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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.

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 favoured in a changing environment, eventually moving away from the optimal shape for migration and increasing transport costs. Data from 20 years of monitoring of two Common Nightingale (*Luscinia megarhynchos*) populations breeding in central Spain, where environmental conditions for breeding have deteriorated during the last 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 favouring 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: climate change, wing shape, trait optimization, apparent survival, population monitoring, *Luscinia megarhynchos*, migration

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 the last decades have been interpreted as adaptive responses to natural selection associated with warmer climate (Lo Cascio Sætre et al. 2017, Weeks et al. 2019), 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 to document 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 favourite 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. 2019). Decades of research and monitoring of bird populations have helped to build comprehensive knowledge of the ecological and evolutionary determinants of variation in migratory behaviour 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 favour individuals that are genetically programmed not only to have optimal morphology and behaviour for travelling, 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 behavioural, 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 characterise 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 phenotype in common garden settings (Wikelski et al. 2003), (3) phenotypic correlations across populations (such as 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 (such as 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. 2019). 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. 2019).

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 the last 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. 2019). 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 favoured 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 to rapid climate change (Chown et al. 2010, Radchuk et al. 2019).

Using the Common Nightingale (*Luscinia megarhynchos*) as 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 analysed variation in wing morphology and phenotype-dependent survival in two closely situated populations of nightingales from central Spain, using individual monitoring data spanning 20 years (1995-2014). In order 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 in advantage if breeding seasons become earlier or shorter in terms of green-up phenology or insect availability (Hahn et al. 2016), whilst 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 recognised as a climate change hostpot 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 might 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 up to promote adaptive change in wing length. But it may favour individuals with 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 favour 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 to 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 favouring 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). Convenient to 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 nestling leave nest at age 10-12 days, although they are able to fly 3-5 days later (Collar 2005).

We used data from two constant effort ringing sites operated weekly. Las Minas (40.2245º N, 03.5475º W) is a reed bed that has been sampled all the year around since 1995. Presa del Rey (40.3010º N, 03.5414º 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 two habitat types represent two 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 15 May to 15 July for breeding birds (31 July 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

In order 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. 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 VIP07 series (Didan et al. 2016; data available from 1982 to 2014) extracted from two nearby extents in central Spain (Supplementary Material S2). We classified NDVI by land uses because phenology is influenced by the type of vegetation (Badeck et al. 2004). Detailed information about the data filtering process may be found in the Supplementary Material S2. The spring was characterized each year by start and end of the season (day 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 elapsed between the two), and spring green-down slope (the difference in NDVI between the maximum and the level at the end of spring, divided by the days elapsed between the two).

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 years, 2.5 degree spatial resolution in [Lat/Lon] 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 elapsed between the two) 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 elapsed between the two).

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 where 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 done with R software v3.5.3 (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 a 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 two 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 to 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 two 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, 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 degree-days, the average hatching temperature of first stages of insect larvae (Jarošík et al. 2011). Only temperatures above 10.4 ºC, the lower developmental threshold temperature of insects (Jarošík et al. 2011), were summed up to obtain accumulated degree-days.

Morphological variables

We analysed temporal trends of change in wing length and tarsus length, two 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 principal components analysis (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 to 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 ANOVA 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 ANOVA 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

In order to explore the relationships between morphological change and possible phenology shifts, we analysed 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. In order 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 of year), and repeated it with the data from all breeding birds captured before 15 May (which roughly corresponds to the end of the first wave of captures in a bimodal distribution, with two 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 analysed phenological trends excluding years with sampling gaps during critical dates (occasionally caused by unfavourable weather). All dates were converted to Julian date (1 January = 1).

Analysis of temporal trends

We analysed temporal trends in environmental, morphological and phenological variables. Temporal trends were assessed by general additive models (GAM) with a smooth function for years estimated through restricted maximum likelihood method (REML) (mgcv package in R; Wood 2017). The effective degrees of freedom (edf) indicate the degree of smoothing. When the data best fitted to a non-linear 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 analysed 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 two 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 trough 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 modelled during the 20 years of nightingale monitoring. In order to explore the long-term patterns of environmental change in our study sites, we also analysed temporal trends of environmental variables during longer periods back in time, which had 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 two 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 ANOVA. We also computed the intensity of survival-associated selection related to 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 $\mathrm{MFA_H}$ 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 modelled with RMark (version 2.2.2; 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 (this year total mist net length changed from 66 m 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 AICc to select the best models (all models with Δ AICc ≤ 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 non-linear pattern in spring earliness (edf = 2.96, F = 3.19, $P = 0.02$; Figure 1; not 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; see Figure 1; the pattern was not significant for the period 1995-2014, *P* = 0.38).

Morphological trends

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 0.6 mm while tarsus length increased 0.4 mm (Table 1). Body size, measured as the PC1 of the two 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: χ^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 ± 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 15 May. We used simple models 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 in 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 and 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 analysis 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 (nine models with Δ AICc ≤ 2 compared to the model with minimum AIC), 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 Δ AICc > 7; Table 2; see all models in Supplementary Material S5). Apparent survival was higher in Presa del Rey (model $\Phi_{\mathrm{Site}} + p_{\mathrm{Age}}$: 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 $\Phi_{\mathrm{Site + Age}} + p_{\mathrm{Age}}$; Las Minas: 0.360 ± 0.047, Presa del Rey: 0.462 ± 0.048) than individuals first captured as 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 ($P > 0.155$). $\mathrm{MFA_{ST}}$ was included in the ninth model with Δ AICc ≤ 2, and it did not have a relevant influence on survival (beta = 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 to their body size in central Spain over two 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, two 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 favoured 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 sum, best-performing migrants were in 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 sub-Sahel area regardless of the flyway they follow (Hahn et al. 2014), and Spanish populations are the ones with shortest migration distance (Hahn et al. 2016). Therefore, the only way in which these populations could reduce migratory distance would be 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 to 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, shortening the breeding season as the consequence. This phenological trend may be a response to the intensifying summer drought (Carbonell et al. 2003): compared to northern latitudes where the summer drought is not so influencing, the change in breeding conditions in these Mediterranean localities may lower 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 favour 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 to 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 has found a generalised decrease in tarsus length but an increase in wing length parallel to climate warming (Weeks et al. 2019). 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. 2019), 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 favoured 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 endeavouring 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 in 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 favour breeding benefits in our interpretation, wing morphology could also change if it is correlated with traits favoured on the wintering grounds, either directly or through diverse carry-over effects on individual fitness (Imlay et al. 2019). In fact, the sub-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 favoured 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). In contrast, nightingales have delayed their arrival during two 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, two direct determinants of breeding success which 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). In order 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 favouring 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 to adapt to climate change is 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 in order to identify such consequences (Stenseth and Mysterud 2002, Winkler et al. 2002). For example, the possibility that natural selection may favour a slow pace of life in some environments could contribute to explain 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.

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FIGURE CAPTIONS

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

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 non-linear 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 = 1st January), (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.

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 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 PCA of these two variables), and an index of the morphology of the flight apparatus (MFA, PC2), which increases with increasing wing length and decreasing tarsus length compared to body size. The models also analyse 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, GAM 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 (1,90)	0.44
Natural selection:							
MFA selection intensity	1	0.136	0.033	0.018		3.24 (1,32)	0.08
Phenology:							
Breeding birds' arrival time *	1	0.119	0.575	0.185		9.62 (1,63)	0.003
Fledging time (earliest young)	1.09	0.264	-0.720	0.232		9.68 (1,32)	0.004
Fledging time (all young)	1.01	0.069	-0.649	0.133		23.68 (1,382)	<0.001
Arrival-breeding interval *	1	0.269	-1.081	0.401		7.26 (1,16)	0.02

* Data from Las Minas only

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-standardised index which increases with increasing wing length and decreasing tarsus length compared to body size) and sampling effort. The models are arranged by Akaike information criterion corrected for small sample sizes. The table shows the nine models that showed the best balance between fit to the data and complexity (those scoring lowest AICc values; models with Δ AICc ≤ 2 compared to the model with lowest AICc 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 (n) and Akaike weights (based on all possible models) are indicated.

Model	n	AICc	Δ AICc	Weight
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: $\boldsymbol{\Phi_{Age * Time + Site + MFA_{ST}} + p_{Age}}$	**11**	**1664.63**	**1.98**	**0.03**
66: $\Phi_{Time} + p_{Age + Site + Sampling\ effort}$	7	1669.82	7.16	0.003

FIGURE 1

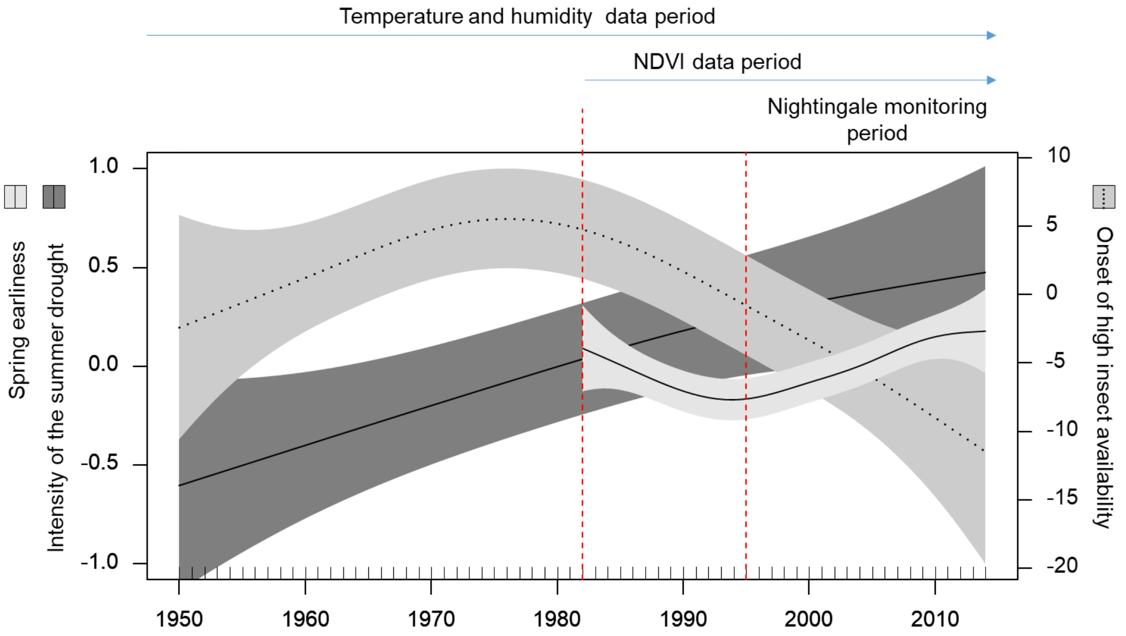

Temperature and humidity data period
NDVI data period
Nightingale monitoring period
Spring earliness
Intensity of the summer drought
Onset of high insect availability
1.0
0.5
0.0
-0.5
-1.0
10
5
0
-5
-10
-15
-20
1950
1960
1970
1980
1990
2000
2010

