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RESEARCH ARTICLE

Climate change and maladaptive wing shortening in a long-distance migratory bird

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ABSTRACT

Contemporary phenotypic trends associated with global change are widely documented, but whether such trends always denote trait optimization under changed conditions remains obscure. Natural selection has shaped the wings of long-distance migratory birds to minimize the costs of transport, and new optimal wing shapes could be promoted by migration patterns altered due to global change. Alternatively, wing shape could vary as a correlated response to selection on other traits favored in a changing environment, eventually moving away from the optimal shape for migration and increasing transport costs. Data from 20 yr of monitoring 2 Common Nightingale (*Luscinia megarhynchos*) populations breeding in central Spain, where environmental conditions for breeding have deteriorated during recent decades due to increased summer drought, show that birds have reduced wing length relative to body size over the period 1995–2014. However, long-winged nightingales survived their first round-trip migration better, and the shorter the average wing length of individuals, the stronger the survival-associated natural selection favoring longer wings. Maladaptive short wings may have arisen because the mortality costs of migration are outweighed by reproductive benefits accrued by short-winged nightingales in these populations. Assuming that the phenotypic integration of morphological and reproductive adaptations of migratory birds has a genetic basis, we hypothesize that the maladaptive trend towards shorter wings may be a correlated response to selection for moderate breeding investment in drying habitat. Our results provide evidence that contemporary phenotypic change may deviate average trait values from their optima, thereby increasing our understanding of the ecological constraints underpinning adaptation to rapid global change.

Keywords: apparent survival, climate change, *Luscinia megarhynchos*, migration, population monitoring, trait optimization, wing shape

Cambio climático y acortamiento maladaptativo del ala en un ave migratoria de larga distancia

RESUMEN

Numerosos estudios han documentado tendencias fenotípicas asociadas con el cambio global, pero no está claro que dichas tendencias representen siempre la optimización de rasgos en condiciones cambiantes. La selección natural ha modelado las alas de las aves migratorias de larga distancia para minimizar los costes de transporte, de modo que la alteración de los patrones migratorios por el cambio global podría promover nuevas morfologías alares óptimas. Sin embargo, una respuesta correlacionada a la selección de otros rasgos que pudieran ser favorables en un ambiente cambiante podría hacer variar también la forma del ala, alejándola de su óptimo para la migración e incrementando los costes de transporte. De acuerdo con los datos de 20 años de seguimiento de dos poblaciones de ruiseñores comunes (*Luscinia megarhynchos*) del centro de España, donde la creciente sequía estival ha deteriorado las condiciones ambientales en época de cría durante las últimas décadas, las aves han reducido la longitud de sus alas relativa al tamaño corporal a lo largo del periodo 1995–2014. Sin embargo, los ruiseñores de alas más largas sobrevivieron mejor a su primer viaje migratorio de ida y vuelta, y cuanto menor fue la longitud media del ala de los individuos, más fuerte fue la selección natural por supervivencia de los individuos de alas más largas. Las alas cortas, un rasgo maladaptativo, podrían haber incrementado su frecuencia en estas poblaciones si los ruiseñores de alas cortas compensasen mediante beneficios reproductivos los costes asociados con la mortalidad durante la migración. Asumiendo que la integración fenotípica de las adaptaciones morfológicas y reproductivas de las aves migratorias tiene una base genética, postulamos que la tendencia maladaptativa hacia alas más cortas puede ser una respuesta correlacionada a la selección a favor de una inversión reproductiva moderada en hábitats cada vez más secos. Nuestros resultados muestran que las poblaciones de aves pueden variar desviándose de su óptimo fenotípico, lo que nos ayuda a comprender mejor las restricciones ecológicas que pueden condicionar su adaptación al rápido cambio global.

Palabras clave: cambio climático, forma del ala, optimización de rasgos, supervivencia aparente, seguimiento de poblaciones, *Luscinia megarhynchos*, migración

INTRODUCTION

Global change has promoted many ecological and evolutionary responses of living beings, including shifting species' ranges, adjustment of seasonal cycles, and morphological adaptation (Parmesan and Yohe 2003, Hoffmann and Sgrò 2011, Radchuk et al. 2019). Phenotypic trends during recent decades have been interpreted as adaptive responses to natural selection associated with warmer climate (Lo Cascio Sætre et al. 2017, Weeks et al. 2020), shifted phenology (Both et al. 2006), or increased human footprint (Johnson and Munshi-South 2017). However, our understanding of the mechanisms underlying adaptation in a rapidly changing world is limited by the difficulty in documenting contemporary evolution in the wild, the lack of knowledge of trait heritabilities, and the complexity of correlated responses that may limit or nullify the fitness advantage of adaptive traits (Merilä 2012, Wegge and Rolstad 2017).

Migratory birds have been a favorite model for the study of adaptive change in the face of global change (Rolshausen et al. 2009, Knudsen et al. 2011, Salewski et al. 2014, Møller et al. 2017, Weeks et al. 2020). Decades of research and monitoring of bird populations have helped to build comprehensive knowledge of the ecological and evolutionary determinants of variation in migratory behavior and its associated phenotypic traits, from the seasonal patterning of annual cycles to morphological adaptations (Helm et al. 2013, Hahn et al. 2016, Vágási et al. 2016). As a general rule, seasonal primary production is considered to be the main driver of the evolution of migration, because fecundity benefits associated with breeding in highly productive habitat compensates the mortality cost of transport incurred by tracking seasonal production pulses (Thorup et al. 2017). In these circumstances, natural selection may favor individuals that are genetically programmed not only to have optimal morphology and behavior for traveling, but also to "live faster" (Wikelski et al. 2003, Piersma et al. 2005, Van Noordwijk et al. 2006, Dingle and Drake 2007, Liedvogel et al. 2011). This adaptive integration of behavioral, physiological, and life-history traits is termed the "migratory syndrome" (Dingle and Drake 2007), which may be viewed as a particular case of the so-called "pace of life syndromes" that position populations, or individuals within populations, on a slow-fast continuum of life-history variation (Ricklefs and Wikelski 2002, Wikelski et al. 2003, Dammhahn et al. 2018). Thus, the most migratory birds not only show morphological adaptations such as long wingspan suited for rapid flight (Tellería et al. 2001, Piersma et al. 2005), but also locate on the fast extreme of the pace of life continuum, showing higher resting metabolic rate, larger clutch size, or shorter lifespan than less migratory birds (Gwinner et al. 1995, Pérez-Tris and Tellería 2002, Wikelski et al. 2003).

