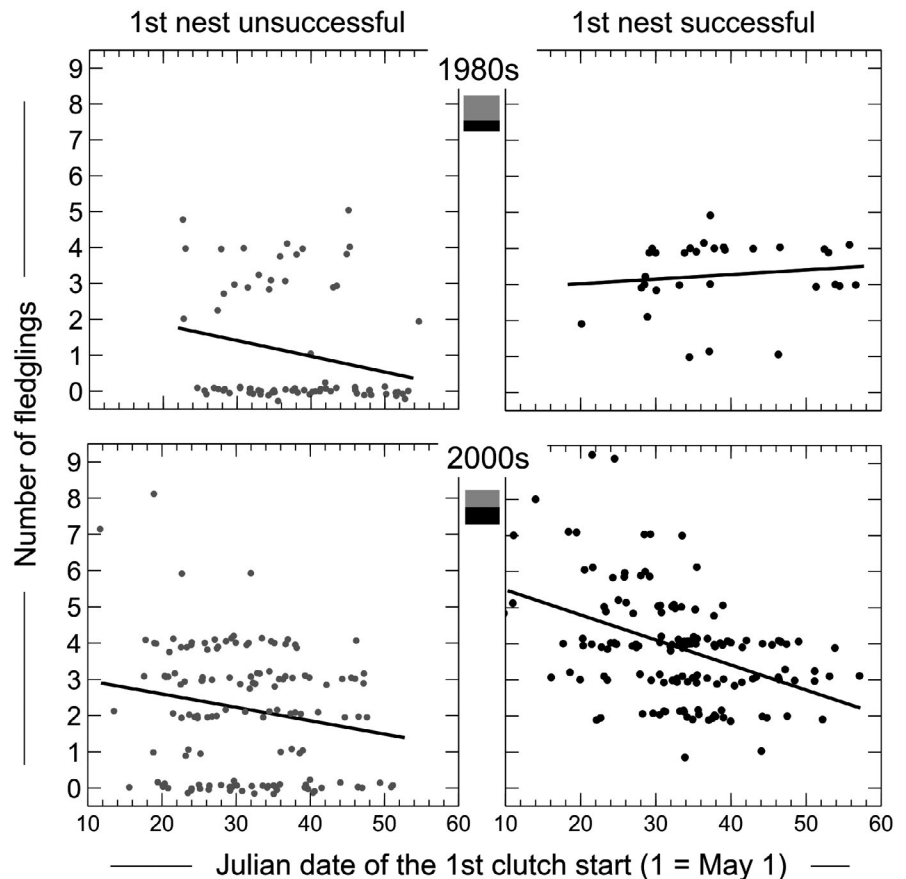


FIGURE 4 Relationships between females' seasonal fledgling production, fate of their first nests and phenology of breeding seasons in the 1980s and 2000s. Proportions of successful (black) and unsuccessful (grey) first nests are shown on stacked bars below labels of study periods. Points, each representing one female, were 'jittered' horizontally and vertically, to avoid over-plotting. Trends are illustrated by simple linear regression lines

TABLE 3 Poisson GLMM explaining variation in the seasonal reproductive output (number of fledglings) in female reed warblers across two study periods covering 12 years. Number of observations was 390, including 343 unique females. Year and identity of female were entered as random factors, but the latter explained a negligible amount of variance (SD of random intercepts $< 10^{-5}$) and was dropped. The middle column lists the model's coefficients with confidence intervals. Beta coefficients with 95% CI not covering a value of zero, are in bold. The right column shows mean coefficients (and their 95% percentile confidence intervals) produced by the resampling procedure using random sets of unique females (see Section 2)