FIGURE 2

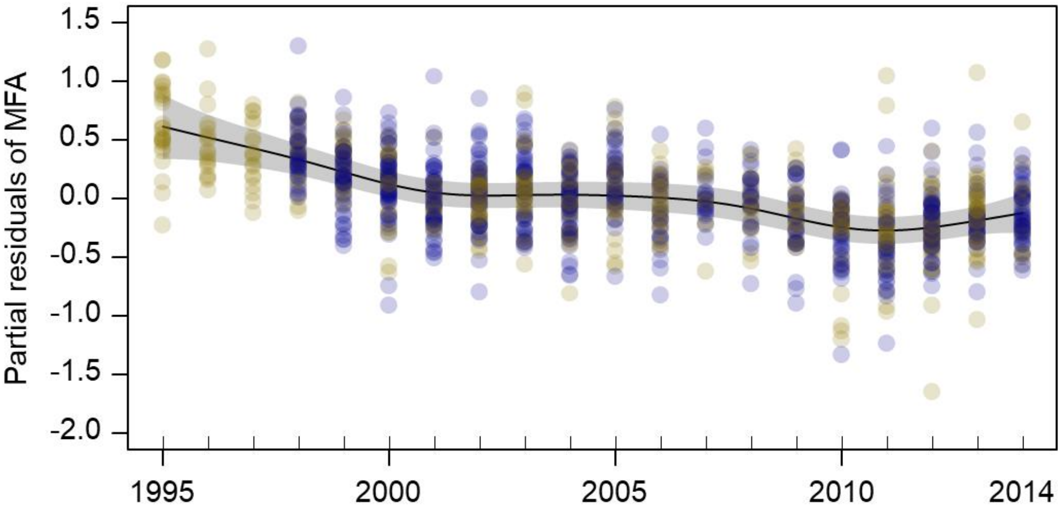

Partial residuals of MFA
1.5
1.0
0.5
0.0
-0.5
-1.0
-1.5
-2.0
1995
2000
2005
2010
2014

FIGURE 3

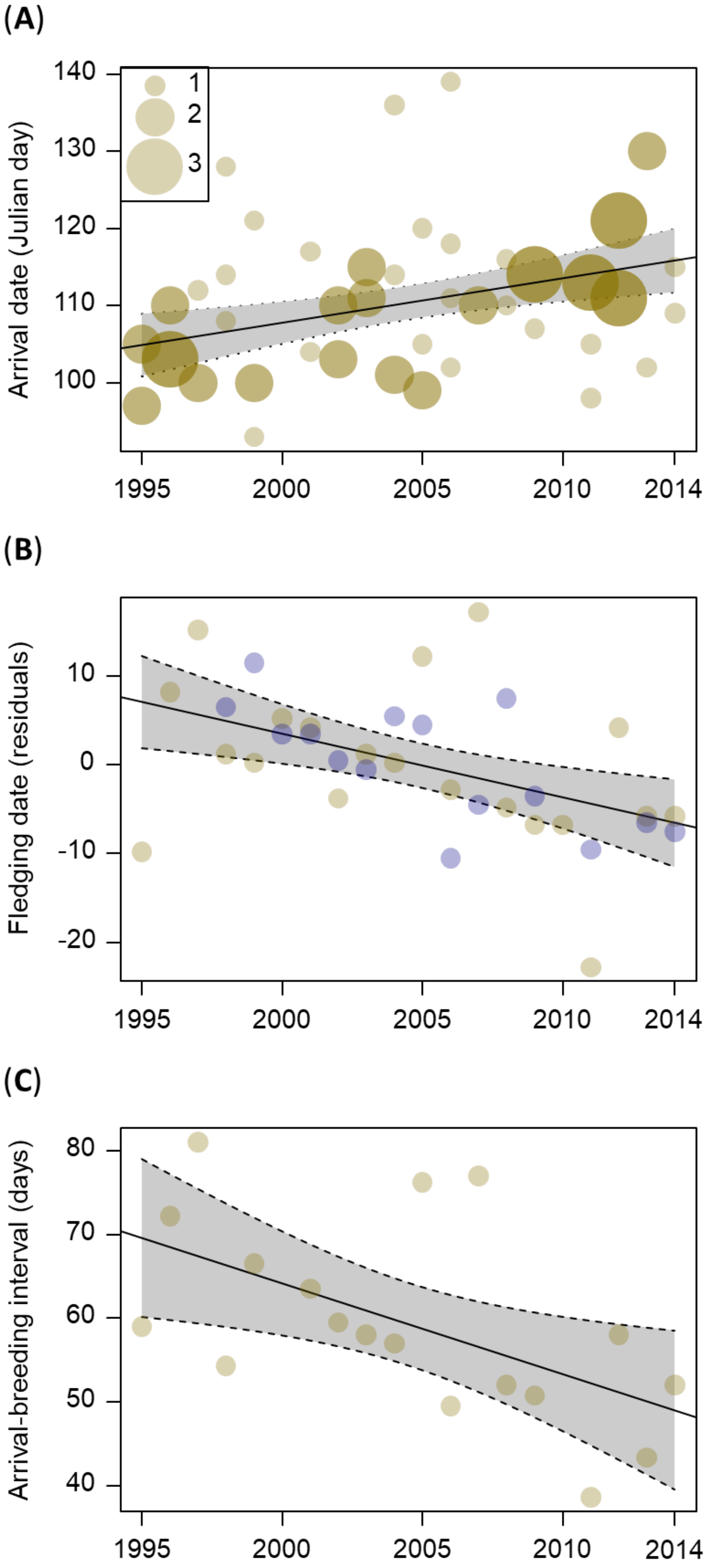
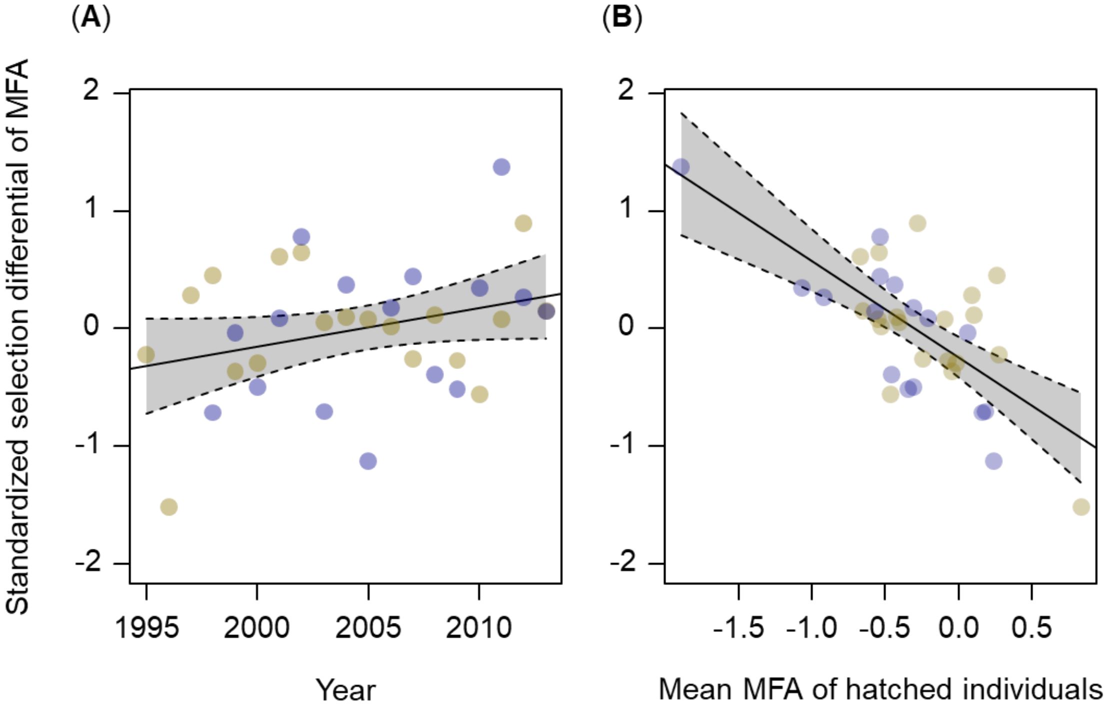

(A)
140
130
120
110
100
1
2
3
Arrival date (Julian day)
1995
2000
2005
2010
2014
(B)
10
0
-10
-20
Fledging date (residuals)
1995
2000
2005
2010
2014
(C)
80
70
60
50
40
Arrival-breeding interval (days)
1995
2000
2005
2010
2014

FIGURE 4


(A)
(B)
Standardized selection differential of MFA
2
1
0
-1
-2
1995
2000
2005
2010
Year
-1.5
-1.0
-0.5
0.0
0.5
Mean MFA of hatched individuals

SUPPLEMENTARY MATERIAL S1

Nightingale data collection and quality control

Temporal frequency of captures

Las Minas is a constant effort year-round ringing station that has been operated weekly since April 1995. Presa del Rey has been operated with less temporal coverage: most years the work on this site aimed at sampling breeding birds, and therefore it was limited to the period April-July (year-round sampling only took place between 1998 and 2002). Total mist net length in Las Minas was 138 m (144 m in 1995 and 132-144 m in 1996). In Presa del Rey, mist net length was 66 m during 1998-2008, and 120 m since 2009. In both sites, nets were visited every hour, five times from sunrise each sampling day. Further details about the sampling protocols and characteristics of the ringing sites may be found in Figure S1.1 and Bermejo (2004).

Data quality control

One crucial step in our analyses was to ensure that we worked with local individuals (breeding birds or locally hatched young). We filtered the data to select those individuals meeting the following criteria:

1. We considered a conservative breeding period between May 15 and July 15 (Julian dates: 134-135 and 195-196). Individuals that were captured at least once in their lifetime within this time window were considered to be local.

2. For young birds, we also included individuals captured between 15 and 31 of July (Julian date: 211-212) to include birds hatched in years with a late breeding season. However, we excluded two birds with fat score > 3 that might be on passage. Birds that were classified as local young following the above criteria were considered to be local recruits if they were captured in subsequent years.

3. Data of adults captured before May 15 or young captured after July 31 were included only when the individual had been observed at least once within the conservative breeding period.