The migratory gene package hypothesis proposes that the phenotypic integration of the various adaptations that characterize migratory birds has a genetic basis (Liedvogel et al. 2011). Empirical evidence in support of this idea comes from (1) quantitative genetic analyses showing genetic correlations among traits (Gwinner et al. 1995, Pulido 2007), (2) divergent populations expressing consistently distinct phenotypes in common garden settings (Wikelski et al. 2003), (3) phenotypic correlations across populations (e.g., long wings associated with high fecundity or increased resting metabolic rate; Gwinner et al. 1995, Pérez-Tris and Tellería 2002, Wikelski et al. 2003), (4) within-population correlations among traits (e.g., arrival date and fecundity; Both and Visser 2005, Teplitsky et al. 2011), or (5) temporal trends of concerted change of phenotypic traits (Weeks et al. 2020). Under the migratory gene package paradigm, ecological influences outside migration periods that change the optimal pace of life may have a correlated effect on other components of the migratory syndrome, either facilitating or constraining adaptation of migratory birds (Merilä 2012, Møller et al. 2017). Therefore, the migratory gene package paradigm provides a convenient framework for interpreting contemporary phenotypic trends, particularly so when different traits change in a concerted manner that is difficult to interpret as adaptive (Weeks et al. 2020).

Long-term population monitoring provides the natural setting in which to link environmental fluctuations with contemporary phenotypic change (Clutton-Brock and Sheldon 2010, Karell et al. 2011, Tellería et al. 2013). Rapid climate warming during recent decades (IPCC 2013) has promoted phenotypic trends of migratory birds, involving traits like body size, arrival time, lay date, or brood size, among others (Both and Visser 2001, 2005, Yom-Tov et al. 2006, Salewski et al. 2014, Usui et al. 2017, Weeks et al. 2020). However, the question remains open whether these trends represent direct responses to selection pushing adaptive traits towards new optima, or they rather arise as correlated responses to selection acting on other traits, or as plastic responses, with newly favored phenotypes being uncorrelated with fitness or even constraining adaptation if maladaptive traits increase frequency. The combined analysis of phenotypic trends and individual fitness may provide insight into the ecological constraints underpinning adaptation of migratory birds confronted with rapid climate change (Chown et al. 2010, Radchuk et al. 2019).

Using the Common Nightingale (*Luscinia megarhynchos*) as a model, we set out to test whether there is a temporal trend of change in wing length relative to body size, a trait important for flight performance in long-distance migratory passerines, parallel to local changes in environmental conditions in the breeding area. If such a trend exists, we aimed to test if the phenotypic change is adaptive (i.e. birds acquire new optimal phenotype) or maladaptive (i.e. phenotypic change impairs migration performance).

To this end, we analyzed variation in wing morphology and phenotype-dependent survival in 2 closely situated populations of nightingales from central Spain, using individual monitoring data spanning 20 yr (1995–2014). To gain insight into the possible influence of local environmental variation on phenotypic change, we also assessed local trends in the environmental variables that may best describe how nightingale habitats have changed over the years, as well as the variation in nightingale arrival or breeding dates. This was deemed important because global climate trends are not always reproduced at lower scales (Wilbanks and Kates 1999), meaning that widespread species may show variable local responses (Hahn et al. 2016). Temporal shifts in spring phenology could be paralleled by adaptive phenotypic trends in local nightingale populations: long-winged, speedier nightingales could be at an advantage if breeding seasons become earlier or shorter in terms of green-up phenology or insect availability (Hahn et al. 2016), while shorter wings could arise as a response to delayed springs, which would relax selection for earliness (Alerstam et al. 2007). However, the Mediterranean region is recognized as a climate change hot spot because of its pronounced warming and decreasing precipitation during spring and summer (Giorgi and Bi 2005, Giorgi 2006, Giorgi and Lionello 2008). Therefore, instead of shifting productivity peaks or changing flight speed necessities, Mediterranean nightingale populations may be facing progressively drier breeding seasons. An intensified summer drought has an impact on bird populations at the end of the breeding season and therefore may not change optimal arrival time to promote adaptive change in wing length. But it may favor individuals with an energetically inexpensive, slower pace of life, because xericity strongly limits the reproductive potential of Mediterranean birds by compromising the viability of offspring, particularly so if young overlap growth with periods of hydric stress (Pérez-Tris et al. 2000, Carbonell et al. 2003, Charmantier et al. 2016). In particular, natural selection for slow pace of life may favor individuals that lay small clutches (whose smaller broods are easier to rear under xeric conditions due to reduced parental effort). If small clutch size and short wings compared with body size are correlated in nightingales, as they are in other closely related passerines (Gwinner et al. 1995, Starck et al. 1995, Pérez-Tris and Tellería 2002, Baldwin et al. 2010), the selective process may result in shortened wing length, not as the result of morphological optimization, but rather as a correlated response to selection favoring another component of the migratory syndrome (Piersma et al. 2005, Van Noordwijk et al. 2006). In this case, wing shortening might impair migration performance up to compromise survival, so that the selected phenotype would be one with a wing shape that is maladaptive for migratory performance. To sum up, the combined analysis of morphological variation and phenotype-dependent survival may help to distinguish adaptive morphological change from maladaptive phenotypic shifts (Radchuk et al. 2019), thereby improving our capacity to correctly interpret contemporary trends of morphological variation in migratory birds.

METHODS

Species and Banding Data

The Common Nightingale is a long-distance migratory passerine widespread in Europe, where it shows morphological variation associated with differences among populations in distance of migration and speed of spring green-up at migration destination (Hahn et al. 2016). Conveniently for our study, nightingales keep juvenile flight feathers until their second summer, moulting them once they have completed the first round-trip migratory journey. This attribute facilitates the direct comparison of the flight apparatus of young birds measured before the first migration with that of recruits that return from sub-Saharan Africa the following year. Nightingales breed mainly in moist lowland woodland, from late April (when first clutches occur) to mid-July (when the latest young reach independence), and usually lay 4–5 eggs. Incubation spans 13–14 days and nestlings leave the nest at age 10–12 days, although they are able to fly 3–5 days later (Collar 2005).

We used data from 2 constant effort ringing sites operated weekly. Las Minas (40.2245°N, 03.5475°W) is a reed bed that has been sampled all year around since 1995. Presa del Rey (40.3010°N, 03.5414°W) is a riverside forest sampled only during the spring–summer period (early April to mid-July), from 1998 to 2014 (Supplementary Material S1 and Figure S2.1 in Supplementary Material S2). These 2 habitat types represent 2 extremes of habitat quality for nightingales, high in the forest and low in the reed bed (Holt et al. 2010), a circumstance that makes our results more generalizable. Nightingales were aged by plumage (Jenni and Winkler 1994), distinguishing among young (hatch-year birds), recruits (second year), and older birds (after-second-year birds, hereafter adults). Many birds were sexed by the presence of a brood patch or protruding cloaca, but juveniles could not be sexed, and therefore we did not include sex in the analyses. Body measures included wing maximum chord (to the nearest 0.5 mm), tarsus length (0.01 mm), fat score (Kaiser 1993), and body mass (to the nearest 0.01 g). Given that birds were measured by many observers, we computed intraclass correlation coefficients (r_i; Lessells and Boag 1987) to estimate the repeatability of wing and tarsus length from measures of the same individual obtained during the same year and with the same plumage (thereby avoiding confusion between measurement error and ontogenetic change). Both traits were repeatable (wing length; $r_i = 0.86$, $F_{324,543} = 17.94$, $P < 0.001$; tarsus length; $r_i = 0.87$, $F_{331,555} = 18.93$, $P < 0.001$).