Term	Coefficients (95% CI)	Resampled coeff. (95% CI)
Intercept	0.166 (-0.071; 0.389)	0.111 (0.021; 0.192)
Study period (1 = the 2000s)	0.503 (0.242; 0.774)	0.513 (0.421; 0.613)
Initiation of female breeding period (Julian date, standardized)	-0.340 (-0.601; -0.088)	-0.263 (-0.336; -0.184)
Success of the first nest in the season (1 = fledged)	1.001 (0.683; 1.318)	1.072 (0.989; 1.166)
Study period : Initiation	0.141 (-0.141; 0.431)	0.085 (-0.005; 0.169)
Study period : Success	-0.345 (-0.697; 0.008)	-0.391 (-0.496; -0.292)
Initiation : Success	0.374 (0.061; 0.693)	0.280 (0.196; 0.360)
Study period : Initiation : Success	-0.342 (-0.695; 0.006)	-0.255 (-0.348; -0.159)
Year (SD of random intercepts)	0.046 (0.000; 0.158)	0.078 (0.045; 0.106)

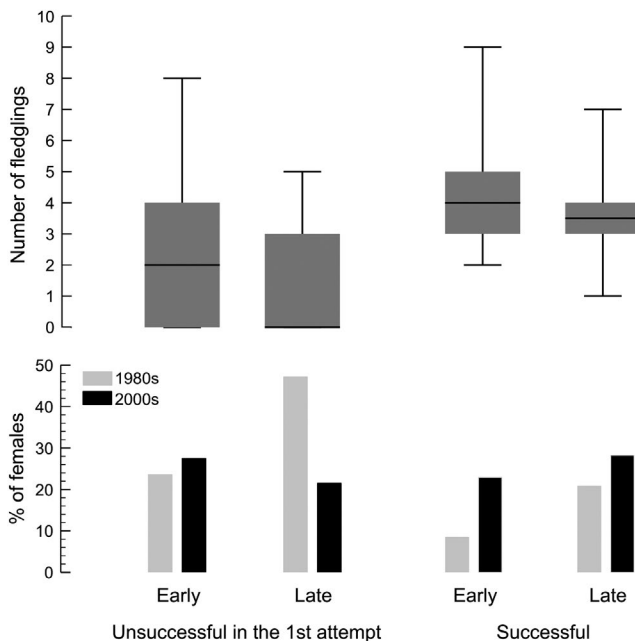


FIGURE 5 Top panel: boxplots (ranges and quartiles) showing production of fledglings by females depending on the initiation of breeding (first-egg laying dates) and the fate of their first nests. Bottom panel: proportion of females in the four classes in both study periods (the sum of lengths of bars of one kind = 100%). 'Early' females started reproduction before the 3rd of June (mean date across the study periods)

the 2000s depended chiefly on a decrease in the proportion of females that began breeding late and were also unsuccessful in their first attempt (Figure 5, bottom panel). The expected three-way interaction between the study period, date of initiation of breeding and nesting success was quite weak (Table 3) and this may reflect relationships between the initiation of breeding and reproductive output: in the 1980s it was flat, whereas in the 2000s it was rather steep, because of the high proportion of

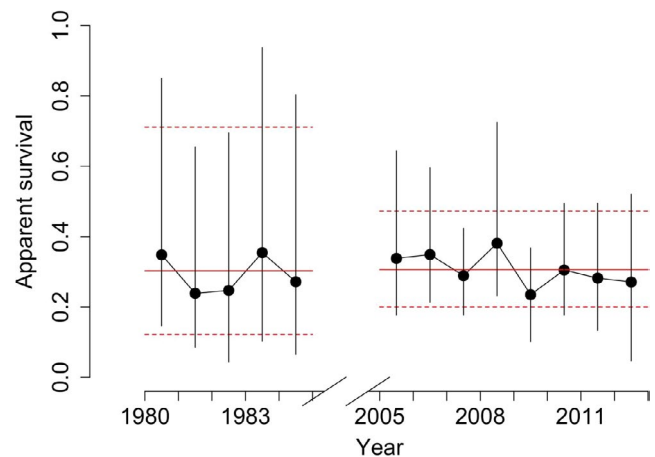


FIGURE 6 Apparent survival estimates of female Reed Warblers for the 1980s and 2000s. Points are yearly means with 95% credible intervals (whiskers), while horizontal red lines show mean apparent survival for the two study periods (means—solid, 95% credible intervals—dashed)

early females that were able to raise two broods in the season (Figure 4).