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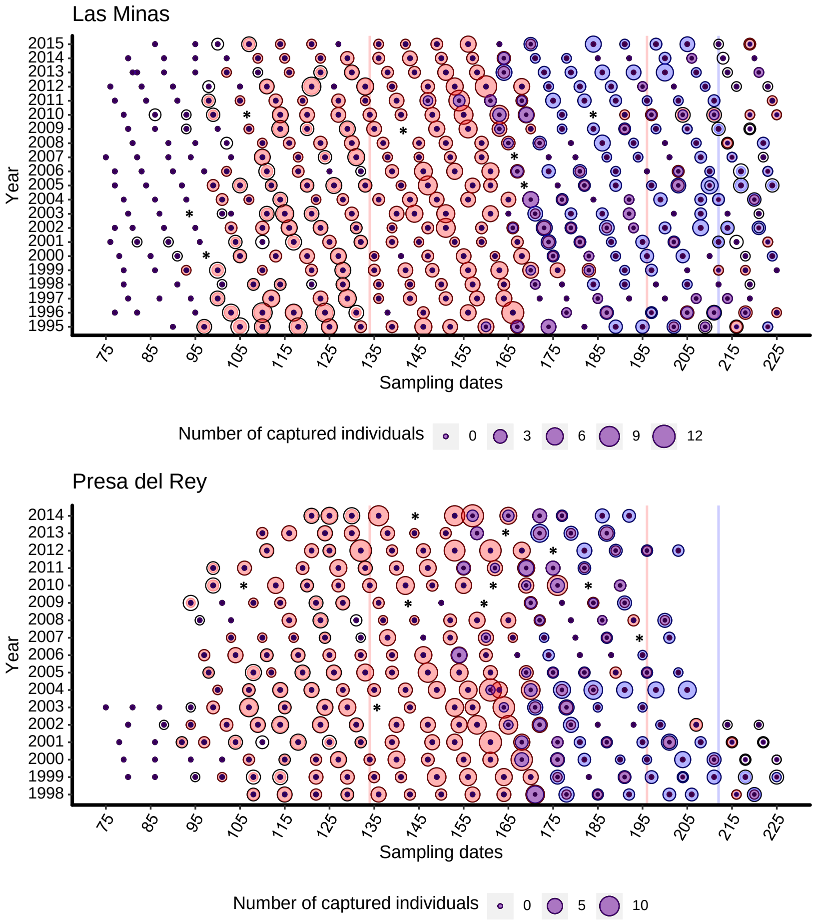


Figure S1.1. Annual distribution of sampling dates and nightingale captures in each ringing station (Las Minas and Presa del Rey). The size of the symbols is proportional to the number of nightingales captured each day. Local young (hatch year birds) and breeding individuals (after-hatch year, second year and after second year) are shown in blue and red respectively. White circles represent individuals that could not be identified as local and therefore were not included in the analyses. Red and blue vertical lines indicate the boundaries of the breeding period (May 15 and July 15) and the end of the period when young were considered to be local (July 31), respectively. Stars indicate sampling gaps.

SUPPLEMENTARY MATERIAL S2

NDVI data filtering process

Grid extent selection

We used standardized NDVI data from VIP07 series (Didan et al. 2016), a database which takes into account the bias due to the incorporation of different advanced very-high-resolution radiometer (AVHRR) sensors during the sampling period. Each image summarizes seven daily images with 0.05-degree spatial resolution (5,600 meters) in geographic (latitude/longitude) grid format. Vegetation phenology is highly dependent on the type of vegetation considered, and signals from different land uses need to be isolated to produce reliable regional NDVI trends (Badeck et al. 2004, Alcaraz-Segura et al. 2009). We extracted NDVI data from a first extent of 285 grids (extent 1, latitude/longitude range: 39.56, 40.30 / -4.0, -3.04), including Las Minas and Presa del Rey ringing stations (Figure S2.1). This area is crossed by the Jarama and Henares rivers, and is dominated by cultivated land with a mosaic of small natural patches mixed with different types of vegetation, such as broad-leaved forest or natural grassland. When NDVI data are excessively influenced by human mediation, as it happens in the agricultural landscape where our study sites are included, considering nearby pixels where natural vegetation predominates may help to correctly capture environmental change in natural habitats (Doktor et al. 2009). Therefore, we incorporated data from a second extent with natural habitat categories, covering 665 grids located also in central Spain (extent 2, latitude/longitude range: 39.77, 40.71 / -5.93, -4.18; Figure S2.1).

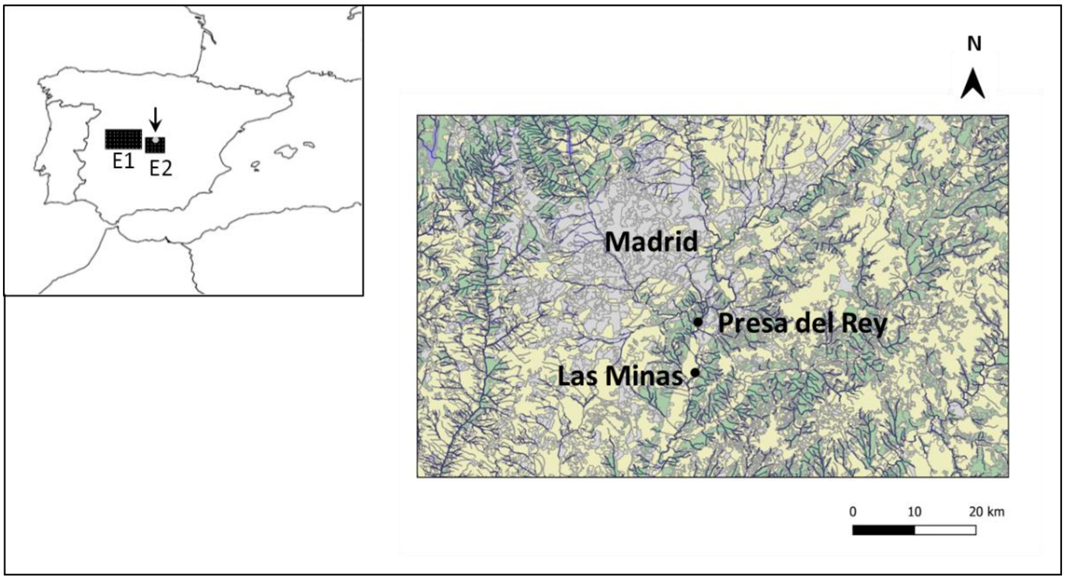


Figure S2.1. Location in the Iberian Peninsula of the spatial extents 1 (E1: 285 grids) and 2 (E2: 685 grids) used for the extraction of NDVI data. An area within extent 2 (indicated by an arrow) is amplified to show the position of the two banding stations (Las Minas and Presa del Rey). Dark blue lines represent rivers and colour polygons indicate CORINE 2012 land uses (grey: artificial land, green: natural areas, yellow: agricultural areas, blue: water areas).

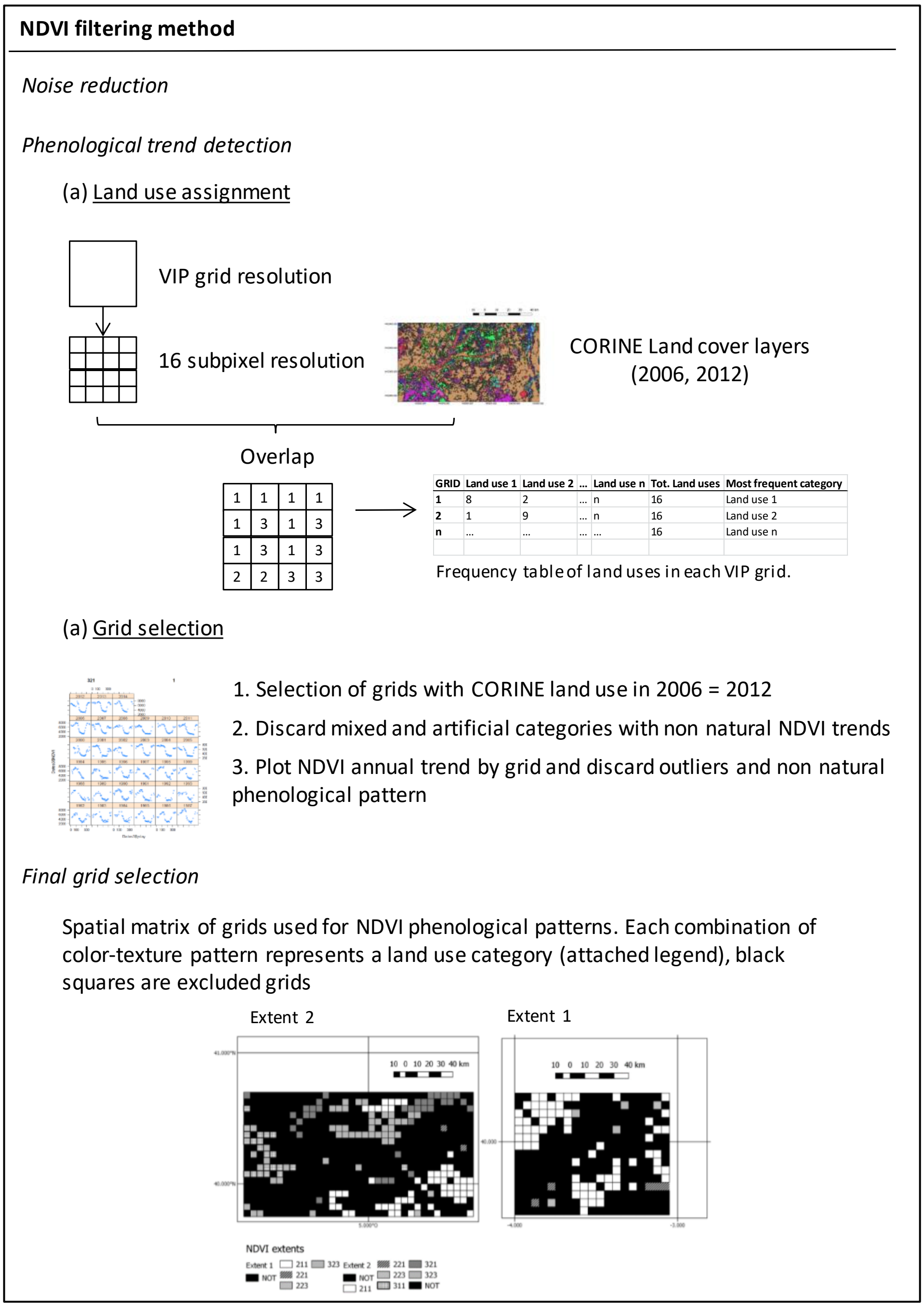
Filtering NDVI data

As a preliminary step, we exhaustively filtered NDVI data to avoid potential sources of bias in the estimation of phenology metrics, like noise by different sources (cloudy days, etc.) and departure from expected gradual vegetation dynamics (mostly by landscape heterogeneity in the grid). The NDVI data filtering procedure is summarized in Figure S2.2, and included the following steps:

Noise reduction. The interference of atmospheric effects and cloud mask with satellite data may be derived from the pixel reliability layer. We included only data with values between 0 and 2 (0 = Excellent, 1 = Good, 2 = Acceptable). Discarded categories range from 3 = Marginal to 11 = Long term average database, and include negative scores representing waterbodies or pixels with no data.