We filtered the data to select records of breeding birds (adults or second-year recruits) and young hatched in the area, based on capture dates and recapture history. We defined a conservative period of absence of birds in passage spanning from May 15 to July 15 for breeding birds (July 31 for young birds). Birds that were captured at least once within this time window were considered to belong to the local breeding population. Each individual was assigned an average morphology each year it was captured, which was computed from mean tarsus and wing lengths measured that year. Data selection is described in detail in Supplementary Material S1.

Environmental Variables

To describe the change in spring and summer environmental conditions faced by local nightingale populations, we used several indices derived from satellite images, temperature and humidity data in a region of central Spain that included both study sites. The spatial and temporal resolution of each variable varied according to the available data.

Spring productivity. The normalized difference vegetation index (NDVI) is widely used as a proxy of vegetation productivity in studies that link animal dynamics to environmental variation (Pettorelli et al. 2005). We used standardized NDVI data from the Vegetation Index and Phenology (VIP) Earth Science Data Records Project, VIP07 series (Didan et al. 2016; data available from 1982 to 2014) extracted from 2 nearby extents in central Spain (Supplementary Material S2). We classified NDVI by land use because phenology is influenced by the type of vegetation (Badeck et al. 2004). Detailed information regarding the data-filtering process is available in Supplementary Material S2. The spring was characterized each year by the start and end of the season (those days with the maximum and minimum slope of NDVI increase, respectively), date of maximum productivity (when NDVI reaches its maximum), spring green-up slope (the difference in NDVI between the maximum and its level at the start of spring, divided by the days which have elapsed between the 2), and spring green-down slope (the difference in NDVI between the maximum and the level at the end of spring, divided by the days which have elapsed between the 2).

Summer temperature and humidity. Nightingale juvenile production peaks during summer (June–July in our study area, see also Collar 2005), which in the Mediterranean is characterized by a drought period that impairs juvenile development (Pérez-Tris et al. 2000). We described summer seasons by temperature and humidity data extracted using R package *RNCEP* from the National Centers for Environmental Prediction (Kemp et al. 2012; data from 1950 to 2014, 2.5° spatial resolution in [latitude/longitude] grid format). We calculated day of maximum temperature, maximum temperature, day of minimum humidity, minimum humidity, speed to reach maximum temperature (the difference in temperature between the maximum and the value at the start of temperature increase, divided by the days which have elapsed between the 2), and speed to reach minimum humidity (the difference in humidity between the minimum and the value at the start of the humidity decrease, divided by the days which have elapsed between the 2).

Computing season indices. The abovementioned spring and summer season variables were estimated using general additive models (GAM, *mgcv* package in R; Wood 2017) for detecting the day when the derivative of smooths with associated standard errors (2-day intervals) was maximum (start of the spring season and start of temperature increase) and minimum (end of the spring season and start of humidity decrease). We also used these models to estimate the dates when predicted NDVI and temperature reached their maximum value, and the date when humidity reached its minimum (day of maximum productivity, day of maximum temperature, and day of minimum humidity, respectively). All computations were performed with R software 3.5.3 (R Development Core Team 2019). Deviances explained by the spline grid models ranged from 19.87 to 85.28% (average = 55.75%) in NDVI data, 75.42 to 89.46% (average = 84.90%) in temperature data, and 34.21 to 69.39% (average = 53.28%) in humidity data. Finally, we performed principal components analyses (PCA) with standardized variables and varimax rotation (*psych* package in R; Revelle 2019) to characterize general patterns of spring or summer season development. We used the factor scores generated as indices of the spring and summer phenology. Spring season was characterized by 2 factors representing spring earliness, which opposes early to late spring seasons and rate of spring advancement, which opposes fast-advancing to slow-advancing spring seasons. Spring earliness (55% explained variance) was positively related with start of spring, day of maximum productivity, and end of spring (loading factors ≥0.88). Rate of spring advancement (24.0% explained variance) was positively related with spring green-up slope and negatively related with spring green-down slope (absolute loading factors ≥0.65). Similarly, summer season was described by 2 factors: the first one was related with the intensity of the summer drought, which opposed rapidly warming hot and dry summers to slowly warming milder ones, and the second with summer earliness, which opposed early-warming to late-warming summer seasons. Intensity of the summer drought (41% explained variance) was positively related with maximum temperature and speed to reach maximum temperature (loading factors ≥0.78). This factor also increased its value in summers when moisture was low, and humidity decreased rapidly and consequently reached its minimum earlier (loading factors ≤–0.54). Summer earliness (27.0%

of explained variance) was positively related with day of maximum temperature and negatively with minimum humidity (absolute loading factors ≥0.62).

Insect phenology. Insects are the main food of passerine nestlings and therefore adjusting the nesting period to insect phenology is key for breeding success (Visser et al. 1998). Following recommendations by Emmenegger et al. (2014) and Hahn et al. (2016), we used accumulated degree-days as a proxy of insect growth or development (Jarošík et al. 2011). We estimated for each year the onset of high availability of insects (FA_{high}, which stands for high food availability) as the day when the accumulated temperature reaches 59.1°C days, the average hatching temperature of first stages of insect larvae (Jarošík et al. 2011). Only temperatures above 10.4°C, the lower developmental threshold temperature of insects (Jarošík et al. 2011), were summed to obtain accumulated degree-days.

Morphological Variables

We analyzed temporal trends of change in wing length and tarsus length, 2 traits that capture important dimensions of the flight apparatus of migratory birds (Tellería and Carbonell 1999). However, variation in body dimensions is primarily dependent on differences in body size. Therefore, we used PCA of wing and tarsus length to obtain orthogonal indices of structural body size and size-independent body shape (Rising and Somers 1989, Pérez-Tris and Tellería 2001). The PC1 explained 61.2% of variance and their scores were positively correlated with both variables (loading = 0.78), thereby representing structural body size. The remaining 38.8% of variance was captured by PC2, which was positively correlated with wing length (loading = 0.62) and negatively correlated with tarsus length (loading = –0.62). Thus, we used individual PC1 scores as an index of structural body size, and PC2 scores as an index of the morphology of the flight apparatus (MFA), which increases with increasing wing length but decreasing tarsus length compared with structural body size.

Birds usually increase wing length as they age, especially during the first complete moult (De la Hera et al. 2014). This source of individual plasticity may be subject to natural selection (Pérez-Tris and Tellería 2001) and therefore contribute to produce morphological trends. We used repeated measures analysis of variance to assess individual variation in wing length. Once we made sure that feather wear did not significantly shorten the wings of birds from hatch year to second year (with freshly grown or worn juvenile feathers, respectively; repeated measures analysis of variance with individuals measured at both ages: $F_{1,32} = 1.30$, $P = 0.26$), we estimated individual plasticity as the mean increment in wing length of individuals measured with juvenile wing feathers (hatch year or second year) and subsequent, adult plumages (older).

