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Climate warming induced a stretch of the breeding season and an increase of second clutches in a passerine breeding at its altitudinal limits

Toni Mingozzi[a], Pierpaolo Storino[a], Giampalmo Venuto[a], Alessandro Massolo[b,c], and Giacomo Tavecchia[d,*]

[a]Department of Biology, Ecology and Earth Sciences (DiBEST), University of Calabria, Via P. Bucci, Rende 87036, Italy, [b]Department of Biology, Ethology Unit, University of Pisa, Via L. Ghini, 13, Pisa 56126, Italy, [c]UMR CNRS 6249 Chrono-environnement, Université Bourgogne Franche-Comté, 16 Route de Gray, Besançon 25030, France, and [d]Animal Demography and Ecology Unit (GEDA-IMEDEA, CSIC -UIB), C. M. Marques, Esporles 07190, Spain

*Address correspondence to Giacomo Tavecchia. E-mail: g.tavecchia@uib.es.

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Abstract

The increase in the average air temperature due to global warming has produced an early onset of the reproduction in many migratory birds of the Palearctic region. According to the "mismatch hypothesis" this response can lead to a decrease in the breeding output when the conditions that trigger the departure from the wintering areas do not match the availability of food resources in the breeding ground. We used 653 brooding events registered during the period 1991–2013 to investigate the link between climatic variables and individual breeding performance of a partially migratory passerine, the Rock Sparrow *Petronia petronia*, breeding at the altitude limit of its distribution. The laying date (LD) of the earliest first clutch was associated with local spring (minimum) temperatures but did not show a significant trend during the period considered. The LD of the latest first clutch had a positive and statistically significant trend, unrelated to local covariates and resulting in a longer breeding season (∼1.5 days/year). A longer breeding season allowed birds to produce more second clutches, which proportion increased from 0.14 to 0.25. The average breeding success was also positively correlated with the average temperature in July and with the duration of the breeding season. Contrary to expectations, the most important climate-dependent effect was a stretch of the breeding season due to a significant increase of the LD of the latest first-clutches rather than an earlier breeding onset. We show how climate changes act on bird populations through multiple paths and stress the need to assess the link between climatic variables and several aspects of the breeding cycle.

Key words: breeding phenology, climate warming, long-term study, *Petronia petronia*, reproductive success

The most common response to the recent global warming (IPCC 2013) by migratory birds in the Palearctic regions is a shift of their breeding phenology (Parmesan and Yohe 2003; Parmesan 2006; Bellard et al. 2012; Foden et al. 2013; Pacifici et al. 2015). Individuals tend to breed earlier than few decades ago (Parmesan and Yohe 2003; Dunn and Winkler 2010) especially in areas where

spring temperature increased more markedly (Both et al. 2004). This plastic response is not always adaptive (Brown and Bomberger Brown 2000; Phillimore et al. 2016) as environmental clues that trigger spring migration might not correlate with those anticipating the peak of resources on the breeding areas, which could lead to a mismatch between food availability and food demand (Weatherhead 2005; Jonzén et al. 2007; Carey 2009; Both 2010; Visser and Gienapp 2019). The evolutionary consequences of this mismatch are difficult to predict and depend on several factors the most important of which is the migratory status and distribution of the species (Brown and Bomberger Brown 2000; Parmesan and Yohe 2003). Individual responses often involve a change in the migratory habit, that is, individuals become more resident, or in behavior, that is, indiviudals change their migratory route or speed (Forchhammer et al. 2002; Sparks et al. 2005; Jonzén et al. 2007). An early arrival can be beneficial (but see for costs Brown and Bomberger Brown 2000; Shipley et al. 2020). This is evident for those individuals living at the northern edge of the species' breeding distribution where the short breeding season oblige a "fast breeding" strategy, chracterized, for example, by rapid laying after arrival, polygamy, and nest desertion (Pilastro et al. 2001; Root et al. 2003; Both et al. 2004; Crick and Sparks 2006). The increase in average temperature made also the distributions of many species to stretch, or shift, northward (Devictor et al. 2008; Auer and King 2014; Lenoir and Svenning 2014; Oliver and Morecroft 2014). If distribution shifts are well documented, the mechanisms involved are often unknown. Earlier egg laying—much more frequent in multiple brooding species (Dunn and Møller 2014)—is frequently associated with larger clutch sizes and greater production of young (Dunn 2004; Dunn and Winkler 2010). Revealing the link between individual breeding performance and climate is of pivotal importance in predicting the effect of climatic changes. Long-term individual-based studies offer the unique opportunity to address questions related to individual life-history strategy and climate variability (Clutton-Brock and Sheldon 2010; Tavecchia et al. 2017). Populations at the altitude limit of the species distribution, where climate change usually exerts more dramatic effects (Chamberlain et al. 2012; Scridel et al. 2018), are expected to exhibit a strong response to climate changes. At higher altitudes, the increase in temperature and the change in rainfall regimes have important cascading effects on the ecosystem (Hitch and Leberg, 2007; Novoa et al. 2008; Lehikoinen et al. 2014). However, the most evident change that birds living at their altitude limit experience is an increase in the duration of the breeding period, characterized by earlier snow melting and warmer summers (Francon et al. 2020). Investigating individual responses to these changes would uncover the constraints that climate imposes on species' breeding distribution, at the same time revealing the environmental drivers of individual strategies.

The Rock Sparrow *Petronia petronia* is a loosely colonial and cavity-nesting passerine, distributed from Southern Europe to Central Asia, in open habitats and under dry and sunny climatic conditions (Cramp and Perrins 1994; Mingozzi and Onrubia 1997). In Europe, this "southern" and heliophilous species (Lebreton 1975) breeds at low density in small groups near villages leading to a natural small and patchy structure of the population (Mingozzi and Onrubia 1997). In the Western Italian Alps, the Rock Sparrow breeds in a few internal valleys (continental xeric sectors), in small and isolated nuclei at the altitudinal limits of its European range (Cramp and Perrins 1994; Mingozzi et al. 1994). This population is a good biological model to assess the responses to climatic variations

(Mingozzi et al. 1994; Pilastro et al. 2001; Tavecchia et al. 2002; Griggio et al. 2003). In such environmental conditions, breeding parameters and performances are expected to be more strongly influenced by variations in temperature and rainfall than in less marginal and more favorable sites for Rock Sparrow (see examples in Karvonen et al. 2012; Reif and Flousek 2012; Martin et al. 2014). Using long-term individual-based data on the Western Italian Alps populations, we aim to reveal the constraint imposed by the marginal environment. We investigated (1) a possible shift in the average laying date (LD) and (2) a possible trend in the earliest and latest observed LD; we also estimated (3) the duration of the breeding period, that is, the time between the earliest and latest clutch recorded; (4) the yearly proportion of second clutches (SCs), and (5) the association between breeding output (BO), that is, number of fledglings, and climatic factors. As found in many multiple-brood species (Halupka and Halupka 2017), we expected to find a progressive advance in the breeding onset and an increase in the breeding period. If a short breeding season prevented birds from laying an SC, we expected an increase in the proportion of SCs as a result of a longer breeding season. Finally, if a long season increased the number of clutches, we expected an increase in the total number of fledglings produced.