Phenological trend detection. We classified VIP07 grids by land cover categories using CORINE layers (Coordination of Information on the Environment, https://land.copernicus.eu/pan-european/corine-land-cover/clc-2012, https://land.copernicus.eu/pan-european/corine-land-cover/clc-2006). CORINE spatial resolution is higher (minimum polygon size 250,000 m^2) than VIP grid resolution (31,360,000 m^2). Therefore, we subdivided each VIP grid in 16 subpixels and overlapped CORINE land cover layers from 2006 and 2012. We assigned to each VIP grid the most frequent land use class. We discarded grids with unreliable trends of NDVI following different criteria: (1) we discarded grids with different land use categories assigned in 2006 and 2012, because land use changes may lead to misleading long-term temporal patterns. (2) Pixels with mixed land uses (when two categories were equally frequent) were discarded because mixed signals resulting from heterogeneous landscape can distort phenological patterns (Doktor et al. 2009). We excluded land use categories with completely artificial phenological pattern: category 212 (permanently irrigated land), category 131 (mineral extraction sites) and category 242 (complex cultivation patters). (3) Phenological trends are strongly influenced by the temporal continuity of NDVI values, for example, long cloudy periods during spring time in some areas and years may bias the analysis of the patterns due to lack of consecutive data. We plotted NDVI trends by grid to discard grids with a significant departure from expected gradual vegetation dynamics. We also excluded outliers by visually inspecting differences of NDVI higher than 1,000 between two consecutive dates. Finally, we calculated the Shannon index of diversity (Shannon

1948) for each grid to have additional information about the landscape heterogeneity when patterns were not gradual.


NDVI filtering method

Noise reduction

Phenological trend detection

(a) Land use assignment

1	1	1	1
1	3	1	3
1	3	1	3
2	2	3	3

GRID	Land use 1	Land use 2	...	Land use n	Tot. Land uses	Most frequent category
1	8	2	...	n	16	Land use 1
2	1	9	...	n	16	Land use 2
n	...	...	...	...	16	Land use n

Frequency table of land uses in each VIP grid.

(a) Grid selection

1. Selection of grids with CORINE land use in 2006 = 2012
2. Discard mixed and artificial categories with non natural NDVI trends
3. Plot NDVI annual trend by grid and discard outliers and non natural phenological pattern

Final grid selection

Spatial matrix of grids used for NDVI phenological patterns. Each combination of color-texture pattern represents a land use category (attached legend), black squares are excluded grids

Figure S2.2. Summary of the NDVI filtering data procedure prior to the computation of environmental indices.

Selected grids

We used the average grid value of CORINE land use categories with a minimum of 4 grids (grids from extent 2 were used when we could not meet this criterion with extent 1). We finally selected 74 out of 285 grids in extent 1 and 106 out of 665 grids in extent 2 (Figure S2.2). We had enough reliable data for the following CORINE land use categories: non-irrigated arable land, vineyards, sclerophyllous vegetation, broad-leaved forest and natural grasslands (Figure S2.3).

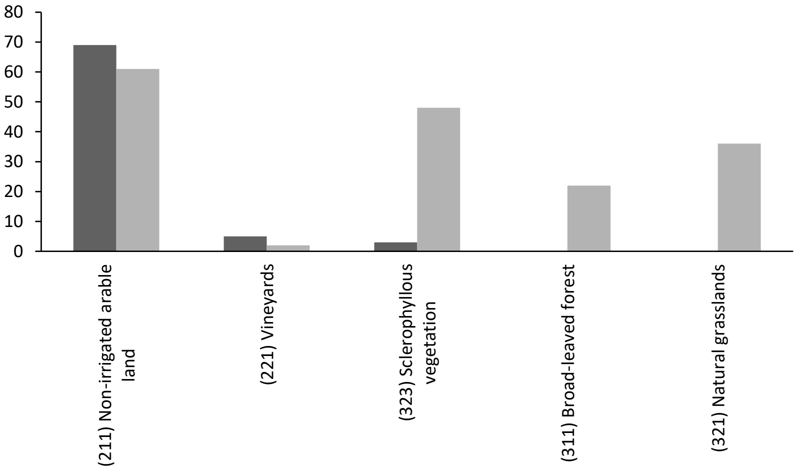


Figure S2.3. Frequencies of selected land use categories in extent 1 (dark grey) and extent 2 (light grey). CORINE land use codes are shown between parentheses.

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SUPPLEMENTARY MATERIAL S3

Post-hoc differences in the fixed term (interaction age by site) for the trend of variation in the morphology of the flight apparatus (MFA)

We performed general mixed models including the interaction between age and site as a fixed factor, year as a covariate and individual identity as a random factor. The morphology of the flight apparatus (MFA) differed between age classes depending on the site. We used Tukey post-hoc tests in emmeans R package (Lenth et al. 2019) to test for pairwise differences between the relevant factor levels. Breeding nightingales had higher MFA values than younger individuals in both areas, nevertheless we found that second-year recruits had higher values than young individuals in Presa del Rey (Figure S3.1, Las Minas comparison age young vs. second-year recruits, $t_{1024} = 0.80$, $P = 0.70$; all other pairwise comparisons $P < 0.01$).

References

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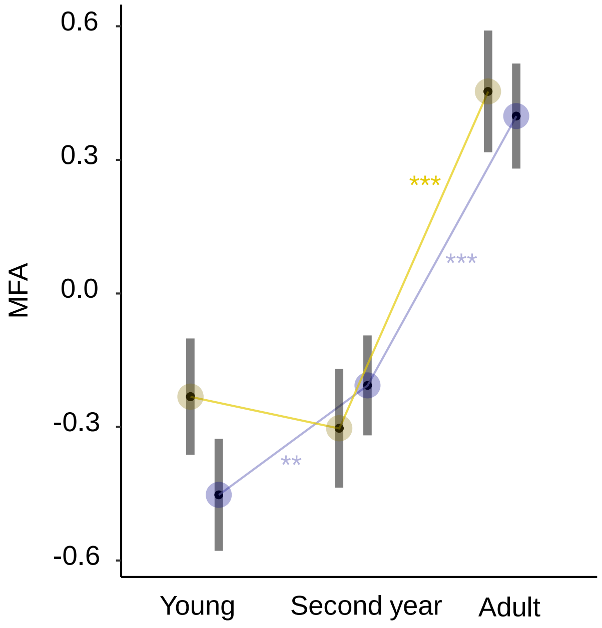

Figure S3.1. Variation in MFA (least square means ± 95% confidence intervals) between age classes in Las Minas (ochre) and Presa del Rey (blue). Statistical significance of the pairwise comparisons was assessed with Tukey method. Young was used as the reference age level within plots (** *P* < 0.01, *** *P* < 0.001).

SUPPLEMENTARY MATERIAL S4

Correlation between phenology and morphological or environmental variables

We further examined phenotypic trends by analysing within-year correlations between morphology and phenology, which might help to gain insight into the drivers of morphological change found in our study. These correlations were analysed with simple or mixed linear models (lme4 package in R; Bates et al. 2015). When the analysis involved individual data, we z-standardized arrival and fledging times within years, Finally, we used simple linear models to analyse the relationships between nightingale phenology and environmental conditions (spring earliness, rate of spring advancement, summer drought, summer earliness, or onset of high availability of insects as estimated from accumulated degree days [FA_{high}]).

Arrival time in Las Minas was not significantly correlated with spring earliness or rate of spring advancement, nor was it correlated with FA_{high}. However, nightingales arrived later in years with more intense summer drought and later summer peak. Individual arrival time (standardized by year) was not correlated with MFA, either considering the earliest 20% individuals (estimate = -0.02, SE = 0.06, $t_{39.1} = -0.42$, P = 0.67) or all breeding individuals caught in the season (estimate = -0.09, SE = 0.05, $t_{320.4} = -1.73$, P = 0.08). We failed to detect a significant correlation between arrival time and average MFA of young nightingales (Table S4.1).

We found a positive relationship between the average date of capture of all young and spring earliness and between the date of capture of the first young and FA_{high}. We did not find any relationship between average fledging time and rate of spring advancement, summer indices, or FA_{high}, nor between date of capture of the first young and spring or summer indices (Table S4.2). However, the relationship between average fledging time and FA_{high} was highly significant when we excluded from the analysis the outlier year 1997 (date of capture of the first young: estimate = 0.41, SE = 0.11, $t_{31} = 3.82$, $P < 0.001$; average date of capture of all young: estimate = 0.32, SE = 0.10, $t_{33} = 3.06$, $P = 0.004$). Fledglings were captured earlier in years when breeding birds had lower mean MFA values if we considered mean date of first capture of all young. However, this relationship was not significant when we analysed it using the date of capture of the first young. At the individual level, fledglings with lower MFA values fledged earlier in the season (relationship between the date of first capture of fledglings standardized among years and MFA of young individuals: estimate = 0.12, SE = 0.05, $t_{342} = 2.28$, $P = 0.02$).

We did not find any significant relationship between arrival-breeding interval and the environmental variables. Arrival-breeding interval in Las Minas tended to be shorter in years when nightingales had low MFA values in average, although the correlation did not reach statistical significance (Table S4.3).

We excluded from the previous analyses various years with sampling gaps, which could have decreased the accuracy of dates. Thus, we excluded from the analysis of arrival time and arrival-breeding interval the years 2000 and 2010. Including all years did not change the results qualitatively, except for the fact that the relationship between arrival time and summer earliness turned not significant ($t_{17} = 1.80$, $P = 0.09$), and we found a significant negative correlation between arrival time and average young MFA (estimate = -5.89, SE = 2.79, $t_{18} = 2.11$, $P = 0.049$). Arrival-breeding interval also became significantly shorter in years when young scored lower values of MFA (estimate = 13.64, SE = 6.08, $t_{18} = 2.24$, $P = 0.04$). In the analyses of date of capture of the first young each year, we excluded the data from Presa del Rey of 2010 and 2012, although including all years did not change the results qualitatively.

Table S4.1. Effects describing the relationships between arrival date of the earliest 20% of breeding nightingales and morphology or environmental variables during the 1995-2014 period. Some effects that changed statistical significance when they were tested including years with sampling gaps are highlighted in red (see key at the foot of the table and details in the main text of this Supplementary Material).

	Arrival date			
	Estimate	SE	t (df)	*P*
Morphological variables:				
MFA of young	-5.76	3.01	-1.92 (16)	0.07*
Environmental variables:				
Spring earliness	2.95	3.24	0.91 (15)	0.38
Rate of spring advancement	0.98	2.18	0.45 (15)	0.66
Summer drought intensity	3.66	1.55	2.37 (15)	0.03
Summer earliness	3.78	1.70	2.23 (15)	0.04[§]
Onset of high availability of insects	0.13	0.10	1.20 (16)	0.25

Statistical significance of the effect when it was tested including years with sampling gaps in the analyses: **P* = 0.049, [§]*P* = 0.09.

Table S4.2. Effects describing the relationships between nightingale fledging time (measured using data of the date of capture of the first fledgling or using data of average date of capture of all fledglings) and morphology or environmental variables during the 1995-2014 period. Some effects that changed statistical significance when they were tested excluding the outlier year 1997 are highlighted in red (see key at the foot of the table and details in the main text of this Supplementary Material).

	Date of capture of the first fledgling				Average date of capture of all fledglings			
	Estimate	SE	t (df)	*P*	Estimate	SE	t (df)	*P*
Morphological variables:								
MFA of breeding birds	6.47	4.66	1.39 (32)	0.17	10.56	3.63	2.91 (34)	0.006
Environmental variables:								
Spring earliness	4.38	3.51	1.25 (31)	0.22	6.26	3.03	2.06 (33)	0.047
Rate of spring advancement	-1.16	2.34	-0.50 (31)	0.62	-1.54	2.05	-0.75 (33)	0.46
Summer drought intensity	1.58	2.03	0.78 (31)	0.44	0.80	1.87	0.43 (33)	0.67
Summer earliness	0.64	1.99	0.32 (31)	0.75	1.79	1.72	1.04 (33)	0.31
Onset of high availability of insects	0.26	0.12	2.28 (32)	0.03*	0.19	0.11	1.75 (34)	0.09[§]

Statistical significance of the effect when the outlier year 1997 was excluded: *$P < 0.001$; [§]$P = 0.004$.