Phenological Variables

To explore the relationships between morphological change and possible phenology shifts, we analyzed temporal trends in the date of first capture of breeding birds and young, which were used as proxies for arrival and fledging times, respectively. We only considered data from Las Minas in the analysis of arrival time, because the sampling in Presa del Rey started in April, when many nightingales had already arrived. To consider possible bias of annual average arrival times by the accumulation of late captures of individuals that arrived earlier, we conducted this analysis using the date of first capture of the earliest 20% individuals ($n = 2$ to 6 birds depending on year), and repeated it with the data from all breeding birds captured before May 15 (which roughly corresponds to the end of the first wave of captures in a bimodal distribution, with 2 peaks separated by a valley of low frequency of captures corresponding to the nesting period). Similarly, for the analysis of fledging time, we conducted the analysis considering the date of first capture of the earliest young individual, and repeated it with the data of all young. The time elapsed from the capture of the earliest 20% breeding birds to the capture of the earliest young in Las Minas was used as an estimate of the time elapsed from arrival to breeding each year (hereafter arrival-breeding interval). Because estimated arrival and fledging times are sensitive to sampling interval, we analyzed phenological trends excluding years with sampling gaps during critical dates (occasionally caused by unfavorable weather). All dates were converted to Julian date (January 1 = 1).

Analysis of Temporal Trends

We analyzed temporal trends in environmental, morphological, and phenological variables. Temporal trends were assessed by GAM with a smooth function for years estimated by the restricted maximum likelihood method (*mgcv* package in R; Wood 2017). The effective degrees of freedom (edf) indicate the degree of smoothing. When the data best fitted to a nonlinear relationship (edf > 1), we also built general linear models (mixed if appropriate) to further explore the linear trend. In individual analyses, we assessed temporal autocorrelation by plotting the residuals of the best model against year (we could not apply alternative analyses such as using autocorrelation functions because they need regular lag times through samples). We analyzed variation in MFA, wing length, tarsus length, and structural body size including year as the smoothing term (or interaction between year and age: young, recruit, or adult, when it was significant). Bird identity was included as a random factor in the analyses conducted at the individual level. Age and site (in the models involving data of the 2 localities) were included as fixed effects, as well as their interaction when it was significant. Land use category was included as a fixed factor for NDVI productivity indices. Statistical significance of the effects was assessed through log-likelihood ratio tests (LRT) using a chi-square distribution with df = 1 for mixed models and *F* statistics for simple models. Temporal trends of variation in environmental variables were modeled during the 20 yr of nightingale monitoring. To explore the long-term patterns of environmental change in our study sites, we also analyzed temporal trends of environmental variables during longer periods back in time, which had a different duration for each variable depending on the temporal coverage of the available data.

Phenotype-Dependent Recruitment and Survival

We evaluated the impact of phenotypic change on nightingale performance using 2 complementary approaches: a comparison of MFA between hatched individuals and second-year recruits, and an analysis of lifelong individual survival dependent on MFA. Because the first migration is an important selective event for long-distance migratory birds, we compared MFA between hatched and recruited nightingales using analysis of variance (ANOVA). We also computed the intensity of survival-associated selection related with the first migratory journey as the difference $MFA_S - MFA_H$ divided by the standard deviation of MFA_H, where MFA_S is the mean MFA of individuals that returned after the first migration (second-year recruits: survivors), and MFA_H is the mean MFA of individuals of the same cohort measured before migration (hatched the preceding calendar year and ringed as young). The intensity of selection thus calculated measures the change in the average trait value before and after the selection event in standard deviation units (Hereford et al. 2004). The sample of surviving birds included both recaptured and un-banded recruits, which assumes that all breeding birds hatched at or near mist-netting sites and therefore breeding dispersal did not affect our results. Supporting this assumption, variation in MFA between recaptured and un-banded second-year recruits was not significant (LRT test of the effect in a mixed linear model with site as a fixed factor and year as a random factor: $\chi^2 = 2.12$, $P = 0.15$). We regressed the intensity of selection against the year of hatching of each cohort (excluding the 2014 cohort, which had no data of recruits). We also regressed intensity of selection against MFA_H to test if the strength of natural selection depends on the population average. Site was included as a fixed effect in these analyses. Finally, we correlated the average MFA of breeding birds measured each year (pooling second-year recruits and older individuals) with MFA of young hatched the same year as a rough proxy of the heritability of MFA.

The lifelong survival probability of nightingales in relation to their MFA was modeled with *RMark* (Laake and Rexstad 2008) using capture–mark–recapture data. This analysis required assigning a MFA value to each individual, but migratory birds increase wing length as they age (Pérez-Tris and Tellería 2001, De la Hera et al. 2014), and nightingales are not an exception (see morphological trends below). Therefore, using average individual morphology values would bias the analysis of MFA-dependent survival, as only survivors attain adult measures and these artificially increase their average MFA. To circumvent this problem, we standardized MFA values within each age category (young, second-year recruits, and adults), and used the average of standardized MFA values of each individual as an age-standardized morphology of the flight apparatus (MFA_{ST}) to be used in the analysis of phenotype-dependent survival. Models were tested with the software *Mark* 6.2 (White and Burnham 1999). We used the Cormack-Jolly-Seber (CJS) open population model. For each model we obtained estimates of apparent survival (Φ) and recapture probabilities between years (*p*). We tested all combinations of the effect of constant, time (linear time trend), age at first capture, site, and MFA_{ST} on survival, and constant, time (as a factor), age at first capture, site, and sampling effort on recapture probability. Sampling effort was included as a dichotomous variable for years before and after 2009 in Presa del Rey (in this year, total mist net length changed from 66 to 120 m). We used the all-combination model strategy of model selection following Doherty et al. (2012). To verify CJS assumptions, we first assessed the goodness of fit of saturated models with *RELEASE* in *RMark* ($P >$ 0.99 in all cases). We used Akaike information criterion corrected for small sample sizes (AIC_c) to select the best models (all models with $\Delta AIC_c \leq 2$ were treated as equally good; Burnham and Anderson 2002).