Materials and Methods

Study area

The study population was located in the Upper Susa Valley (Italian Cottian Alps, province of Turin; Figure 1), in an area of ~13 km^2 (municipalities of Sestriere and Cesana Torinese) between 1,350 and 1,800–2000 m above the sea level, characterized by xeric pastures and montane meadows on the right bank of the Ripa river with mountain slopes facing S and SW. Traditional agricultural practices as field cultivation (potatoes, cereals, and fodder crops), cattle grazing, and grass mowing were declining throughout the last decades following a widespread trend of agro-pastoral abandonment (Laiolo et al. 2004; Orlandi et al. 2016). A total of 24–52 nest boxes/year (average ± SD: 38.0 ± 4.6) were installed in 5 small villages for periods ranging from 9 to 22 years: 1991–2013, San Sicario (SS; 1,570 m a.s.l), and Champlas Janvier (CJ; 1,784 m a.s.l); 1991–2000, Champlas Seguin (1,780 m); 2005–2013, Champlas du Col (1,760 m a.s.l.), and Thures (TH; 1,720 m a.s.l.). The nest boxes (11 × 12 cm and 50 cm long with an oval entrance hole of 5 × 3 cm) were especially designed for this species and equipped to work, when necessary, as trapping devices (Mingozzi et al. 1994). Birds exhibit a marked preference for nest boxes versus natural nest in deep holes of building (Mingozzi et al. 1994). As a result, since 1994 all known natural nests have been abandoned and virtually all the population was breeding in artificial nest boxes.

Data collection

During the period 1991–2013 (22 years), the nesting population was monitored every day from mid-May to the beginning of September, that is, from the start of nest building until the last nest fledged. Nest boxes were checked at 2-day intervals to measure reproductive and phenology population parameters (with the exception of 2009 in which the information on clutch number was missing). All breeding adults and nestlings were individually marked each year with a unique combination of 1 aluminum ring (numbered) and 3 plastic color rings (Mingozzi et al. 1994), so that bird identity and social pair bonds were daily ascertained on the field through direct
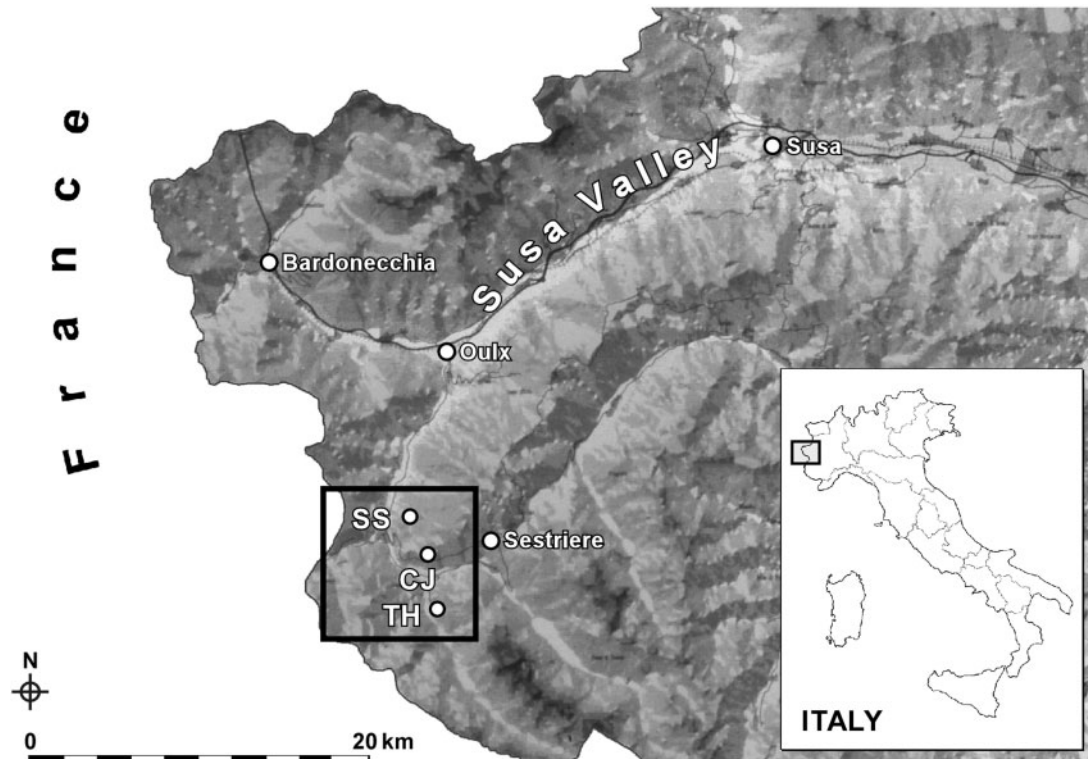
Figure 1. Location of the study area (black square) of the rock sparrow breeding population monitored from 1991 to 2013 in the Italian Western Alps. The main 3 breeding sites are highlighted.

observations. SCs were determined by identifying one or both members of the pair that have been found in another nest earlier in the season. Considering that nearly all breeding pairs in our study area were monitored, we assumed that unmarked breeding birds were immigrants from neighboring nesting sites, most likely from the larger population on the French side of the Alps (Tavecchia et al. 2002). Adults were measured and weighed immediately after capture and nestlings at 12 ± 1 days after hatching date. For each nest monitored, we considered the following parameters:

i. the LD of the first egg (Julian) and the length of the breeding period (i.e., the difference in LDs between the earliest and the latest observed clutch).
ii. the proportion of SCs.
iii. the breeding success (BS; i.e., the probability of fledgling at least one chick).
iv. the yearly BO of successful nests (i.e., the total number of fledged chicks each year).