Table S4.3. Effects describing the relationships between nightingale arrival-breeding interval and morphology or environmental variables during the 1995-2014 period. Significant effects are highlighted in bold. An effect that changed statistical significance when it was tested including years with sampling gaps is highlighted in red (see key at the foot of the table and details in the main text of this Supplementary Material).

	Arrival-breeding interval			
	Estimate	SE	t (df)	*P*
Morphological variables:				
MFA of breeding birds	12.33	6.85	1.80 (16)	0.09
MFA of young	12.81	6.46	1.98 (16)	0.07*
Environmental variables:				
Spring earliness	0.77	7.14	0.11 (15)	0.92
Rate of spring advancement	-3.88	4.80	-0.81 (15)	0.43
Summer drought intensity	-2.89	3.98	-0.73 (15)	0.48
Summer earliness	-3.69	4.37	-0.84 (15)	0.41
Onset of high availability of insects	0.12	0.23	0.50 (16)	0.63

Statistical significance of the effect when it was tested including years with sampling gaps in the analyses: **P* = 0.04.

SUPPLEMENTARY MATERIAL S5

Cormack-Jolly-Seber models of variation in apparent survival and probability of recapture of nightingales

Table S5.1. Complete list of Cormack-Jolly-Seber models of variation in apparent survival (Φ) and probability of recapture (p) of nightingales. The list includes all possible simple and double interactions combining age at first capture, site, linear time trend and MFA_{ST} for Φ, and simple combinations of age at first capture, site, time as factor and sampling effort for "p". Models were ordered by Δ AICc, from lowest (the best model according to the balance between fit to the data and model complexity) to highest values.

Model	n	AICc	Δ AICc	Weight
Phi (~Age * Time + Site) p(~Age)	10	1662.65	0.00	0.09
Phi (~Site + Time) p(~Age)	6	1663.25	0.59	0.07
Phi (~Age + Site + Time) p(~Age)	8	1663.82	1.17	0.05
Phi (~Site) p(~Age)	5	1664.27	1.61	0.04
Phi (~Age * Time + Site) p(~Age + Site)	11	1664.47	1.82	0.04
Phi (~Age * Time + Site) p(~Age + Site + Sampling effort)	12	1664.52	1.87	0.04
Phi (~Age + Site) p(~Age)	7	1664.58	1.93	0.03
Phi (~Site + Time) p(~Age + Site + Sampling effort)	8	1664.62	1.97	0.03
Phi (~Age * Time + Site + MFAst) p(~Age)	11	1664.63	1.98	0.03
Phi (~Site * Time) p(~Age)	7	1665.05	2.39	0.03
Phi (~Site + Time) p(~Age + Site)	7	1665.09	2.44	0.03
Phi (~MFAst + Time + Site) p(~Age)	7	1665.24	2.59	0.02
Phi (~Site * Time + Age) p(~Age)	9	1665.68	3.03	0.02
Phi (~Age + Site + Time) p(~Age + Site + Sampling effort)	10	1665.68	3.03	0.02
Phi (~Age + Site + Time) p(~Age + Site)	9	1665.70	3.05	0.02
Phi (~MFAst + Time + Site + Age) p(~Age)	9	1665.79	3.14	0.02
Phi (~Site + MFAst) p(~Age)	6	1666.00	3.35	0.02
Phi (~Site) p(~Age + Site)	6	1666.15	3.50	0.02

Phi (~Age + Site + MFAst) p(~Age)	8	1666.24	3.59	0.02
Phi (~Age * Time + Site + MFAst) p(~Age + Site)	12	1666.45	3.80	0.01
Phi (~Age + Site) p(~Age + Site)	8	1666.50	3.85	0.01
Phi (~Age * Time + Site + MFAst) p(~Age + Site + Sampling effort)	13	1666.51	3.86	0.01
Phi (~Site * Time) p(~Age + Site + Sampling effort)	9	1666.60	3.95	0.01
Phi (~MFAst + Time + Site) p(~Age + Site + Sampling effort)	9	1666.63	3.98	0.01
Phi (~Site * Time) p(~Age + Site)	8	1666.88	4.23	0.01
Phi (~Site * Time + MFAst) p(~Age)	8	1667.05	4.40	0.01
Phi (~MFAst + Time + Site) p(~Age + Site)	8	1667.09	4.44	0.01
Phi (~Age * Site + Time) p(~Age)	10	1667.10	4.45	0.01
Phi (~MFAst * Site + Time) p(~Age)	8	1667.22	4.57	0.01
Phi (~Age * Time + Site) p(~1)	8	1667.25	4.60	0.01
Phi (~Site * Time + Age) p(~Age + Site)	10	1667.55	4.90	0.01
Phi (~Site * Time + Age + MFAst) p(~Age)	10	1667.65	5.00	0.01
Phi (~MFAst + Time + Site + Age) p(~Age + Site + Sampling effort)	11	1667.67	5.02	0.01
Phi (~Site * Time + Age) p(~Age + Site + Sampling effort)	11	1667.67	5.02	0.01
Phi (~MFAst + Time + Site + Age) p(~Age + Site)	10	1667.68	5.03	0.01
Phi (~Site) p(~Age + Site + Sampling effort)	7	1667.70	5.05	0.01
Phi (~MFAst * Site + Age + Time) p(~Age)	10	1667.78	5.13	0.01
Phi (~MFAst * Age + Site + Time) p(~Age)	11	1667.78	5.13	0.01
Phi (~Site + MFAst) p(~Age + Site)	7	1667.89	5.24	0.01
Phi (~MFAst * Site) p(~Age)	7	1667.99	5.34	0.01
Phi (~Age * Site) p(~Age)	9	1668.13	5.48	0.01
Phi (~Age + Site + MFAst) p(~Age + Site)	9	1668.16	5.51	0.01
Phi (~Age + Site) p(~Age + Site + Sampling effort)	9	1668.21	5.56	0.01
Phi (~MFAst * Site + Age) p(~Age)	9	1668.24	5.59	0.01
Phi (~MFAst * Age + Site) p(~Age)	10	1668.33	5.67	0.01
Phi (~Age + Site + Time) p(~1)	6	1668.38	5.73	0.01
Phi (~Age * Time + Site) p(~Sampling effort)	9	1668.49	5.83	0.00
Phi (~MFAst * Site + Time) p(~Age + Site + Sampling effort)	10	1668.52	5.87	0.00
Phi (~Site * Time + MFAst) p(~Age + Site + Sampling effort)	10	1668.61	5.96	0.00
Phi (~Site * Time + MFAst) p(~Age + Site)	9	1668.89	6.24	0.00
Phi (~Age * Site + Time) p(~Age + Site)	11	1668.93	6.28	0.00
Phi (~Age * Site + Time) p(~Age + Site + Sampling effort)	12	1668.96	6.31	0.00
Phi (~Age * Time + Site) p(~Site)	9	1668.99	6.34	0.00
Phi (~MFAst * Site + Time) p(~Age + Site)	9	1669.08	6.43	0.00
Phi (~Age * Site + Time + MFAst) p(~Age)	11	1669.10	6.45	0.00
Phi (~Age * Time + Site + MFAst) p(~1)	9	1669.20	6.55	0.00

Phi (~Age + Site) p(~1)	5	1669.23	6.58	0.00
Phi (~Site + MFAst) p(~Age + Site + Sampling effort)	8	1669.36	6.71	0.00
Phi (~Site * Time + Age + MFAst) p(~Age + Site)	11	1669.53	6.88	0.00
Phi (~Age + Site + Time) p(~Sampling effort)	7	1669.58	6.93	0.00
Phi (~MFAst * Site + Age + Time) p(~Age + Site + Sampling effort)	12	1669.59	6.94	0.00
Phi (~Site * Time + Age + MFAst) p(~Age + Site + Sampling effort)	12	1669.66	7.01	0.00
Phi (~MFAst * Age + Site + Time) p(~Age + Site)	12	1669.67	7.01	0.00
Phi (~MFAst * Site + Age + Time) p(~Age + Site)	11	1669.68	7.02	0.00
Phi (~Age + Site + MFAst) p(~Age + Site + Sampling effort)	10	1669.81	7.15	0.00
Phi (~Time) p(~Age + Site + Sampling effort)	7	1669.82	7.17	0.00
Phi (~Age * Site + MFAst) p(~Age)	10	1669.83	7.18	0.00
Phi (~MFAst * Age + Site + Time) p(~Age + Site + Sampling effort)	13	1669.87	7.21	0.00
Phi (~MFAst * Site) p(~Age + Site)	8	1669.89	7.24	0.00
Phi (~Age * Site) p(~Age + Site)	10	1670.02	7.37	0.00
Phi (~MFAst * Site + Age) p(~Age + Site)	10	1670.17	7.52	0.00
Phi (~Age + Site + Time) p(~Site)	7	1670.18	7.53	0.00
Phi (~MFAst * Age + Site) p(~Age + Site)	11	1670.24	7.59	0.00
Phi (~Site * Time + Age) p(~1)	7	1670.26	7.61	0.00
Phi (~MFAst + Time + Site + Age) p(~1)	7	1670.34	7.69	0.00
Phi (~Age * Time + Site + MFAst) p(~Sampling effort)	10	1670.45	7.80	0.00
Phi (~Age * Time) p(~Age + Site + Sampling effort)	11	1670.59	7.94	0.00
Phi (~Age + Time) p(~Age + Site + Sampling effort)	9	1670.63	7.98	0.00
Phi (~Time) p(~Age + Site)	6	1670.77	8.12	0.00
Phi (~Age + Site + MFAst) p(~1)	6	1670.85	8.20	0.00
Phi (~Age * Site + Time + MFAst) p(~Age + Site)	12	1670.94	8.29	0.00
Phi (~Age * Time + Site + MFAst) p(~Site)	10	1670.95	8.30	0.00
Phi (~Age * Time) p(~Age + Site)	10	1670.97	8.32	0.00
Phi (~Age * Site + Time + MFAst) p(~Age + Site + Sampling effort)	13	1670.97	8.32	0.00
Phi (~Age + Time) p(~Age + Site)	8	1671.04	8.39	0.00
Phi (~Age + Site) p(~Site)	6	1671.08	8.43	0.00
Phi (~Age + Site) p(~Sampling effort)	6	1671.23	8.58	0.00
Phi (~1) p(~Age + Site)	5	1671.26	8.61	0.00
Phi (~Age) p(~Age + Site)	7	1671.29	8.64	0.00
Phi (~MFAst * Site) p(~Age + Site + Sampling effort)	9	1671.34	8.69	0.00
Phi (~MFAst + Time + Site + Age) p(~Sampling effort)	8	1671.55	8.90	0.00
Phi (~Age * Site + Time) p(~1)	8	1671.56	8.91	0.00