RESULTS

Environmental Trends

During the nightingale monitoring period, springs have been linearly delaying (spring earliness, edf = 4.87, estimate = 0.023, SE = 0.009, $F_{1,93} = 6.95$, $P = 0.01$; Figure 1) while rate of spring advancement has been oscillating cyclically (edf = 6.19, $F = 3.73$, $P = 0.001$). In the long term (1982–2014) we only detected a nonlinear pattern in spring earliness (edf = 2.96, $F = 3.19$, $P = 0.02$; Figure 1; not a significant pattern for rate of spring advancement, $P = 0.15$). All spring season indices varied between land use categories (all P values < 0.001). Regarding the summer season, we found a linear increase in intensity of summer drought in the period 1950–2014 (edf = 1.34, estimate = 0.017, SE = 0.006, $F_{1,63} = 7.64$, $P = 0.007$; see Figure 1; all other P values ≥ 0.44). In relation to insect phenology, the onset of high insect availability ranged from Julian day 101 to 163 during the period 1950–2014. Insect phenology varied among years only in the long term (edf = 2.58, $F = 4.02$, $P = 0.01$), with a nearly significant negative linear trend (estimate = −0.156, SE = 0.080, $F_{1,63} = 3.83$, $P = 0.055$;

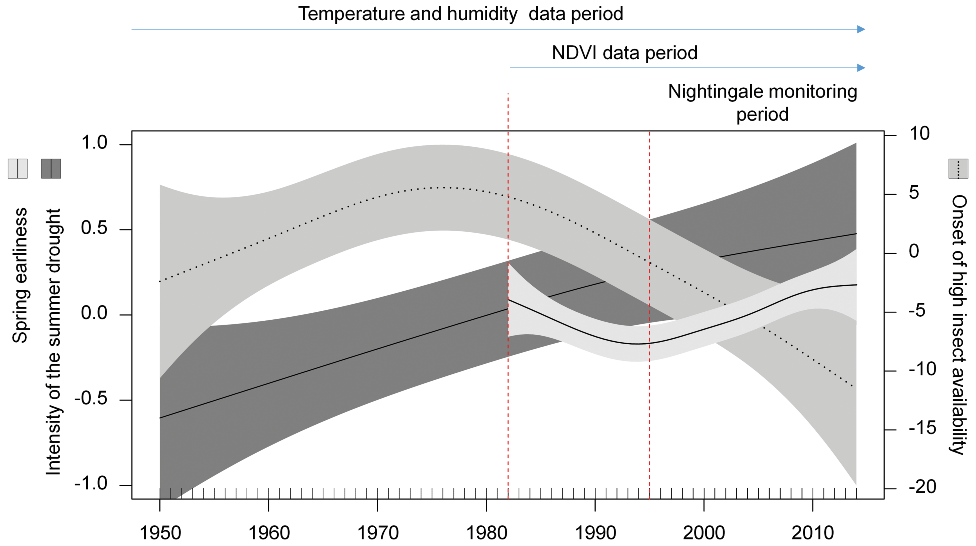

FIGURE 1. Temporal trend of spring earliness (light gray and continuous line), summer drought intensity (dark gray and continuous line), and onset of high insect availability (medium gray and dashed line) as smooth functions of the years. Shaded areas represent 95% confidence intervals.

TABLE 1. Results of the analysis of temporal trends of change in morphology (and its variation within and among individuals) and phenology of nightingales. Morphological traits include wing length and tarsus length, an index of structural body size (PC1 from a principal components analyses [PCA] of these 2 variables), and an index of the morphology of the flight apparatus (MFA, PC2), which increases with increasing wing length and decreasing tarsus length compared with body size. The models also analyze temporal trends in wing length plasticity (individual increase in wing length after the first complete moult) and intensity of natural selection on MFA associated with the first migratory journey. Phenological variables are breeding birds' arrival time (date of first capture of the earliest 20% breeding birds captured each year, measured in Las Minas alone), fledging time (date of first capture of either the earliest young individual or all young captured in the season), and arrival-breeding interval (time elapsed from breeding birds' arrival to the date of capture of the first young individual, measured in Las Minas alone). The trends were tested using general additive models (GAM), but linear trends were also tested using linear models. For each trend, the effect size (adjusted R^2) and linear estimates of temporal change in each variable (with standard errors) are provided. When edf = 1, general additive models are equivalent to linear models. Statistical significance of the linear trend (*P*) was derived from likelihood ratio tests (for mixed effects models, χ^2) or *F* statistics (for linear models with fixed effects).

	GAM				Linear model			
	edf	Adj. R^2	Estimate	SE	χ^2	*F*	df	*P*
Morphology								
MFA	5.06	0.179	-0.034	0.005	38.90			<0.001
Wing length	3.91	0.238	-0.030	0.012	6.28			0.01
Tarsus length	5.23	0.026	0.021	0.004	24.11			<0.001
Body size	4.44	0.105	0.011	0.005	4.26			0.04
Individual plasticity								
Wing length increase	1	–0.007	0.022	0.029		0.60	1 and 90	0.44
Natural selection								
MFA selection intensity	1	0.136	0.033	0.018		3.24	1 and 32	0.08
Phenology								
Breeding birds' arrival time[a]	1	0.119	0.575	0.185		9.62	1 and 63	0.003
Fledging time (earliest young)	1.09	0.264	-0.720	0.232		9.68	1 and 32	0.004
Fledging time (all young)	1.01	0.069	-0.649	0.133		23.68	1 and 382	<0.001
Arrival-breeding interval[a]	1	0.269	-1.081	0.401		7.26	1 and 16	0.02

[a] Data from Las Minas only.

see Figure 1; the pattern was not significant for the period 1995–2014, $P = 0.38$).

Morphological Trends

The average MFA of nightingales decreased during the study period (Table 1, Figure 2). Both uncorrected wing length and tarsus length of nightingales changed during the study period: wing length decreased by 0.6 mm while tarsus length increased by 0.4 mm (Table 1). Body size, measured as the PC1 of the 2 morphological traits, showed a slight but significant trend to increase during the study period (Table 1). Temporal trends in MFA, wing length, tarsus length, and body size of nightingales did not significantly change between age classes (all P values > 0.12). For MFA, there was a small but significant interaction between age and site (LRT: $\chi^2 = 7.27$, $P = 0.03$, see Supplementary Material S3 for post-hoc differences in the fixed term). None of the other variables differed between sites (all P values > 0.12), but body size and wing length were larger in adults ($P < 0.001$). Individual nightingales elongated their wings after the first complete moult (mean ± standard error [SE], juvenile plumage: 82.02 ± 0.20 mm; post-juvenile plumage: 84.04 ± 0.18 mm; within-subjects ANOVA $F_{1,92} = 180.11$, $P < 0.001$). We did not find any temporal pattern of variation in the strength of this plastic change (Table 1).

Phenological Trends

In Las Minas, average arrival time of the earliest 20% individuals ranged between April 12 in 1995 ($n = 4$) and May 2 in 2013 ($n = 3$), representing a 20-day difference between the earliest and the latest year. Nightingales delayed arrival by 10.9 days during the study period (Table 1, Figure 3A). Results did not change when we computed arrival time as the average date of first capture of all breeding birds captured before May 15. We used simple models

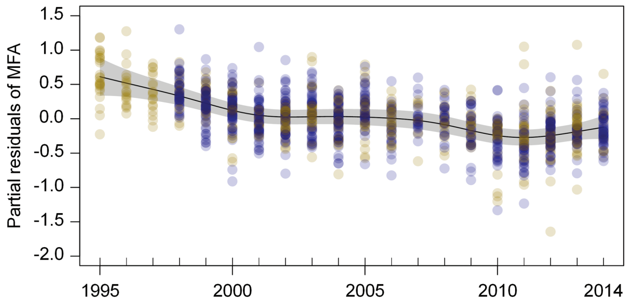

FIGURE 2. Temporal trend of variation in the morphology of the flight apparatus of nightingales (MFA, an index which increases with increasing wing length and decreasing tarsus length relative to body size) during the period 1995–2014 (edf = 5.06). The graph shows the best nonlinear fit (smooth function of the years with 95% confidence intervals). Ochre circles represent values for Las Minas and blue circles for Presa del Rey.