Regional weather data

Climate data (1991–2013) were obtained from ARPA Piemonte (https://www.arpa.piemonte.it/rischinaturali/accesso-ai-dati/annali_meteoidrologici/annali-meteo-idro/banca-dati-meteorologica.html) and referred to a regional meteorological station located in Oulx-Gad (1,135 m a.s.l.), 9 km north of the study area. To avoid data dredging, we focused on temperature (°C) and precipitation (mm) which are climatic variables known to affect bird phenology and reproduction success (Chambers et al. 2013; Dunn and Møller 2014; Martin et al. 2014). We calculated monthly mean and minimum values from daily during the laying period (May to June), and during the main brooding period (July). The minimum temperature in June

had a clear increasing trend (minimum June temperature: $\beta_{trend} = 0.101$, $t = 2.594$, $P = 0.017$), but the other variables did not. The correlation between temperature and rainfall was not statistically significant in any of the periods considered (April: $N = 22$, $r = -0.18$; $P = 0.405$; May–June: $N = 22$; $r = -0.23$, $P = 0.282$, July: $N = 22$, $r = -0.35$, $P = 0.114$). To avoid building a large number of models with all possible combinations of explanatory variables, we assessed the influence of each covariate alone and added a second covariate only when the first one was statistically significant or close to be. We never assessed the effect of 3 covariates simultaneously (see also below). We also add year as a continuous covariate to account for possible trends, if any.

Statistical analyses

We began by analyzing the variation in the LD to assess variations in reproductive onset and termination along the study period. We focused on the extreme values of the earliest and latest clutches but first assessed whether these were representative of the whole distribution by assessing their correlation with the 10th and 90th percentiles ($10th_{perc}$ and $90th_{perc}$) of the LD distribution. Temporal variations in the earliest and latest LD and the length of the breeding period and their association with climatic variables were investigated by means of multiple regressions in program R (R Core Team 2018). In these analyses, the significance of each covariate (see above) was assessed by the estimate of its linear coefficient (t-distribution, $\alpha = 0.05$).

The proportion of SC versus first clutches was modeled through logistic regression by coding "0" and "1" the first and SCs, respectively. SCs were confirmed by the identity of at least 1 bird of the pair. Replacement clutches were excluded. As predictors of SC, we used year (first as a factor and subsequently as a continuous

variable) and the weather covariates measured during the whole laying period (namely, May–June and June–July temperature and rainfall). We did not find evidence of extra-binomial variance ($\chi^2_{536} = 559$; $P = 0.24$, dispersion parameter $= 1.04$) and it was not considered further. As above, the significance of a specific covariate was assessed by the estimate of its linear coefficient (z-distribution, $\alpha = 0.05$).

The average LD, the BS, and the reproductive output (BO) were modeled through generalized linear mixed models using data from all known broods with known LD. In the analysis of the average LD, we only considered clutches between Days 145 and 187 to avoid outliers ("boxplot" procedure in program R) and meet the normality assumptions. In the other analyses all data were considered unless specified (see the "Results" section). The probability of BS, that is, the probability that at least one chick is fledged, was modeled as a binary response through logistic regressions. In this analysis, we also considered the LD (a linear as well as quadratic relationship) as a possible predictor of the BS. The quadratic term was added to investigate a possible optimum in the onset of the reproduction. This was not done for the climatic covariates because the species breeds typically in areas with higher spring and summer temperature and rainfall values. BO of each nest, that is, number of young fledged, was log-transformed ($+1$) and modeled through linear mixed models with normal error structure (note that mixed models with a Poisson error had singularity problems). The total number of fledged chicks produced each year was modeled using Poisson regression to assess for a possible trend.

When comparing several competing mixed models, we used the Bayesian Information Criterion (BIC; Burnham and Anderson 2002). The model with the lowest BIC value was considered as the best compromise between deviance explained and model complexity. Note that we preferred the BIC over the Akaike's Information Criterion (AIC) to guide the choice of generalized mixed models only, as it is more conservative (Burnham and Andreson 2002). Models within 2 point of BIC were considered equivalent. In all mixed models, we used nest identity and year as random effects. The first was used to account for the heterogeneity within the population, for example, the difference in quality across territories and/or among parents, and the second to correct for pseudoreplications that is, the nests within a given year are not independent. We did not consider bird identity because (1) some birds remained unknown, (2) the presence of polygamy and sequential nest desertion (Pilastro et al. 2001) would complicate results, (3) on average, individuals have been seen less than twice during the 22-year period (1.36 and 1.65 for females and males, respectively; Tavecchia et al. 2002), and (4) high-quality individuals tend to acquire high-quality territories (Sergio and Newton 2001) making the information partially redundant. Finally, when testing for the influence of weather covariates, we included a linear effect of time to correct for a possible spurious relationship induced by a temporal trend (Noriega and Ventosa-Santaulària 2007; Haest et al. 2018). Linear mixed models were implemented using the package "lmer" (Bates 2019). The significance of each covariate was measured by Wald tests (χ^2-distribution).

Results

During the 22-year period, a total of 2,802 birds were ringed (228 adults and 2,574 nestlings) and an average of 29.8 ± 8.5 SD nests was monitored each year (range: 15–45). In the overall period (1991–2013), we recorded $N = 653$ brooding events, 430 of which were first clutches with known LD.

Average LD

To avoid biases due to extreme values, we kept only clutches with an LD between 145 and 187 ($N = 409$). The average LD changed significantly over the years ($\sim$3 days over the whole period; Figure 2) but without a trend ($\beta_{\text{linear_trend}} = -0.128$, $\chi^2_1 = 0.7912$, $P = 0.374$; Table 1 and Figure 2). The model with the lowest BIC was the one assuming an effect of the average rainfall before and during laying (May–June; Model 11, Table 1, $\beta_{\text{rainfall\_May}} = 2.85979$, $\chi^2_1 = 29.2940$, $P < 0.001$). The other covariates were not significant. The difference across territories in the average LD was important ($\sigma_{\text{nest\_id}}$: 3.85) indicating an additive role of territorial/bird quality in the variation of LD.

Earliest and latest LD, duration of breeding period, and proportion of SCs

We used all first clutches ($N = 430$) with known LD to investigate the yearly variation in the earliest and latest first-clutch. Outliers were kept in the analysis because the normality assumption of the LD distribution within each year was no longer important, as for each year we only considered the earliest and latest first clutch. Although they influenced the overall distribution, the LDs of the earliest and latest first-clutch observed were correlated with the $10\text{th}_{\text{perc}}$ and $90\text{th}_{\text{perc}}$ of the distribution of LD ($R^2 = 0.83$, $t = 57.7$, $P < 0.001$ and $R^2 = 0.41$, $t = 21.35$, $P < 0.001$, respectively), suggesting that extreme cases correctly represent the left and right tail of the distribution.