Phi (~Time) p(~Age)	5	1671.61	8.96	0.00
Phi (~Site * Time + Age) p(~Sampling effort)	8	1671.61	8.96	0.00
Phi (~Age + Site + MFAst + Time + Site:Age + Site:Time + Age:Time + MFAst:Site + MFAst:Age) p(~Age)	17	1671.69	9.03	0.00
Phi (~Age * Site + MFAst) p(~Age + Site)	11	1671.72	9.07	0.00
Phi (~Age * Site) p(~Age + Site + Sampling effort)	11	1671.78	9.13	0.00
Phi (~MFAst * Site + Age) p(~Age + Site + Sampling effort)	11	1671.80	9.15	0.00
Phi (~MFAst + Time) p(~Age + Site + Sampling effort)	8	1671.83	9.18	0.00
Phi (~Age + Time) p(~Age)	7	1671.92	9.27	0.00
Phi (~MFAst * Age + Site) p(~Age + Site + Sampling effort)	12	1671.99	9.34	0.00
Phi (~Age * Time) p(~Age)	9	1672.01	9.36	0.00
Phi (~Site * Time + Age) p(~Site)	8	1672.05	9.40	0.00
Phi (~1) p(~Age)	4	1672.10	9.45	0.00
Phi (~MFAst + Time + Site + Age) p(~Site)	8	1672.15	9.50	0.00
Phi (~Age) p(~Age)	6	1672.18	9.53	0.00
Phi (~Site * Time + Age + MFAst) p(~1)	8	1672.23	9.57	0.00
Phi (~MFAst * Site + Age + Time) p(~1)	8	1672.31	9.66	0.00
Phi (~MFAst * Age + Site + Time) p(~1)	9	1672.39	9.74	0.00
Phi (~1) p(~Age + Site + Sampling effort)	6	1672.42	9.77	0.00
Phi (~Age * Time + MFAst) p(~Age + Site + Sampling effort)	12	1672.60	9.95	0.00
Phi (~Age + MFAst + Time) p(~Age + Site + Sampling effort)	10	1672.63	9.98	0.00
Phi (~Age * Site) p(~1)	7	1672.68	10.02	0.00
Phi (~Age) p(~Age + Site + Sampling effort)	8	1672.69	10.04	0.00
Phi (~Age + Site + MFAst) p(~Site)	7	1672.70	10.05	0.00
Phi (~MFAst + Time) p(~Age + Site)	7	1672.78	10.13	0.00
Phi (~Age * Site + Time) p(~Sampling effort)	9	1672.79	10.14	0.00
Phi (~MFAst * Site + Age) p(~1)	7	1672.83	10.18	0.00
Phi (~Age + Site + MFAst) p(~Sampling effort)	7	1672.84	10.19	0.00
Phi (~MFAst * Age + Site) p(~1)	8	1672.97	10.32	0.00
Phi (~Age * Time + MFAst) p(~Age + Site)	11	1672.98	10.33	0.00
Phi (~Age + MFAst + Time) p(~Age + Site)	9	1673.04	10.39	0.00
Phi (~Age + MFAst) p(~Age + Site)	8	1673.07	10.42	0.00
Phi (~MFAst) p(~Age + Site)	6	1673.09	10.44	0.00
Phi (~Age * Site + Time) p(~Site)	9	1673.35	10.70	0.00
Phi (~Age * Site + MFAst) p(~Age + Site + Sampling effort)	12	1673.42	10.77	0.00
Phi (~Age + Site + MFAst + Time + Site:Age + Site:Time + Age:Time + MFAst:Site + MFAst:Age) p(~Age + Site)	18	1673.44	10.79	0.00
Phi (~MFAst * Site + Age + Time) p(~Sampling effort)	9	1673.48	10.83	0.00
Phi (~Age * Site + Time + MFAst) p(~1)	9	1673.55	10.90	0.00
Phi (~Site * Time + Age + MFAst) p(~Sampling effort)	9	1673.59	10.93	0.00

Phi (~MFAst + Time) p(~Age)	6	1673.63	10.98	0.00
Phi (~MFAst * Age + Site + Time) p(~Sampling effort)	10	1673.74	11.09	0.00
Phi (~Age + Site + MFAst + Time + Site:Age + Site:Time + Age:Time + MFAst:Site + MFAst:Age) p(~Age + Site + Sampling effort)	19	1673.84	11.19	0.00
Phi (~Age + MFAst + Time) p(~Age)	8	1673.93	11.28	0.00
Phi (~MFAst) p(~Age)	5	1673.96	11.31	0.00
Phi (~Age + MFAst) p(~Age)	7	1673.99	11.34	0.00
Phi (~Site * Time + Age + MFAst) p(~Site)	9	1674.02	11.37	0.00
Phi (~Age * Time + MFAst) p(~Age)	10	1674.03	11.38	0.00
Phi (~MFAst * Site + Age + Time) p(~Site)	9	1674.13	11.48	0.00
Phi (~MFAst) p(~Age + Site + Sampling effort)	7	1674.16	11.50	0.00
Phi (~MFAst * Age + Site + Time) p(~Site)	10	1674.19	11.54	0.00
Phi (~Age * Site + MFAst) p(~1)	8	1674.34	11.69	0.00
Phi (~Age + MFAst) p(~Age + Site + Sampling effort)	9	1674.38	11.73	0.00
Phi (~Age * Site) p(~Site)	8	1674.52	11.87	0.00
Phi (~MFAst * Site + Age) p(~Site)	8	1674.69	12.04	0.00
Phi (~Age * Site) p(~Sampling effort)	8	1674.70	12.05	0.00
Phi (~Age * Site + Time + MFAst) p(~Sampling effort)	10	1674.79	12.14	0.00
Phi (~MFAst * Site + Age) p(~Sampling effort)	8	1674.82	12.17	0.00
Phi (~MFAst * Age + Site) p(~Site)	9	1674.82	12.17	0.00
Phi (~MFAst * Age + Site) p(~Sampling effort)	9	1674.99	12.34	0.00
Phi (~MFAst * Age + Time) p(~Age + Site + Sampling effort)	12	1675.06	12.41	0.00
Phi (~MFAst * Age + Time) p(~Age + Site)	11	1675.29	12.63	0.00
Phi (~Age * Site + Time + MFAst) p(~Site)	10	1675.35	12.70	0.00
Phi (~MFAst * Age) p(~Age + Site)	10	1675.39	12.74	0.00
Phi (~Age * Time) p(~Sampling effort)	8	1675.70	13.05	0.00
Phi (~Age + Time) p(~Sampling effort)	6	1675.73	13.08	0.00
Phi (~Age * Time) p(~Site)	8	1675.86	13.21	0.00
Phi (~Age + Time) p(~Site)	6	1675.94	13.29	0.00
Phi (~Age + Site + MFAst + Time + Site:Age + Site:Time + Age:Time + MFAst:Site + MFAst:Age) p(~1)	15	1676.14	13.49	0.00
Phi (~Age * Site + MFAst) p(~Site)	9	1676.18	13.53	0.00
Phi (~MFAst * Age + Time) p(~Age)	10	1676.22	13.57	0.00
Phi (~Age) p(~Site)	5	1676.24	13.59	0.00
Phi (~Age * Site + MFAst) p(~Sampling effort)	9	1676.35	13.70	0.00
Phi (~MFAst * Age) p(~Age)	9	1676.36	13.70	0.00
Phi (~Age + Time) p(~1)	5	1676.72	14.06	0.00
Phi (~MFAst * Age) p(~Age + Site + Sampling effort)	11	1676.82	14.17	0.00
Phi (~Age * Time) p(~1)	7	1676.82	14.17	0.00

Phi (~Age) p(~1)	4	1677.02	14.36	0.00
Phi (~Age * Time + Site) p(~Age + time)	28	1677.53	14.88	0.00
Phi (~Site + Time) p(~Age + time)	24	1677.67	15.02	0.00
Phi (~Age + Site + MFAst + Time + Site:Age + Site:Time + Age:Time + MFAst:Site + MFAst:Age) p(~Sampling effort)	16	1677.69	15.04	0.00
Phi (~Age * Time + MFAst) p(~Sampling effort)	9	1677.71	15.06	0.00
Phi (~Age + MFAst + Time) p(~Sampling effort)	7	1677.74	15.09	0.00
Phi (~Age + Site + MFAst + Time + Site:Age + Site:Time + Age:Time + MFAst:Site + MFAst:Age) p(~Site)	16	1677.85	15.20	0.00
Phi (~Age * Time + MFAst) p(~Site)	9	1677.86	15.21	0.00
Phi (~Age + MFAst + Time) p(~Site)	7	1677.94	15.28	0.00
Phi (~Age) p(~Sampling effort)	5	1677.97	15.32	0.00
Phi (~Age + MFAst) p(~Site)	6	1678.00	15.35	0.00
Phi (~Age + MFAst + Time) p(~1)	6	1678.72	16.07	0.00
Phi (~Age + MFAst) p(~1)	5	1678.81	16.16	0.00
Phi (~Age * Time + MFAst) p(~1)	8	1678.83	16.18	0.00
Phi (~Age + Site + Time) p(~Age + time)	26	1678.95	16.30	0.00
Phi (~Site) p(~Age + time)	23	1679.18	16.53	0.00
Phi (~Age + Site) p(~Age + time)	25	1679.42	16.76	0.00
Phi (~Age * Time + Site) p(~Age + time + Sampling effort)	29	1679.53	16.88	0.00
Phi (~Age * Time + Site) p(~Age + Site + time)	29	1679.61	16.96	0.00
Phi (~Age * Time + Site + MFAst) p(~Age + time)	29	1679.62	16.96	0.00
Phi (~Age + MFAst) p(~Sampling effort)	6	1679.67	17.02	0.00
Phi (~Site * Time) p(~Age + time)	25	1679.70	17.05	0.00
Phi (~Site + Time) p(~Age + time + Sampling effort)	25	1679.73	17.08	0.00
Phi (~MFAst + Time + Site) p(~Age + time)	25	1679.76	17.10	0.00
Phi (~Site + Time) p(~Age + Site + time)	25	1679.76	17.10	0.00
Phi (~MFAst * Age + Time) p(~Site)	9	1680.26	17.61	0.00
Phi (~MFAst * Age + Time) p(~Sampling effort)	9	1680.29	17.64	0.00
Phi (~MFAst * Age) p(~Site)	8	1680.39	17.74	0.00
Phi (~Age + Site + Time) p(~Age + time + Sampling effort)	27	1680.97	18.31	0.00
Phi (~Age + Site + Time) p(~Age + Site + time)	27	1681.02	18.37	0.00
Phi (~Site * Time + Age) p(~Age + time)	27	1681.02	18.37	0.00
Phi (~MFAst + Time + Site + Age) p(~Age + time)	27	1681.03	18.38	0.00
Phi (~MFAst * Age + Time) p(~1)	8	1681.10	18.45	0.00
Phi (~Site + MFAst) p(~Age + time)	24	1681.12	18.46	0.00
Phi (~Site) p(~Age + time + Sampling effort)	24	1681.12	18.47	0.00
Phi (~Site) p(~Age + Site + time)	24	1681.20	18.55	0.00
Phi (~MFAst * Age) p(~1)	7	1681.25	18.60	0.00
Phi (~Age + Site) p(~Age + time + Sampling effort)	26	1681.28	18.63	0.00