3.5 | Annual survival

Female apparent survival was similar in both study periods with mean survival rates of 0.30 (± 0.14 SD , including temporal variance) in the 1980s and 0.31 (± 0.07 SD) in the 2000s (Figure 6). Re-encounter probabilities were more variable in the 1980s (0.15–0.58) than in the 2000s (0.43–0.74, except for the last year when it dropped to 0.22), which translated to less precise survival estimates for the former study period. Despite unequal precision, the similarity of both estimated mean survival rates indicates little or no changes between the two periods; however, the process variance (temporal, i.e. between-years) was much larger in the 1980s than in the 2000s (Table S4).

4 | DISCUSSION

Our study has found that the duration of breeding periods of reed warbler females extended between 1980s and the current century, and we also observed an increase in the female annual productivity. Higher number of annually produced young by a breeding female in 2000s compared to the 1980s was the combined effect of earlier start of nesting and higher nest success.

The important result of our study is a positive relationship between the lengthening of the breeding season of the study population of reed warblers (the period from the beginning of nest-building by the earliest pair in the population until the end of parental care by the latest pair in a season) and breeding periods of individual females (the time period an average female devoted to parental care annually). This result was not obvious as the arrival and start of breeding (as well as the cessation of breeding) are very asynchronous in our population of reed warblers, and hence the breeding season of the whole population is much longer than a breeding period of an average female. Therefore, it might be expected that an earlier arrival of birds observed in recent years would result in longer seasons (Ambrosini et al., 2019) and even greater breeding asynchrony, but not necessarily changes in breeding periods of individual females. However, we found that breeding periods of single females became extended between the two study periods by 13.5 days (2 weeks), which resulted both from earlier start of nesting but also their later cessation of breeding.

Although the annual number of clutches, as well as clutch size and the total number of eggs laid in the season were similar in the two study periods, the annual number of young produced by a breeding female increased from 1.6 to 2.8. This resulted primarily from the decline in the proportion of females that did not produce any young annually (from 48.1% to 15.5%) and the increase in the share of females rearing second broods after a successful first brood (from 2.7% to 23.6%). In 2000s, some double-brooded females were successful in both broods, producing 6–9 young annually (this never occurred in the 1980s), and hence individual heterogeneity was higher than in the 1980s. High number of double-brooding females in recent years was associated with their earlier arrival and initiation of breeding (it appears that only females starting nest-building in May have a chance for a second brood; Figure 4), and much higher success of first broods. High success of first broods in the 2000s also contributed to the low proportion of females that did not produce any young annually. Because nest concealment has been recognized as a crucial factor affecting nest survival in the species (Halupka, Halupka, et al., 2014; Schulze-Hagen et al., 1996), we suggest that the higher success of first broods in the 2000s was associated with the advanced reed development (the effect of much warmer springs) and hence better nest concealment. In the 1980s, new reeds at the beginning of breeding season were much shorter compared to the 2000s (118.8 ± 27.6 vs. 196.6 ± 25.4 cm above water level) and early nests were built among sparser reeds. The comparison of these reed heights indicates that reed warblers, despite the earlier start of breeding in the 2000s, are now delayed in relation to reed phenology, compared to the situation in the 1980s.

In our population, the higher number of annually produced young was related to the earlier initiation of nesting of individual females (and hence longer breeding periods), and this trend was found also for females whose first brood was unsuccessful (Figure 4, left panel; Figure 5). Similar results were described in a few passerine species studied in areas where climatic conditions did not change throughout the study period (Lv et al., 2019; Tarwater & Arcese, 2018; Townsend et al., 2013; see Section 1 for details). Research analysing links between season duration and fecundity, in the areas where climate has changed, are very rare. In one of them, multi-brooded barn swallows increased fledging success over time, and this was related to longer inter-clutch intervals (Møller, 2007), and longer breeding seasons (Møller et al., 2010). Gullet et al. (2013) found that the duration of breeding season of single-brooded long-tailed tits shortened by 33% over 17 years, and they estimated it should result in a substantial loss in reproductive opportunity. The significant advancement in seasonal termination dates in the British population of long-tailed tits was probably a response to phenological shift in food supply associated with warmer Aprils (Gullet et al., 2013). We can expect that if climatic conditions change the period of availability of food resources, this may affect the length of breeding seasons but also female fecundity and survival (Seward et al., 2013).