The LD of the earliest clutch (Figure 3) advanced about 1 day every 3 years ($\sim$3 days/decades) but the trend was not significant ($N = 22$, $\beta_{\text{trend}} = -0.279$, $t = -1.506$, $P = 0.1477$). The day of the earliest clutch showed a negative and significant association with May–June temperature (minimum temperature: $\beta_{\text{min\_temP}} = -3.01$, $t = -2.661$, $P = 0.015$; average temperature: $\beta_{\text{temP}} = -2.84$, $t = -2.03$, $P = 0.056$; note that as expected these 2 variables were correlated, $R^2 = 0.56$, $t_{20} = 5.11$, $P < 0.001$) but independent of the mean rainfall for the same period ($\beta_{\text{raiN}} = 2.492$, $t = 1.197$, $P = 0.245$). In contrast, the LD of the latest first-clutch had a positive and statistically significant trend over time ($\beta_{\text{trend}} = 1.304$, $t = 4.224$, $P < 0.001$; Figure 3) but independent from
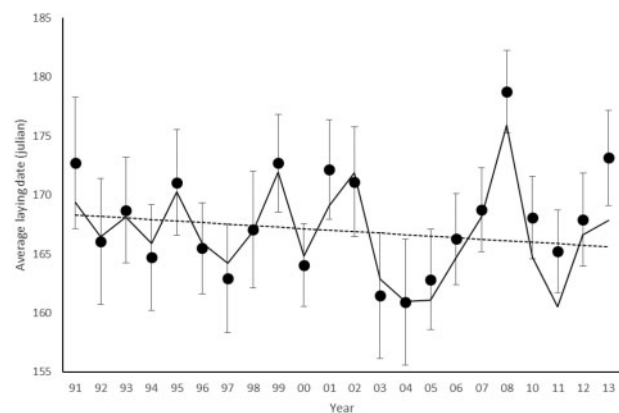

Figure 2. Change in the average LD of first clutches ($N = 406$) of the rock sparrow over the study period (1991–2013) in the Western Italian Alps. Solid line is the model assuming an effect of mean rainfall during the laying period (May and June; Model 1, Table 2). Dashed line indicates the expected values of a model assuming a temporal trend. Vertical lines are the 95% confidence interval.

Table 1. Modeling the average LDs of 409 first-clutches through mixed linear models

Model	Effects	np	BIC	ΔBIC
10	**Rain_M+linear trend**	**6**	**2,800.949**	**0**
0	Constant	4	2,807.571	6.62
6	Rain_MJ+linear trend	6	2812.363	11.41
2	Linear trend	5	2,812.805	11.85
7	Temp_MJ+linear trend	6	2,816.37	15.43
5	Temp_MJ+Rain_MJ+linear trend	7	2,816.953	16.00
4	minTemp_J +linear trend	6	2,817.455	16.51
3	minTemp_MJ +linear trend	6	2,884.70	17.39
8	RainJ+linear trend	6	2,818.607	17.66
9	minT_J+RainJ+linear trend	7	2,823.343	22.39
1	Year	24	2,862.706	61.76

Year (factors) was considered as a random variable together with nest identity. np, number of parameters in the model; ΔBIC = difference with the lowest BIC. Rain, mean rainfall; Temp, mean temperature, minTemp, minimum temperature; _MJ, May–June, _J, June, _M, May, _JL, July. When testing for weather covariates, we included a linear effect of the year to account for possible trend of the covariate. The model retained is in bold.
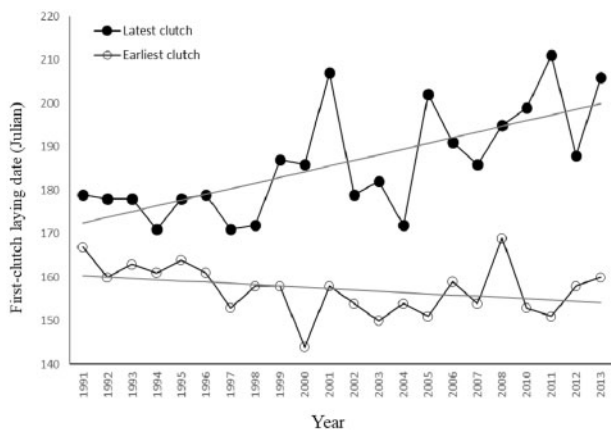
Figure 3. Change in the earliest ($N = 22$, empty symbols) and latest ($N = 22$, solid symbols) first-clutch LDs of the rock sparrow over the study period (1991–2013). Straight gray lines indicate the linear trend of each series. The increasing trend over time of the latest first-clutch is statistically significant (see the text).

the May–June covariates ($\beta_{min\_temP} = -1.9615$, $t = -0.913$, $P = 0.37$; $\beta_{temP} = -2.701$, $t = -1.126$, $P = 0.273$; $\beta_{raiN} = 3.627$, $t = 1.106$, $P = 0.282$). The difference between the earliest and latest first-clutch each year, that is, the length of first-clutch laying period, increased significantly over the study period ($\beta_{length} = 1.599$, $t = 4.581$, $P < 0.001$), from 12 days in 1991 to 46 in 2013 (~1.5 days/year; Figure 3).

The proportion of SCs was estimated from 558 clutches, 112 of which (20%) were SCs. It varied markedly, ranging from 3% to nearly 40%, and showed a statistically significant increase over the study period ($\beta_{trend-prop\_second\_cl} = 0.03$, $z = 2.00$, $P = 0.045$; Table 2 and Figure 4). Despite several models assuming an effect of covariates had a similar AIC values (<2 points), none of the weather variables was significant or close to be, playing the role of "pretending variables" (Burnham and Anderson 2002). Indeed, the probability of SC was not associated to May–June weather ($\beta_{min\_temp} = -0.185$, $z = -1.411$, $P = 0.158$; $\beta_{temP} = 0.011$, $z = 0.084$, $P = 0.933$;

Table 2. Modeling the proportion of SCs through logistic regression

| Model	Effects	np	AIC	ΔAIC
4	**RainMJ+linear trend**	**3**	**558.679**	**0**
2	**Linear trend**	**2**	**559.454**	**0.775**
9	**TempMJ+linear trend**	**3**	**559.455**	**0.776**
5	**TempMJ+RainMJ+linear trend**	**4**	**560.550**	**1.871**
7	RainJL+linear trend	3	561.162	2.483
6	TempJL+linear trend	3	561.238	2.558
3	TempMJ+linear trend	3	561.447	2.768
0	Constant	1	561.556	2.876
8	TempJL+Rain_JL+linear trend	4	562.690	4.010
1	Year	22	563.050	4.371

np, number of parameters in the model; AIC = Akaike's Information Criterion; ΔAIC, difference with the lowest AIC; Temp_MJ, mean temperature in May–June; rain_MJ, mean rainfall in May–June; temp_JL, mean temperature in July; rain_JL, mean rainfall in July. When testing for weather covariates, we included a linear effect of the year to account for possible trend of the covariate.

$\beta_{raiN} = -0.327$, $z = -1.663$, $P = 0.096$, respectively), nor to July covariates ($\beta_{temP} = -0.042$, $z = -0.466$, $P = 0.641$ and $\beta_{raiN} = -0.103$, $z = -0.538$, $P = 0.593$; Table 2).