Phi (~Age + Site + MFAst) p(~Age + time)	26	1681.32	18.67	0.00
Phi (~Age + Site) p(~Age + Site + time)	26	1681.38	18.72	0.00
Phi (~Age * Time + Site + MFAst) p(~Age + time + Sampling effort)	30	1681.62	18.97	0.00
Phi (~Age * Time + Site) p(~Age + time + Site + Sampling effort)	30	1681.65	19.00	0.00
Phi (~MFAst * Site + Time) p(~Age + time)	26	1681.67	19.02	0.00
Phi (~Age * Time + Site + MFAst) p(~Age + Site + time)	30	1681.70	19.05	0.00
Phi (~Age * Time + Site) p(~time)	26	1681.75	19.10	0.00
Phi (~Site * Time + MFAst) p(~Age + time)	26	1681.79	19.14	0.00
Phi (~Site * Time) p(~Age + Site + time)	26	1681.79	19.14	0.00
Phi (~Site * Time) p(~Age + time + Sampling effort)	26	1681.80	19.15	0.00
Phi (~MFAst + Time + Site) p(~Age + time + Sampling effort)	26	1681.82	19.17	0.00
Phi (~Site + Time) p(~Age + time + Site + Sampling effort)	26	1681.83	19.18	0.00
Phi (~MFAst + Time + Site) p(~Age + Site + time)	26	1681.85	19.20	0.00
Phi (~MFAst * Age) p(~Sampling effort)	8	1682.23	19.58	0.00
Phi (~Age * Site + Time) p(~Age + time)	28	1682.34	19.69	0.00
Phi (~MFAst * Site + Age + Time) p(~Age + time)	28	1682.96	20.31	0.00
Phi (~MFAst + Time + Site + Age) p(~Age + time + Sampling effort)	28	1683.04	20.39	0.00
Phi (~Age * Site) p(~Age + time)	27	1683.05	20.40	0.00
Phi (~Site + MFAst) p(~Age + time + Sampling effort)	25	1683.06	20.41	0.00
Phi (~MFAst * Site) p(~Age + time)	25	1683.06	20.41	0.00
Phi (~Age + Site + Time) p(~Age + time + Site + Sampling effort)	28	1683.07	20.42	0.00
Phi (~Site * Time + Age) p(~Age + time + Sampling effort)	28	1683.07	20.42	0.00
Phi (~MFAst + Time + Site + Age) p(~Age + Site + time)	28	1683.10	20.45	0.00
Phi (~Site * Time + Age) p(~Age + Site + time)	28	1683.10	20.45	0.00
Phi (~Site * Time + Age + MFAst) p(~Age + time)	28	1683.11	20.45	0.00
Phi (~Site + MFAst) p(~Age + Site + time)	25	1683.14	20.49	0.00
Phi (~Age + Site) p(~time)	23	1683.15	20.50	0.00
Phi (~Age + Site + MFAst) p(~Age + time + Sampling effort)	27	1683.19	20.54	0.00
Phi (~Site) p(~Age + time + Site + Sampling effort)	25	1683.20	20.55	0.00
Phi (~MFAst * Site + Age) p(~Age + time)	27	1683.27	20.62	0.00
Phi (~Age + Site + MFAst) p(~Age + Site + time)	27	1683.29	20.64	0.00
Phi (~Age + Site) p(~Age + time + Site + Sampling effort)	27	1683.35	20.70	0.00
Phi (~Age + Site + Time) p(~time)	24	1683.36	20.71	0.00
Phi (~MFAst * Age + Site + Time) p(~Age + time)	29	1683.41	20.75	0.00
Phi (~MFAst * Age + Site) p(~Age + time)	28	1683.63	20.98	0.00
Phi (~MFAst * Site + Time) p(~Age + time + Sampling effort)	27	1683.72	21.07	0.00
Phi (~Age * Time + Site + MFAst) p(~Age + time + Site + Sampling effort)	31	1683.73	21.08	0.00

Phi (~MFAst * Site + Time) p(~Age + Site + time)	27	1683.76	21.11	0.00
Phi (~Age * Time + Site + MFAst) p(~time)	27	1683.81	21.16	0.00
Phi (~Age * Time + Site) p(~Site + time)	27	1683.81	21.16	0.00
Phi (~Site * Time + MFAst) p(~Age + Site + time)	27	1683.89	21.24	0.00
Phi (~Site * Time + MFAst) p(~Age + time + Sampling effort)	27	1683.89	21.24	0.00
Phi (~Site * Time) p(~Age + time + Site + Sampling effort)	27	1683.90	21.25	0.00
Phi (~MFAst + Time + Site) p(~Age + time + Site + Sampling effort)	27	1683.93	21.28	0.00
Phi (~Time) p(~Age + Site + time)	24	1684.02	21.36	0.00
Phi (~Age) p(~Age + Site + time)	25	1684.14	21.49	0.00
Phi (~Age * Time) p(~Age + Site + time)	28	1684.16	21.51	0.00
Phi (~Age * Site + Time) p(~Age + time + Sampling effort)	29	1684.40	21.75	0.00
Phi (~1) p(~Age + Site + time)	23	1684.43	21.78	0.00
Phi (~Age * Site + Time + MFAst) p(~Age + time)	29	1684.44	21.79	0.00
Phi (~Age * Site + Time) p(~Age + Site + time)	29	1684.44	21.79	0.00
Phi (~Age + Time) p(~Age + Site + time)	26	1684.66	22.01	0.00
Phi (~MFAst * Site + Age + Time) p(~Age + time + Sampling effort)	29	1684.95	22.30	0.00
Phi (~MFAst * Site) p(~Age + time + Sampling effort)	26	1684.97	22.31	0.00
Phi (~Age * Site) p(~Age + time + Sampling effort)	28	1684.97	22.32	0.00
Phi (~Age * Site + MFAst) p(~Age + time)	28	1684.99	22.34	0.00
Phi (~MFAst * Site + Age + Time) p(~Age + Site + time)	29	1685.03	22.38	0.00
Phi (~Age + Site + MFAst) p(~time)	24	1685.05	22.39	0.00
Phi (~Age * Site) p(~Age + Site + time)	28	1685.07	22.42	0.00
Phi (~MFAst * Site) p(~Age + Site + time)	26	1685.09	22.43	0.00
Phi (~MFAst * Site + Age) p(~Age + time + Sampling effort)	28	1685.09	22.44	0.00
Phi (~Age + Site) p(~Site + time)	24	1685.13	22.48	0.00
Phi (~Site + MFAst) p(~Age + time + Site + Sampling effort)	26	1685.15	22.50	0.00
Phi (~MFAst + Time + Site + Age) p(~Age + time + Site + Sampling effort)	29	1685.15	22.50	0.00
Phi (~Site * Time + Age + MFAst) p(~Age + time + Sampling effort)	29	1685.16	22.51	0.00
Phi (~Site * Time + Age) p(~Age + time + Site + Sampling effort)	29	1685.18	22.53	0.00
Phi (~Site * Time + Age + MFAst) p(~Age + Site + time)	29	1685.18	22.53	0.00
Phi (~MFAst * Site + Age) p(~Age + Site + time)	28	1685.23	22.58	0.00
Phi (~Age + Site + MFAst) p(~Age + time + Site + Sampling effort)	28	1685.27	22.61	0.00
Phi (~Age + Site + Time) p(~Site + time)	25	1685.40	22.75	0.00
Phi (~MFAst + Time + Site + Age) p(~time)	25	1685.42	22.77	0.00
Phi (~Site * Time + Age) p(~time)	25	1685.45	22.80	0.00

Phi (~MFAst * Age + Site + Time) p(~Age + time + Sampling effort)	30	1685.46	22.81	0.00
Phi (~MFAst * Age + Site + Time) p(~Age + Site + time)	30	1685.49	22.84	0.00
Phi (~MFAst * Age + Site) p(~Age + time + Sampling effort)	29	1685.58	22.93	0.00
Phi (~MFAst * Age + Site) p(~Age + Site + time)	29	1685.63	22.98	0.00
Phi (~MFAst * Site + Time) p(~Age + time + Site + Sampling effort)	28	1685.83	23.17	0.00
Phi (~Age * Time + Site + MFAst) p(~Site + time)	28	1685.88	23.22	0.00
Phi (~Time) p(~Age + time + Site + Sampling effort)	25	1685.88	23.23	0.00
Phi (~Age * Time + Site) p(~Site + time + Sampling effort)	28	1685.88	23.23	0.00
Phi (~Age) p(~Age + time + Site + Sampling effort)	26	1685.90	23.25	0.00
Phi (~Age * Time) p(~Age + time + Site + Sampling effort)	29	1685.95	23.30	0.00
Phi (~Site * Time + MFAst) p(~Age + time + Site + Sampling effort)	28	1686.00	23.35	0.00
Phi (~MFAst + Time) p(~Age + Site + time)	25	1686.11	23.46	0.00
Phi (~Age + MFAst) p(~Age + Site + time)	26	1686.13	23.47	0.00
Phi (~1) p(~Age + time + Site + Sampling effort)	24	1686.19	23.54	0.00
Phi (~Age) p(~Age + time + Sampling effort)	25	1686.21	23.55	0.00
Phi (~Age * Time + MFAst) p(~Age + Site + time)	29	1686.26	23.60	0.00
Phi (~Time) p(~Age + time + Sampling effort)	24	1686.28	23.63	0.00
Phi (~1) p(~Age + time + Sampling effort)	23	1686.36	23.71	0.00
Phi (~MFAst) p(~Age + Site + time)	24	1686.44	23.78	0.00
Phi (~Age + Time) p(~Age + time + Site + Sampling effort)	27	1686.49	23.84	0.00
Phi (~Age * Site + Time + MFAst) p(~Age + time + Sampling effort)	30	1686.50	23.85	0.00
Phi (~Age * Site + Time) p(~Age + time + Site + Sampling effort)	30	1686.51	23.86	0.00
Phi (~Age * Site + Time + MFAst) p(~Age + Site + time)	30	1686.54	23.89	0.00
Phi (~Age * Time) p(~Age + time + Sampling effort)	28	1686.58	23.93	0.00
Phi (~Age * Site) p(~time)	25	1686.68	24.02	0.00
Phi (~Age * Site + Time) p(~time)	26	1686.70	24.05	0.00
Phi (~Time) p(~Age + time)	23	1686.73	24.08	0.00
Phi (~Age + MFAst + Time) p(~Age + Site + time)	27	1686.75	24.10	0.00
Phi (~Age * Site + MFAst) p(~Age + time + Sampling effort)	29	1686.91	24.26	0.00
Phi (~Age + Time) p(~Age + time + Sampling effort)	26	1686.95	24.30	0.00
Phi (~MFAst * Site + Age) p(~time)	25	1686.95	24.30	0.00
Phi (~Age * Site + MFAst) p(~Age + Site + time)	29	1687.01	24.36	0.00
Phi (~Age + Site + MFAst) p(~Site + time)	25	1687.03	24.38	0.00
Phi (~MFAst * Site + Age + Time) p(~Age + time + Site + Sampling effort)	30	1687.06	24.40	0.00
Phi (~MFAst * Site) p(~Age + time + Site + Sampling effort)	27	1687.06	24.41	0.00