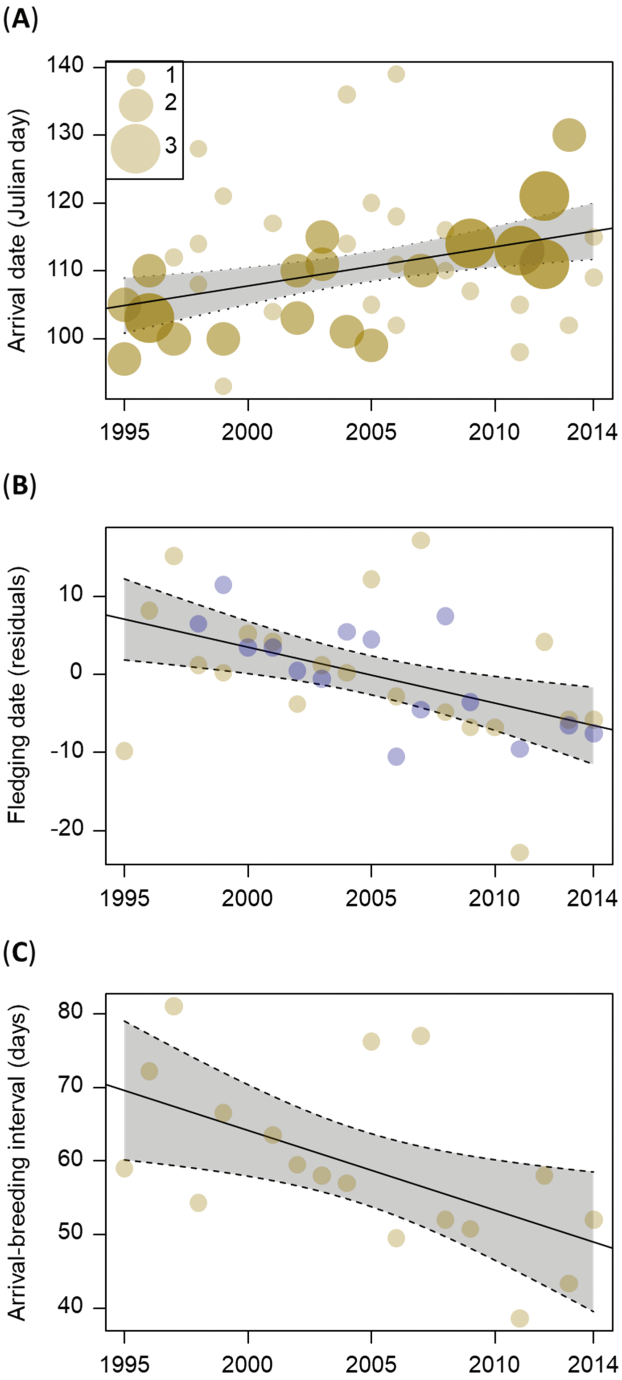

FIGURE 3. Temporal trends of variation in phenology of nightingales during the period 1995–2014. Phenological variables are (**A**) breeding birds' arrival time (date of first capture of the earliest 20% of breeding birds captured each year, measured in Las Minas alone, circle size is proportional to sample size; day 1 = January 1), (**B**) fledging time (residual date of first capture of the earliest young individual controlling by site), and (**C**) arrival-breeding interval (time elapsed from breeding birds' arrival to the date of capture of the first young individual, measured in Las Minas alone). The graph shows the best linear fit with 95% confidence intervals. Ochre circles represent values for Las Minas and blue circles for Presa del Rey.

due to lack of convergence in mixed model and random variances close to zero.

The date of capture of the first young was May 28 in 2011 and July 7 in 2007, representing a 40-day interval between the earliest and the latest year. We found a linear trend towards earlier fledging during the study period, which was significant both when we used the date of capture of the earliest young individual (which advanced 13.7 days over the study period; Table 1, Figure 3B), and when all young were included in the analysis (average date of capture advanced 12.3 days; Table 1). Nightingales fledged on average earlier in Presa del Rey than in Las Minas (estimate = −3.494, SE = 1.489, $F_{1,382} = 5.51$, $P = 0.02$), but the date of capture of the first young did not differ between sites ($F_{1,32} = 3.41$, $P = 0.07$). Arrival-breeding interval in Las Minas varied from 38.6 days in 2011 to 81 days in 1997, representing a 42.4-day difference between the shortest and the longest years, respectively. Arrival-breeding interval linearly decreased, becoming 20.5 days shorter during the study period (Table 1, Figure 3C). We excluded from these analyses the years with sampling gaps (2000 and 2010 of Las Minas in the analyses of arrival time and arrival-breeding interval, and 2010 and 2012 of Presa del Rey in the analyses of date of capture of the first young captured each year), although including all years did not change the results qualitatively. Results of correlations between phenology and morphological and environmental variables are available in Supplementary Material S4.

Phenotype-Dependent Recruitment and Survival

Overall, second-year recruits captured after their first round-trip migration had larger MFA values than young measured before the first migration (ANOVA: $F_{1,692} = 4.73$, $P = 0.03$). The intensity of selection on MFA associated with the first migration tended to increase during the study period, but the temporal trend did not reach statistical significance (Table 1, Figure 4A). Nevertheless, natural selection for long-winged nightingales was stronger in cohorts with low MFA values (estimate = −0.886, SE = 0.156, $F_{1,32} = 32.46$, $P < 0.001$; Figure 4B). MFA of breeding birds was positively correlated with MFA of young (estimate = 0.472, SE = 0.095, $r = 0.76$, $F_{1,18} = 24.77$, $P < 0.001$).