BS and BO

BS was modeled by considering 419 first-clutches with known LD. It varied over the year, increasing from 0.72 (SE = 0.13) in 1992 to 0.92 (SE = 0.05) in 2010 and 1.00 during the last 3 years of the study (Figure 5). The model with the lowest BIC value (Table 3) was the one assuming a linear trend over the year (Table 3) but a model assuming an effect of the average July temperature had only a slightly larger BIC value and should be considered an equally good model (Table 3 and Figure 5). This covariate had a positive and statistically significant effect ($\beta_{temp\_JL} = 0.319$, $z = 2.25$, $P = 0.02$). The length of the breeding period, that is, the interval between the earliest and the latest first clutch, was also significantly correlated with the annual BS ($\beta_{length} = 0.0364$, $z = 2.799$, $P < 0.013$), whereas the rainfall was not statistically associated in any of the 2 periods considered ($\beta_{rain\_MJ} = -0.45967$, $z = -1.413$, $P = 0.158$, $\beta_{rain\_JL} = -0.04597$, $z = -0.148$, $P = 0.882$, for May–June and July, respectively).

The number of fledged chicks was modeled using 432 first-clutches in which at least one egg had hatched. The model with the
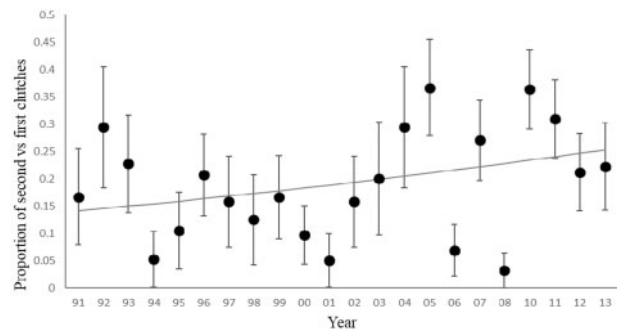
Figure 4. Proportion of second versus first clutches of the rock sparrow over the study period (1991–2013, $N = 558$). Vertical lines are the 95% confidence interval.
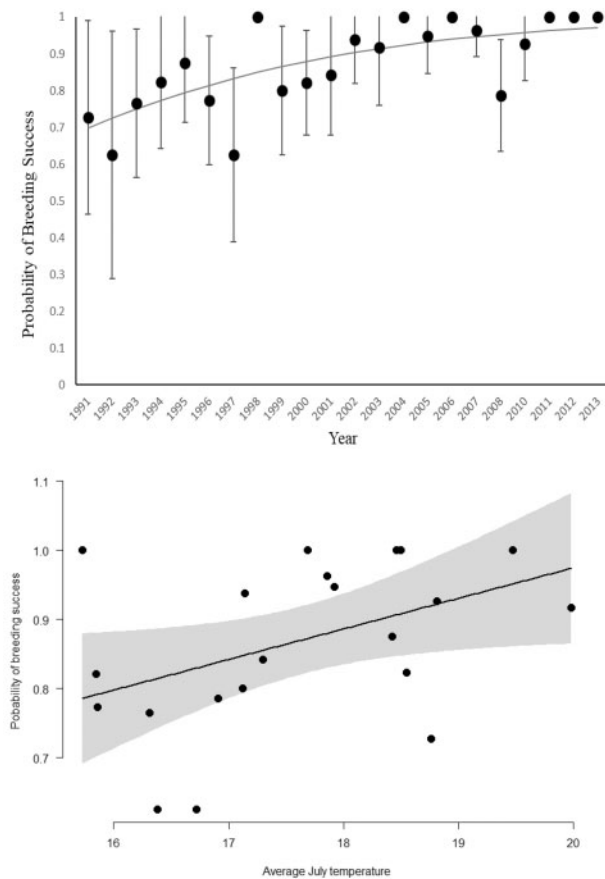
Figure 5. Upper panel: First clutches ($N=419$) BS variation over the study area (range 0.625–1.00). Straight line indicates the linear trend. Vertical lines are the 95% confidence interval. Lower panel: BS according to average July temperature.

lowest BIC was the one assuming a constant value, however, the average number of fledglings per nest increased significantly ($\chi_1^2=7.31$, $P=0.007$) from 3.4 to 4.7 over the study period. The model assuming an association between the number of fledglings and the average July temperature has the lowest BIC among those including weather covariates (Table 4). The effect of this covariate was positive and close to be statistically significant ($\chi_1^2=3.679$, $P=0.055$). The total number of fledglings produced by all monitored nests ($N=615$) increased significantly over the study period (Poisson regression, $\beta_{\text{trend}}=0.0357$, $z=11.05$, $P<0.01$, $N=22$), from an average value of 93 fledglings produced during the first 5-year period (1991–1995) to 150 during the last one (2008–2013, note that 2009 was excluded).

Discussion

We found no evidence of a significant advance in the onset of the reproduction over the 22 years of the study. In contrast, there was evidence of a progressive increase in the length of the breeding season and of an increase in the frequency of SCs. We also found that the probability of nest success and the average number of fledglings produced increased significantly over the study period. Next success was significantly correlated with July temperature. The association of this covariate with the number of fledglings produced in first clutches was also positive and close to be statistically significant

Table 3. Modeling BS through general linear mixed models in which nest identity and year (as a factor) were considered as a random effect

Model	Effect	np	BIC	ΔBIC
1	**Linear trend**	**4**	**305.888**	**0**
7	**TempJL+linear trend**	**5**	**307.323**	**1.435**
4	RainMJ+linear trend	5	309.88	4.001
3	TempMJ+linear trend	5	310.009	4.121
6	LD	5	311.012	5.124
12	minTempMJ+linear trend	5	311.186	5.298
8	RainJL+linear trend	5	311.904	6.016
11	TempJL+TempMJ+linear trend	6	320.157	6.327
9	TempJL+RainJL+linear trend	6	325.377	6.702
10	TempJL+RainMJ+linear trend	6	390.206	7.039
5	TempMJ+RainMJ+linear trend	6	314.301	8.413
0	Constant	2	315.063	9.175
2	Year	24	396.243	90.355

np, number of parameters in the model; BIC, Bayesian Information Criterion; ΔBIC, difference with the lowest BIC; Temp_MJ, mean temperature in May and June; Rain_MJ, mean rainfall in May and June; Temp_JL, mean temperature in July; and Rain_JL, mean rainfall in July. Retained models are marked in bold. When testing for weather covariates, we included a linear effect of the year to account for possible trend of the covariate.