Our study has revealed that in recent years females apparently allocated more in reproduction compared to females nesting in the 1980s: they spent more time caring for their offspring and raised more young in the season, which is costly in terms of energy (Harshman & Zera, 2007). Despite this, the increased parental effort was not associated with a declined survival: female apparent survival was almost identical in the two study periods. Several explanations for such a result are possible (van Noordwijk & de Jong, 1986; Santos & Nakagawa, 2012). For example, higher reproductive effort (reducing condition and survival) could be compensated for by higher availability of food, increasing condition and survival (Seward et al., 2013; van Noordwijk & de Jong, 1986). Preliminary data from our study site suggest that food resources were indeed higher in the 2000s than in the 1980s (A. Dyrz & L. Halupka, unpubl. data). Our results of survival analysis are consistent with the patterns found in the meta-analysis examining relationships between parental effort and survival in birds (Santos & Nakagawa, 2012). The authors revealed that experimental females, that experienced the increased parental effort, were just as likely to survive to the next season as control females, in line with our findings. This suggests that the trade-off between parental effort and survival is more complex than previously assumed.

Temporal advances in mean laying dates have been found in the majority of bird species studied at temperate and higher latitudes (Dunn & Møller, 2014; Radchuk et al., 2019), but they have not been related to the changes in the duration of reproductive seasons (Halupka & Halupka, 2017). Theoretically, the climate-driven extension of breeding season and hence increased re-nesting opportunities can be expected to positively affect fecundity primarily in multi-brooded species (Halupka & Halupka, 2017). The opposite pattern, shortening of breeding seasons and a decline in fecundity, is expected in single-brooded species as they often fine-tune their breeding cycle with short-lasting food resources, and their

reproduction may be mistimed due to unequal phenological changes across trophic levels (Both et al., 2009; Marra et al., 2005). The number of studies reporting phenological mismatches has been rising (Thomas et al., 2017), but at the same time recent evidence suggests that some single-brooded species may become double-brooded under changing climatic conditions, and so may benefit from climate change (Both et al., 2019). In contrast, in some regions conditions in late spring or in summer may deteriorate due to climate change, causing earlier cessation of the breeding season and reducing fecundity (Miller-Rushing et al., 2010; Tarwater & Arcese, 2018).

In sum, we are still far from understanding how climate change affects bird fecundity and population productivity. Few data collected so far suggest that some species suffer from climate change (e.g. Gullet et al., 2013; Halupka, Czyż, et al., 2020) while other seem to benefit (e.g. Møller, 2007; this study). Therefore, long-term studies examining fecundity effects of advancing laying dates and changes in the duration of avian breeding seasons are urgently needed. In addition, we should complement long-term studies with more additional data and experiments to obtain the better knowledge about at the underlying mechanisms (e.g. the effects related to changes in food availability or parental effort).

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AUTHORS' CONTRIBUTIONS

L.H. conceived the study, designed the experiment, collected the data in the current century and led the writing of the manuscript; K.H. performed most statistical analyses, contributed to experimental design and writing of the manuscript; M.B. collected the first batch of data; G.N. performed survival analysis and contributed to writing of the manuscript. All authors read and approved the final manuscript.

DATA AVAILABILITY STATEMENT

The data used to obtain conclusions in this paper are available at <https://doi.org/10.6084/m9.figshare.13241975> (Halupka, Borowiec, et al., 2020).

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SUPPORTING INFORMATION

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