Age at first capture, site, a linear temporal trend, and interactions between these effects were frequently included in the best CJS models of apparent survival (9 models with $\Delta AIC_c \leq 2$ compared with the model with minimum AIC_c), although only the effect of site was recovered by all models (the best model without an effect of site on Φ was model number 66, with $\Delta AIC_c > 7$; Table 2; see all models in Supplementary Material S5). Apparent survival was higher in Presa del Rey (model $\Phi_{Site} + p_{Age}$: estimate = 0.543, SE = 0.024) than in Las Minas (estimate = 0.436, SE = 0.029). In both sites, nightingales that were first captured as hatch year scored lower apparent survival (estimates ± SE in the model $\Phi_{Site + Age} + p_{Age}$; Las Minas: 0.360 ± 0.047, Presa del Rey: 0.462 ± 0.048) than individuals first captured as

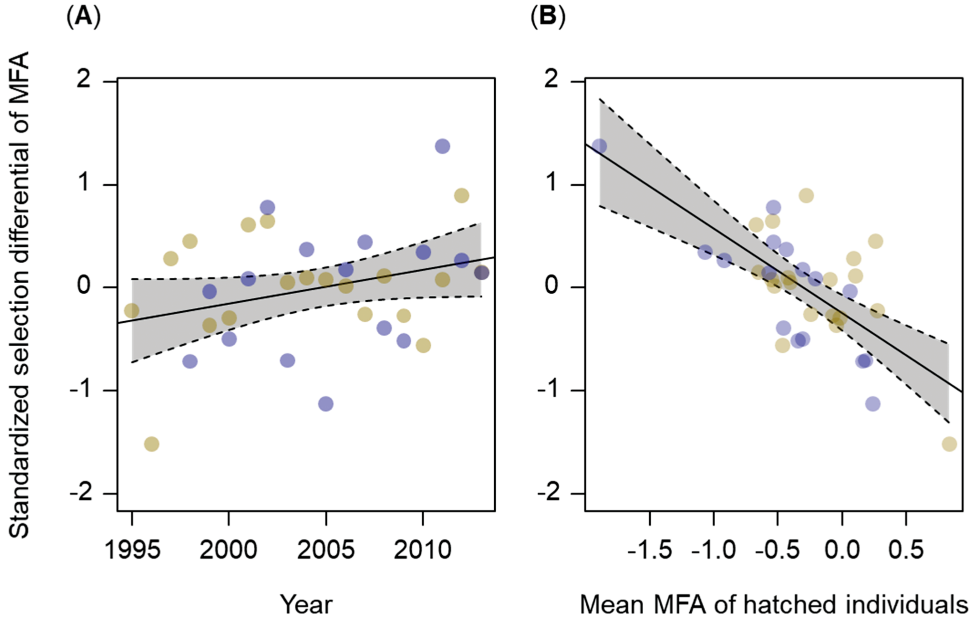

FIGURE 4. Variation in the intensity of selection on the morphology of the flight apparatus (MFA) associated with the first round-trip migratory journey of nightingales (best linear fit with 95% confidence intervals). The graphs show the temporal trend (**A**) of change in the intensity of selection during the period 1995–2014, and the relationship between the average MFA in the population before selection and the intensity of selection (**B**). Ochre circles represent values for Las Minas and blue circles for Presa del Rey. Deletion of extreme points in plot B did not change the results.

TABLE 2. Best Cormack-Jolly-Seber models of variation in apparent survival (Φ) and probability of recapture (*p*) of nightingales as functions of age at first capture, site, time (effect of a linear temporal trend), MFA$_{ST}$ (an age-standardized index which increases with increasing wing length and decreasing tarsus length compared with body size), and sampling effort. The models are arranged by Akaike information criterion corrected for small sample sizes (AIC$_c$). The table lists the 9 models that showed the best balance between fit to the data and complexity (those scoring lowest AIC$_c$ values; models with ΔAIC$_c$ ≤ 2 compared with the model with lowest AIC$_c$ are considered equally good). The best model including MFA$_{ST}$ is highlighted in bold. The best model that did not include an effect of site on Φ is also shown at the bottom of the table. The number of parameters in each model (*k*) and Akaike weights (w_i, based on all possible models) are indicated.

Model	*k*	AIC$_c$	ΔAIC$_c$	w_i
1: $\Phi_{Age * Time + Site} + p_{Age}$	10	1662.65	0.00	0.09
2: $\Phi_{Site + Time} + p_{Age}$	6	1663.25	0.59	0.07
3: $\Phi_{Age + Site + Time} + p_{Age}$	8	1663.82	1.17	0.05
4: $\Phi_{Site} + p_{Age}$	5	1664.27	1.61	0.04
5: $\Phi_{Age * Time + Site} + p_{Age + Site}$	11	1664.47	1.82	0.04
6: $\Phi_{Age * Time + Site} + p_{Age + Site + Sampling\ effort}$	12	1664.52	1.87	0.04
7: $\Phi_{Age + Site} + p_{Age}$	7	1664.58	1.93	0.03
8: $\Phi_{Site + Time} + p_{Age + Site + Sampling\ effort}$	8	1664.62	1.97	0.03
9: $\Phi_{Age * Time + Site + MFAST} + p_{Age}$	**11**	**1664.63**	**1.98**	**0.03**
66: $\Phi_{Time} + p_{Age + Site + Sampling\ effort}$	7	1669.82	7.16	0.003

second year (Las Minas: 0.463 ± 0.038, Presa del Rey: 0.568 ± 0.033) or adult birds (Las Minas: 0.448 ± 0.040, Presa del Rey: 0.553 ± 0.036). Note that natal dispersal of hatch-year individuals (and higher fidelity to breeding sites in second-year and after-second-year birds) might also contribute to the differences in apparent survival. Nevertheless, the effect of age at first capture on apparent survival did not reach statistical significance in likelihood ratio tests comparing competing models with or without the effect ($P > 0.155$). MFA$_{ST}$ was included in the ninth model with ΔAIC$_c$ ≤ 2, and it did not have a relevant influence on survival (β = 0.019, SE = 0.074; Table 2).

DISCUSSION

Global change has been paralleled by contemporary phenotypic change of many migratory birds, although little is known about the interplay of adaptation and constraint driving these trends. Nightingales have shortened wing length compared with their body size in central Spain over 2 decades of monitoring (1995–2014). However, body size increased slightly during the same period, meaning that nightingales changed the shape of the flight apparatus rather than becoming smaller over time (Dunn et al. 2017). The trend was replicated in a reed bed and a forest, 2 habitat types with contrasting structure and quality for nightingales (Holt et al. 2010). Our combined analysis of morphological trends and phenotype-dependent survival shows that average wing shape moved away from the optimal shape for migration: natural selection during the first migratory journey favored long-winged individuals, and the shorter the average wing length in the population, the stronger the selection for longer wings. Although we failed to find conclusive evidence that long-winged nightingales remained better survivors at all ages, they had better chances to recruit and yet their frequency in the population decreased across generations. In summary, best-performing migrants were at a clear disadvantage, which rules out the possibility that nightingales have shortened wing length as a consequence of relaxed natural selection associated with reduced costs of transport. Geolocator data are showing that nightingales winter in the Sahel area regardless of the flyway they follow (Hahn et al. 2014), and Spanish populations are the ones with the shortest migration distance (Hahn et al. 2016). Therefore, the only way in which these populations could reduce migratory distance would be by establishing pre-Saharan wintering grounds. However, to the best of our knowledge, nightingales have never been reported wintering north of the Sahara.

The change in wing length of nightingales paralleled environmental and phenological trends. In central Spain, springs have delayed and the summer drought has increased intensity, while temperature has allowed insects to thrive earlier, a pattern that fits with the general climate change trend in the Mediterranean region (Giorgi and Bi 2005). In this scenario, nightingales have delayed arrival but raise their offspring earlier, consequently shortening the breeding season. This phenological trend may be a response to the intensifying summer drought (Carbonell et al. 2003): compared with northern latitudes where the summer drought is not so influencing, the change in breeding conditions in these Mediterranean localities may lower the fitness of individuals that fail to rear offspring before the environment deteriorates (Pérez-Tris et al. 2000).