($P=0.055$). Despite reported as one of the most common response of numerous organisms to recent climate change (McCleery and Perrins 1998; Brown et al. 1999; Crick and Sparks 1999; Dunn and Winkler 1999; Matthysen et al. 2011; Dunn and Møller 2014), Rock sparrows did not advance the onset of the reproduction. Proximate causes of LD include multiple local factors such as precipitation (Leitner et al. 2003; Rodríguez and Bustamante 2003; Martin et al. 2014), photoperiod (Wingfield et al. 2003), local

Table 4. Modeling the number of fledgling in first clutches where at least 1 egg had hatched through linear mixed models in which nest identity and year were considered as a random effect

Model	Effect	np	BIC	ΔBIC
1	**– (constant)**	**4**	**816.9942**	**0**
2	Linear trend	5	824.1599	7.1657
7	TempJL+linear trend	6	831.7372	14.743
5	RainMJ+linear trend	6	831.8683	14.8741
8	RainJL+linear trend	6	833.5796	16.5854
4	TempMJ+linear trend	6	833.8535	16.8593
10	RainMJ+ RainJL+linear trend	7	840.1814	23.1872
9	TempJL+RainJL+linear trend	7	840.334	23.3398
11	TempJL+TempMJ+linear trend	7	841.7367	24.7425
6	TempMJ+RainMJ+linear trend	7	841.7687	24.7745
3	Year	24	935.3414	118.3472

np, number of parameters in the model, BIC, Bayesian Information Criterion; ΔBIC, difference with the lowest BIC value. Temp_MJ, mean temperature in May and June; Rain_MJ, mean rainfall in May and June; Temp_JL, mean temperature in July; Rain_JL, mean rainfall in July. In bold, the model with the lowest AIC value. The model retained is in bold.

weather conditions (e.g., snow cover; Hendrics 2003 and temperature Phillimore et al. 2016), the quality, abundance and availability of food (Reed et al. 2013), age and endogenous factors (Goutte et al. 2010), and their interactions (Carey 2009). We found that breeding onset, that is, the average and earliest LD of first clutches, varied with May–June weather conditions, which can influence food availability (e.g., grasshoppers; Biddau et al. 1995). However, the covariates considered, with the exception of June minimum temperature, did not show a clear increasing trend over time (see also Fletcher et al. 2013; Lv et al. 2020 for similar results on Red Grouse *Lagopus lagopus* and Superb Fairy-Wrens *Malurus cyaneus*, respectively). This contrasts with the long-term tendency of climate in the Alps (Gobiet et al. 2014), and was probably due to the relative short time series and the aberrant values of the LD distribution registered in 2008, for which we do not have a clear explanation. Also, topography, microclimate, orientation of slope, and type of plant cover can modulate the way in which climate warming influences biological responses (Durand et al. 2009). Tomás (2015) argue that hatching date should be a more reliable variable to study optimal timing of breeding than LD. We have focused on this latter for comparative purposes because many studies on bird phenology reported a shift in this parameter, especially for migratory birds (Crick et al. 1997). It is also possible that local spring snow cover, which largely depends on the very variable precipitations during late winter, sets a constraint to the onset of the reproduction (see also Hendrics 2003; Jenny and Kéry 2003; Scridel et al. 2018). However, we did not have quantitative snow cover data for the local population and we were not able to explore this potential proximate cause.

The most important change that we found was a stretch of the breeding period represented by a significant delay of the latest first-clutches, leading to a statistically significant extension of the breeding period (∼1.5 days/year, see also Halupka and Halupka 2017). We recorded an increase in the proportion of SCs, likely due to this extension, and in the total number of fledged chicks in the population. This was in agreement with results from long-term studies on 24 populations of tits (*Parus* sp.) from 6 European countries that suggested a link between rising temperatures and the frequency of second broods (Visser et al. 2003). A delay in the LD of the latest first clutches can result from low-quality phenotypes or later arrivals that would have struggled to breed when breeding season was short. Further investigations using for example a measure of individual quality (e.g., Griggio et al. 2003) should be conducted to clarify this point. An increase in the frequency of SCs and on the average number of fledglings does indicate that birds were constrained by the short length of the breeding season during the early years.

Climatic variables can play a different role according to the parameter considered (e.g., Mattyshen et al. 2011). This interplay can make difficult to generalize the impact of and the individual responses to climatic changes. Climate change has been shown to extend breeding period in multiple brood species of birds of ∼0.43 days/year (Møller et al. 2010), but in our case, and contrary to what previously thought, this extension is due to a progressive delay in the LD of the latest first clutches (Halupka and Halupka 2017). The earliest arrival and the average BS were associated to spring and summer temperature showing a clear positive relation with warmer weather, but these covariates did not explain the increasing LD of the latest clutches, responsible for the stretch of the breeding period. Similar results were found for the Superb Fairy-Wren in which the breeding onset is associated with spring temperature but warmer temperatures did not result in earlier breeding over the year (Lv et al. 2020).

In conclusion, climatic changes in the Alpine region are favoring the rock sparrow through a higher BS and a longer breeding period. Despite our population might be limited by the number of nest boxes, we expect an increase in the occupation rate and/or colonization of new areas. These changes are expected to play a role in slowing down the "fast breeding" strategy observed in the individuals of this population, characterized for example by a high frequency of polygamy and female nest desertion. Our results suggested that the low number of SCs recorded during the early years of the study resulted from a constrain due to the short breeding season (see also Pilastro et al. 2001). Further work should focus on other aspects of the breeding strategy of the rock sparrow, which can be potentially affected by an extended breeding period, such as, for example the frequency of nest desertion or the probability of permanent dispersal (Pilastro et al. 2001; Tavecchia et al. 2002).

Author Contributions

T.M. coordinated the project because of its inception and with A.M. and G.T. designed the experiments and analyzed the data. P.S. and G.V. collected the data (1999–2013) and contributed to data analysis. All authors edited and contributed to the article and approved the final manuscript.

Compliance with Ethical Standards

All authors have examined and agreed on the manuscript, have agreed to be listed, and contributed to the research reported. The authors declare that they have no conflict of interest. The study complies with institutional, national, and international ethics guidelines concerning the use of animals in research and/or the sampling of endangered species. None of the procedures used in the study met the criteria to define them "experiments" as defined in Article 2 of the EEC Directive 86/609/EEC regarding the protection of animals used for experimental and other scientific purposes.

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Conflict of Interest

There are no conflicts of interest in the current work.

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References

Auer SK, King DI, 2014. Ecological and life-history traits explain recent boundary shifts in elevation and latitude of western North American songbirds. *Glob Ecol Biogeogr* **23**:867–875.

Bates D, 2019. R topics documented. Package "lmer4". Available from: https://cran.r-project.org/web/packages/lme4/lme4.pdf (last visited 16 May 2019).

Bellard C, Bertelsmeier C, Leadley P, Thuiller W, Courchamp F, 2012. Impacts of climate change on the future of biodiversity. *Ecol Lett* **15**: 365–377.