Short wings lowered nightingale survival during the first round-trip migration, and therefore the observed phenotypic trend is most likely driven by breeding benefits accrued by short-winged individuals. Life-history theory predicts that in impoverished breeding environments natural selection should favor trait combinations that reduce the cost of offspring rearing (Grant and Grant 2002, Ricklefs and Wikelski 2002). Therefore, nightingales confronted with a shrinking time frame of suitable breeding conditions may benefit from reducing reproductive investment, in particular if they tend to overlap offspring rearing with periods of intense drought due to climate change. If the new optimal clutch size has fewer eggs, a cliff-edge effect would strongly penalize individuals that keep laying clutches of the historical optimal clutch size (Boyce and Perrins 1987). Under the migratory gene package paradigm, natural selection for smaller clutch size may shorten wing length as a correlated response (Van Noordwijk et al. 2006, Merilä 2012). In fact, comparisons of populations of migratory passerines positioned along the slow-fast continuum of life-history variation provide compelling evidence that heritable slow pace of life is associated with shorter wings compared with body size and larger structural body size (Gwinner et al. 1995, Starck et al. 1995, Pérez-Tris and Tellería 2002, Wikelski et al. 2003, Baldwin et al. 2010). Remarkably, a recent study of 52 species of North American migratory birds found a generalized decrease in tarsus length but an increase in wing length parallel to climate warming (Weeks et al. 2020). This morphological trend, which our study replicates in the opposite direction, further supports the idea that the different pieces of the migratory syndrome may change in concert in the face of rapid environmental change. The correlated expression of different traits may align with fitness to boost adaptation (Weeks et al. 2020), but it may harm more than help if maladaptive traits—such as short wings of nightingales—arise in the population (Radchuk et al. 2019).

We have no data of breeding success of nightingales, but different lines of evidence support our interpretation that maladaptive morphological change may be a correlated response to selection on life-history traits promoted in an impoverished environment. Late laying associated with delayed arrival could promote smaller clutch size (Rowe et al. 1994, Smith and Moore 2005), which may be further favored if reduced breeding investment allows late-arriving nightingales to advance reproduction. Upon arrival, nightingales that are able to produce smaller clutches (or less costly to rear offspring) may become ready for laying earlier than those endeavoring larger breeding investments (Rowe et al. 1994). Supporting this interpretation, young nightingales with short wings appeared earlier than long-winged young in our study areas. Early hatched, short-winged nightingales may be at a further advantage because they avoid overlapping growth with stressful drought (Pérez-Tris et al. 2000) and have time to attain better condition before migration (Gill et al. 2014). According to this view, short-winged nightingales would increase their fitness via reproductive benefits, increasing their frequency over time. Although we favor breeding benefits in our interpretation, wing morphology could also change if it is correlated with traits favored on the wintering grounds, either directly or through diverse carry-over effects on individual fitness (Imlay et al. 2019). In fact, the Sahel area is among the clearest examples of desertification associated with global warming (Huang et al. 2016), which might contribute to selection for slow pace of life if individuals with lower resting metabolic rates are favored in these circumstances.

In most European localities, warmer springs have promoted earlier arrival of migratory birds (Usui et al. 2017, Mayor et al. 2017), although long-distance migrants show less evident responses than short-distance migrants (Rubolini et al. 2010). By contrast, nightingales have delayed their arrival during 2 decades of monitoring in central Spain, parallel to a trend towards delayed springs in this region, but clearly at odds with both an earlier period of insect proliferation and an intensified summer drought, 2 direct determinants of breeding success that should promote early arrival (Saino et al. 2011). However, the observation is consistent with the idea that long-distance migrants are more constrained to advance their arrival to match habitat productivity, not only by migration distance but also by their morphology (Møller et al. 2017). To arrive earlier, nightingales may need to be assisted by longer wings necessary to gain flight speed (Hahn et al. 2016). In fact, nightingales were subject to survival selection favoring migratory performance, and the shorter the wings, the stronger the selection for long wings. However, a breeding disadvantage of long-winged birds under impaired conditions may impede an adaptive increase in frequency of long wings in nightingales.

By uncovering a link between selected morphology of the flight apparatus and reduced recruitment in nightingales, our study challenges the idea that morphological trends of migratory birds necessarily represent adaptive biomechanical fitting (Radchuk et al. 2019), paving the ground for alternative interpretations of phenotypic trends, such as maladaptive trait evolution due to genetic constraints. Our interpretation assumes that the observed trends have a genetic basis (Gienapp et al. 2008, Hoffmann and Sgrò 2011, Teplitsky and Millien 2014). Supporting this idea, we did not find evidence of plasticity underlying morphological change: there was no trend in the magnitude of plastic change in wing length, and the morphological trend was found in all age classes. In addition, MFA of young was correlated with MFA of breeding birds within years, supporting the heritability of the trait. In fact, wing length is heritable in many birds (Merilä and Sheldon 2000, Teplitsky et al. 2009) and nightingales are likely not an exception (Kipper et al. 2006).

Whether migratory birds will be capable of adapting to climate change is a cause of concern (Radchuk et al. 2019), and several studies have investigated the consequences of climate change on bird demography (Sæther et al. 2004). With its impact on phenology, climate change may affect different life-history traits, calling for a comprehensive examination to identify such consequences (Stenseth and Mysterud 2002, Winkler et al. 2002). For example, the possibility that natural selection may favor a slow pace of life in some environments could contribute to explaining negative population trends in species that have not shifted arrival dates (Møller et al. 2008, Saino et al. 2011), or increasing phenological mismatch between spring green-up and arrival of migratory birds (Mayor et al. 2017). However, the evolution of slow life histories could put migratory bird populations at risk (Siliceo and Díaz 2010, Møller et al. 2017, Wegge and Rolstad 2017). The number and size of our gaps of knowledge are proportional to the complexity of possible population responses, putting forward the importance of long-term population monitoring of morphological and life-history variation (Clutton-Brock and Sheldon 2010, Tellería et al. 2013, Radchuk et al. 2019), including, if possible, the quantification of environmental and genetic influences on trait variation as a tool for understanding avian adaptive responses to global change.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *The Auk: Ornithological Advances* online.

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Author contributions: CRe and JPT conceived the study; CRe, JPT, CRo, and JP curated the database; CRe, JPT, and CRo analyzed the data; CRe and JPT drafted the manuscript. All authors contributed critically to the final version and gave their final approval for publication.

Data depository: Analyses reported in this article can be reproduced using the data provided by Remacha et al. (2020). According to the journal policy regarding the ethical re-use of data, and considering the effort that the members of the SEO-Monticola ringing group put into assembling this database, we would appreciate that anyone interested in re-using the data contact the corresponding author in order to agree to a collaboration when appropriate.

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