Biddau L, Mingozzi T, Fedrighini N, 1995. Trophic resource availability and mating systems: a progressive study concerning an Alpine population of *Petronia petronia* (L). *Suppl Ric Biol Selv* **22**:225–230.

Both C, 2010. Food availability, mistiming, and climatic change. In: Moller AP, Fiedler W, Berthold P, editors. *Effects of Climate Change on Birds*. Oxford: Oxford University Press. 129–147.

Both C, Artemyev AV, Blaauw B, Cowie RJ, Dekhuijzen AJ et al., 2004. Large-scale geographical variation confirms that climate change causes birds to lay earlier. *Proc R Soc Lond Ser B Biol Sci* **271**:1657–1662.

Brown CR, Bomberger Brown M, 2000. Weather-mediated natural selection on arrival time in cliff swallows *Petrochelidon pyrrhonota*. *Behav Ecol Sociobiol* **47**:339–345.

Brown JL, Li SH, Bhagabati N, 1999. Long-term trend toward earlier breeding in an American bird: a response to global warming? *Proc Nat Acad Sci U S A* **96**:5565–5569.

Burnham KP, Anderson DR, 2002. *Model Selection and Inference: A Practical Information-Theoretic Approach*. 2nd edn. New York (NY): Springer.

Carey C, 2009. The impact of climate change on the annual cycle of birds. *Phil Trans R Soc B* **364**:3321–3330.

Chamberlain D, Arlettaz R, Caprio E, Maggini R, Pedrini P et al., 2012. The altitudinal frontier in avian climate impact research. *Ibis* **154**:205–209.

Chambers LE, Altwegg R, Barbraud C, Barnard P, Beaumont LJ et al., 2013. Phenological changes in the southern hemisphere. *PLoS ONE* **8**:e75514.

Cramp S, Perrins CM, 1994. *Handbook of the Birds of Europe, the Middle East, and North Africa: The Birds of the Western Palearctic Volume IX: Buntings and New World Warblers*. Oxford: Oxford University Press.

Crick HQP, Dudley C, Glue DE, Thomson DL, 1997. UK birds are laying eggs earlier. *Nature* **388**:526.

Crick HQP, Sparks TH, 1999. Climate change related to egg-laying trends. *Nature* **399**:423–423.

Crick HQP, Sparks TH, 2006. Changes in the phenology of breeding and migration in relation to global climate change. *Acta Zool Sin* **52**:154–157.

Clutton-Brock T, Sheldon B, 2010. Individuals and populations: the role of long-term, individual-based studies of animals in ecology and evolutionary biology. *Trend Ecol Evol* **25**:562–573.

Devictor V, Julliard R, Couvet D, Jiguet F, 2008. Birds are tracking climate warming, but not fast enough. *Proc R Soc B Biol Sci* **275**:2743–2748.

Dunn P, 2004. Breeding dates and reproductive performance. In: Moller WFA, Berthold P, editors. *Advances in Ecological Research*. Vol. **35**. Cambridge (MA): Academic Press. 69–87.

Dunn PO, Møller AP, 2014. Changes in breeding phenology and population size of birds. *J Anim Ecol* **83**:729–739.

Dunn PO, Winkler DW, 1999. Climate change has affected the breeding date of tree swallows throughout North America. *Proc R Soc B Biol Sci* **266**: 2487–2490.

Dunn PO, Winkler DW, 2010. Effects of climate change on timing of breeding and reproductive success in birds. In: Moller AP, Fiedler W, Berthold P, editors. *Effects of Climate Change on Birds*. Oxford: Oxford University Press. 336.

Durand Y, Giraud G, Laternser M, Etchevers P, Mérindol L et al., 2009. Reanalysis of 47 years of climate in the French Alps (1958–2005): climatology and trends for snow cover. *J Appl Meteorol Climatol* **48**:2487–2512.

Fletcher K, Howarth D, Kirby A, Dunn R, Smith A, 2013. Effect of climate change on breeding phenology, clutch size and chick survival of an upland bird. *Ibis* **155**:456–463.

Foden WB, Butchart SHM, Stuart SN, Vié JC, Akçakaya HR et al., 2013. Identifying the world's most climate change vulnerable species: a systematic trait-based assessment of all birds, amphibians and corals. *PLoS ONE* **8**: e65427.

Forchhammer MC, Post E, Stenseth NC, 2002. North Atlantic oscillation timing of long- and short-distance migration. *J Anim Ecol* **71**:1002–1014.

Francon L, Corona C, Till-Bottraud I, Choler P, Carlson BZ et al., 2020. Assessing the effects of earlier snow melt-out on alpine shrub growth: the sooner the better? *Ecol Indicat* **115**:106455.

Gobiet A, Kotlarski S, Beniston M, Heinrich G, Rajczak J et al., 2014. 21st century climate change in the European Alps: a review. *Sci Total Environ* **493**:1138–1151.

Goutte A, Antoine É, Weimerskirch H, Chastel O, 2010. Age and the timing of breeding in a long-lived bird: a role for stress hormones? *Funct Ecol* **24**: 1007–1016.

Griggio M, Tavecchia G, Biddau L, Mingozzi T, 2003. Mating strategies in the rock sparrow *Petronia petronia*: the role of female quality. *Ethol Ecol Evol* **15**:389–398.

Haest B, Hüppop O, Bairlein F, 2018. Challenging a 15-year-old claim: the North Atlantic oscillation index as a predictor of spring migration phenology of birds. *Glob Chang Biol* **24**:1523–1537.

Halupka L, Halupka K, 2017. The effect of climate change on the duration of avian breeding seasons: a meta-analysis. *Proc R Soc B Biol Sci* **284**: 20171710.

Hitch AT, Leberg PL, 2007. Breeding distributions of North American bird species moving north as a result of climate change. *Conserv Biol* **21**: 534–539.

Hendrics P, 2003. Spring snow conditions, laying date, and clutch size inan alpine population of American Pipits. *J Field Ornithol* **74**:423–429.

IPCC, 2013. *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. New York (NY): Cambridge University Press.

Jenny L, Kéry M, 2003. Timing of autumn bird migration under climate change: advances in long-distance migrants, delays in short-distance migrants. *Proc Biol Sci* **270**:1467–1471.

Jonzén N, Hedenström A, Lundberg P, 2007. Climate change and the optimal arrival of migratory birds. *Proc R Soc B Biol Sci* **274**:269–274.

Karvonen J, Orell M, Rytkönen S, Broggi J, Belda E, 2012. Population dynamics of an expanding passerine at the distribution margin. *J Avian Biol* **43**: 102–108.

Laiolo P, Dondero F, Ciliento E, Rolando A, 2004. Consequences of pastoral abandonment for the structure and diversity of the alpine avifauna. *J App Ecol* **41**:294–304.

Lebreton JD, 1975. Distribution française du Moineau soulcie *P. petronia* (L). *L'Oiseau et R.F.O* **45**:65–71.

Lehikoinen A, Green M, Husby M, Kålås JA, Lindström Å, 2014. Common montane birds are declining in northern Europe. *J Avian Biol* **45**:3–14.

Leitner S, Van't Hof TJ, Gahr M, 2003. Flexible reproduction in wild canaries is independent of photoperiod. *Gen Comp Endocrinol* **130**:102–108.

Lenoir J, Svenning JC, 2014. Climate-related range shifts: a global multidimensional synthesis and new research directions. *Ecography* **38**:15–28.

Lv L, Liu Y, Osmond HL, Cockburn A, Kruuk LEB, 2020. When to start and when to stop: effects of climate on breeding in a multi-brooded songbird. *Glob Chang Biol* **26**:443–457.

Martin RO, Sebele L, Koeslag A, Curtis O, Abadi F et al., 2014. Phenological shifts assist colonisation of a novel environment in a range-expanding raptor. *Oikos* **123**:1457–1468.

Matthysen E, Adriaensen F, Dhondt AA, 2011. Multiple responses to increasing spring temperatures in the breeding cycle of blue and great tits (*Cyanistes caeruleus, Parus major*). *Glob Chang Biol* **17**:1–16.

McCleery RH, Perrins CM, 1998. …temperature and egg-laying trends. *Nature* **391**:30–31.

Mingozzi T, Biddau L, Rinaldi F, Rosselli D, 1994. The rock sparrow *Petronia petronia* in the Western Alps: a multidisciplinary research programme. *VI Convegno Italiano di Ornitologia, Mus. Reg. Sc. Nat., Torino*. 363–374.

Mingozzi T, Onrubia A, 1997. *Petronia petronia* rock sparrow. In: Hagemeijer EJM, Blair M, editors. *The Ebcc Atlas of European Breeding Birds: Their Distribution and Abundance*. London: Academic Press. p. 699.

Møller AP, Flensted-Jensen E, Klarborg K, Mardal W, Nielsen JT, 2010. Climate change affects the duration of the reproductive season in birds. *J Anim Ecol* 79:777–784.

Noriega AE, Ventosa-Santaulària D, 2007. Spurious regression and trending variables. *Oxford Bull Econ Stat* 69:439–444.

Novoa C, Besnard A, Brenot JF, Ellison LN, 2008. Effect of weather on the reproductive rate of rock ptarmigan *Lagopus muta* in the eastern Pyrenees. *Ibis* 150:270–278.

Oliver TH, Morecroft MD, 2014. Interactions between climate change and land use change on biodiversity: attribution problems, risks, and opportunities. *Clim Chang* 5:317–335.

Orlandi S, Probo M, Sitzia T, Trentanovi G, Garbarino M et al., 2016. Environmental and land use determinants of grassland patch diversity in the western and eastern Alps under agro-pastoral abandonment. *Biodivers Conserv* 25:275–293.

Pacifici M, Foden WB, Visconti P, Watson JEM, Butchart SHM et al., 2015. Assessing species vulnerability to climate change. *Nat Climate Chang* 5: 215–224.

Parmesan C, 2006. Ecological and evolutionary responses to recent climate change. *Ann Rev Ecol Evol Syst* 37:637–669.

Parmesan C, Yohe G, 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421:37–42.

Phillimore AB, Leech DI, Pearce-Higgins JW, Hadfiled JD, 2016. Passerines may be sufficiently plastic to track temperature-mediated shifts in optimum lay date. *Glob Chang Biol* 22:3259–3272.

Pilastro A, Biddau L, Marin G, Mingozzi T, 2001. Female brood desertion increases with number of available mates in the rock sparrow. *J Avian Biol* 32:68–72.

Reed TE, Jenouvrier S, Visser ME, 2013. Phenological mismatch strongly affects individual fitness but not population demography in a woodland passerine. *J Anim Ecol* 82:131–144.

Reif J, Flousek J, 2012. The role of species' ecological traits in climatically driven altitudinal range shifts of central European birds. *Oikos* 121: 1053–1060.

Rodríguez C, Bustamante J, 2003. The effect of weather on lesser kestrel breeding success: can climate change explain historical population declines? *J Anim Ecol* 72:793–810.

Root TL, Price JT, Hall KR, Schneider SH, Rosenzweig C et al., 2003. Fingerprints of global warming on wild animals and plants. *Nature* 421: 57–60.

Scridel D, Brambilla M, Martin K, Lehikoinen A, Iemma A et al., 2018. A review and meta-analysis of the effects of climate change on Holarctic mountain and upland bird populations. *Ibis* 160:489–515.

Sergio F, Newton I, 2001. Occupancy as a measure of territory quality. *J Anim Ecol* 72:857–865.

Shipley JR, Twining CW, Taff CC, Vitousek MN, Flack A et al., 2020. Birds advancing lay dates with warming springs face greater risk of chick mortality. *Proc Natl Acad Sci U S A* 117:25590–25594.

Sparks TH, Bairlein F, Bojarinova JG, Hüppop O, Lehikoinen EA et al., 2005. Examining the total arrival distribution of migratory birds. *Glob Chang Biol* 11:22–30.

Tavecchia G, Pradel R, Lebreton JD, Biddau L, Mingozzi T, 2002. Sex-biased survival and breeding dispersal probability in a patchy population of the rock sparrow *Petronia petronia*. *Ibis* 144:E79–E89.

Tavecchia G, Oro D, Sanz-Aguilar A, Bechet A, 2017. The multidimensional value of long-term individual-based studies: more than lots of data. *Avocetta* 41:19–21.

Tomás G, 2015. Hatching date vs laying date: what should we look at to study avian pptimal timing of reproduction? *J Avian Biol* 46: 107–112.

Visser ME, Adriaensen F, Van Balen JH, Blondel J, Dhondt AA et al., 2003. Variable responses to large-scale climate change in European *Parus* populations. *Proc R Soc B Biol Sci* 270:367–372.

Visser ME, Gienapp P, 2019. Evolutionary and demographic consequences of phenological mismatches. *Nat Ecol Evol* 3:879–885.

Weatherhead PJ, 2005. Effects of climate variation on timing of nesting, reproductive success, and offspring sex ratios of red-winged blackbirds. *Oecologia* 144:168–175.

Wingfield JC, Hahn TP, Maney DL, Schoec SJ, Wada M et al., 2003. Effects of temperature on photoperiodically induced reproductive development, circulating plasma luteinizing hormone and thyroid hormones, body mass, fat deposition and molt in mountain white-crowned sparrows, *Zonotrichia leucophrys oriantha*. *Gen Comp Endocrinol* 131:143–158.