Phi (~Age * Site) p(~Age + time + Site + Sampling effort)	29	1687.07	24.42	0.00
Phi (~MFAst * Site + Age) p(~Age + time + Site + Sampling effort)	29	1687.17	24.52	0.00
Phi (~Age + Site) p(~Site + time + Sampling effort)	25	1687.18	24.53	0.00
Phi (~Site * Time + Age + MFAst) p(~Age + time + Site + Sampling effort)	30	1687.26	24.61	0.00
Phi (~Age + Site + MFAst + Time + Site:Age + Site:Time + Age:Time + MFAst:Site + MFAst:Age) p(~Age + time)	35	1687.31	24.65	0.00
Phi (~1) p(~Age + time)	22	1687.31	24.66	0.00
Phi (~MFAst * Site + Age + Time) p(~time)	26	1687.32	24.67	0.00
Phi (~Age) p(~Age + time)	24	1687.36	24.70	0.00
Phi (~MFAst * Age + Site) p(~time)	26	1687.39	24.73	0.00
Phi (~MFAst + Time + Site + Age) p(~Site + time)	26	1687.47	24.81	0.00
Phi (~Age + Site + Time) p(~Site + time + Sampling effort)	26	1687.48	24.82	0.00
Phi (~Site * Time + Age) p(~Site + time)	26	1687.50	24.85	0.00
Phi (~Site * Time + Age + MFAst) p(~time)	26	1687.51	24.86	0.00
Phi (~MFAst * Age + Site + Time) p(~Age + time + Site + Sampling effort)	31	1687.57	24.92	0.00
Phi (~MFAst * Age + Site) p(~Age + time + Site + Sampling effort)	30	1687.66	25.01	0.00
Phi (~Age * Time) p(~Age + time)	27	1687.67	25.01	0.00
Phi (~Age + Time) p(~Age + time)	25	1687.70	25.05	0.00
Phi (~MFAst * Age + Site + Time) p(~time)	27	1687.79	25.14	0.00
Phi (~Age + MFAst) p(~Age + time + Site + Sampling effort)	27	1687.89	25.24	0.00
Phi (~Age * Time + Site + MFAst) p(~Site + time + Sampling effort)	29	1687.95	25.30	0.00
Phi (~MFAst + Time) p(~Age + time + Site + Sampling effort)	26	1687.98	25.33	0.00
Phi (~Age * Time + MFAst) p(~Age + time + Site + Sampling effort)	30	1688.05	25.40	0.00
Phi (~Age) p(~Site + time)	23	1688.16	25.51	0.00
Phi (~MFAst) p(~Age + time + Site + Sampling effort)	25	1688.20	25.55	0.00
Phi (~Age + MFAst) p(~Age + time + Sampling effort)	26	1688.20	25.55	0.00
Phi (~MFAst) p(~Age + time + Sampling effort)	24	1688.37	25.72	0.00
Phi (~MFAst + Time) p(~Age + time + Sampling effort)	25	1688.37	25.72	0.00
Phi (~Age * Time) p(~Site + time)	26	1688.40	25.75	0.00
Phi (~Age + MFAst + Time) p(~Age + time + Site + Sampling effort)	28	1688.58	25.93	0.00
Phi (~Age * Site + MFAst) p(~time)	26	1688.60	25.95	0.00
Phi (~Age * Site + Time + MFAst) p(~Age + time + Site + Sampling effort)	31	1688.62	25.97	0.00
Phi (~MFAst * Age) p(~Age + Site + time)	28	1688.67	26.02	0.00
Phi (~Age * Time + MFAst) p(~Age + time + Sampling effort)	29	1688.67	26.02	0.00

Phi (~Age * Site) p(~Site + time)	26	1688.68	26.03	0.00
Phi (~Age * Site + Time) p(~Site + time)	27	1688.76	26.11	0.00
Phi (~Age * Site + Time + MFAst) p(~time)	27	1688.78	26.13	0.00
Phi (~MFAst + Time) p(~Age + time)	24	1688.82	26.17	0.00
Phi (~MFAst * Site + Age) p(~Site + time)	26	1688.92	26.27	0.00
Phi (~Age * Site + MFAst) p(~Age + time + Site + Sampling effort)	30	1689.01	26.36	0.00
Phi (~Age + MFAst + Time) p(~Age + time + Sampling effort)	27	1689.04	26.39	0.00
Phi (~Site + Time) p(~1)	4	1689.07	26.42	0.00
Phi (~Age + Site + MFAst) p(~Site + time + Sampling effort)	26	1689.08	26.43	0.00
Phi (~Age + Time) p(~Site + time)	24	1689.12	26.46	0.00
Phi (~MFAst * Age + Time) p(~Age + Site + time)	29	1689.33	26.67	0.00
Phi (~MFAst) p(~Age + time)	23	1689.33	26.68	0.00
Phi (~MFAst * Site + Age + Time) p(~Site + time)	27	1689.36	26.71	0.00
Phi (~Age + MFAst) p(~Age + time)	25	1689.37	26.72	0.00
Phi (~MFAst * Age + Site) p(~Site + time)	27	1689.39	26.74	0.00
Phi (~Age + Site + MFAst + Time + Site:Age + Site:Time + Age:Time + MFAst:Site + MFAst:Age) p(~Age + time + Sampling effort)	36	1689.41	26.76	0.00
Phi (~Age + Site + MFAst + Time + Site:Age + Site:Time + Age:Time + MFAst:Site + MFAst:Age) p(~Age + Site + time)	36	1689.44	26.79	0.00
Phi (~MFAst + Time + Site + Age) p(~Site + time + Sampling effort)	27	1689.54	26.89	0.00
Phi (~Site * Time + Age + MFAst) p(~Site + time)	27	1689.56	26.91	0.00
Phi (~Site * Time + Age) p(~Site + time + Sampling effort)	27	1689.58	26.93	0.00
Phi (~Age * Time + MFAst) p(~Age + time)	28	1689.77	27.12	0.00
Phi (~Age + MFAst + Time) p(~Age + time)	26	1689.80	27.15	0.00
Phi (~MFAst * Age + Site + Time) p(~Site + time)	28	1689.85	27.20	0.00
Phi (~Age) p(~Site + time + Sampling effort)	24	1690.09	27.44	0.00
Phi (~Site + Time) p(~Sampling effort)	5	1690.13	27.47	0.00
Phi (~Age + MFAst) p(~Site + time)	24	1690.15	27.49	0.00
Phi (~Age * Time) p(~Site + time + Sampling effort)	27	1690.34	27.69	0.00
Phi (~Site) p(~1)	3	1690.49	27.84	0.00
Phi (~Age * Time + MFAst) p(~Site + time)	27	1690.49	27.84	0.00
Phi (~MFAst * Age) p(~Age + time + Site + Sampling effort)	29	1690.52	27.86	0.00
Phi (~Age * Site + MFAst) p(~Site + time)	27	1690.61	27.96	0.00
Phi (~Age * Site) p(~Site + time + Sampling effort)	27	1690.74	28.09	0.00
Phi (~Age * Site + Time) p(~Site + time + Sampling effort)	28	1690.85	28.20	0.00
Phi (~Age * Site + Time + MFAst) p(~Site + time)	28	1690.85	28.20	0.00
Phi (~Site + Time) p(~Site)	5	1690.93	28.28	0.00
Phi (~Site * Time) p(~1)	5	1690.93	28.28	0.00

Phi (~MFAst * Age) p(~Age + time + Sampling effort)	28	1690.94	28.29	0.00
Phi (~MFAst * Site + Age) p(~Site + time + Sampling effort)	27	1690.95	28.30	0.00
Phi (~Age + Time) p(~Site + time + Sampling effort)	25	1691.08	28.43	0.00
Phi (~MFAst + Time + Site) p(~1)	5	1691.08	28.43	0.00
Phi (~Age + MFAst + Time) p(~Site + time)	25	1691.20	28.54	0.00
Phi (~MFAst * Age + Time) p(~Age + time + Site + Sampling effort)	30	1691.22	28.57	0.00
Phi (~Age + Site + MFAst + Time + Site:Age + Site:Time + Age:Time + MFAst:Site + MFAst:Age) p(~time)	33	1691.31	28.66	0.00
Phi (~Age) p(~time)	22	1691.42	28.77	0.00
Phi (~MFAst * Site + Age + Time) p(~Site + time + Sampling effort)	28	1691.42	28.77	0.00
Phi (~MFAst * Age + Site) p(~Site + time + Sampling effort)	28	1691.48	28.82	0.00
Phi (~Age + Site + MFAst + Time + Site:Age + Site:Time + Age:Time + MFAst:Site + MFAst:Age) p(~Age + time + Site + Sampling effort)	37	1691.56	28.91	0.00
Phi (~Site * Time + Age + MFAst) p(~Site + time + Sampling effort)	28	1691.65	29.00	0.00
Phi (~MFAst * Age + Time) p(~Age + time + Sampling effort)	29	1691.80	29.15	0.00
Phi (~MFAst * Age) p(~Age + time)	27	1691.94	29.29	0.00
Phi (~MFAst * Age + Site + Time) p(~Site + time + Sampling effort)	29	1691.96	29.30	0.00
Phi (~Age + MFAst) p(~Site + time + Sampling effort)	25	1692.08	29.43	0.00
Phi (~Age * Time) p(~time)	25	1692.12	29.47	0.00
Phi (~MFAst + Time + Site) p(~Sampling effort)	6	1692.13	29.48	0.00
Phi (~Site * Time) p(~Sampling effort)	6	1692.15	29.50	0.00
Phi (~Site + MFAst) p(~1)	4	1692.21	29.56	0.00
Phi (~Site) p(~Site)	4	1692.38	29.73	0.00
Phi (~Age + Time) p(~time)	23	1692.39	29.74	0.00
Phi (~MFAst * Age + Time) p(~Age + time)	28	1692.41	29.76	0.00
Phi (~Age * Time + MFAst) p(~Site + time + Sampling effort)	28	1692.43	29.78	0.00
Phi (~Site) p(~Sampling effort)	4	1692.49	29.84	0.00
Phi (~Age * Site + MFAst) p(~Site + time + Sampling effort)	28	1692.68	30.03	0.00
Phi (~MFAst * Age) p(~Site + time)	26	1692.73	30.07	0.00
Phi (~Site * Time) p(~Site)	6	1692.78	30.12	0.00
Phi (~MFAst + Time + Site) p(~Site)	6	1692.94	30.28	0.00
Phi (~Site * Time + MFAst) p(~1)	6	1692.94	30.28	0.00
Phi (~Age * Site + Time + MFAst) p(~Site + time + Sampling effort)	29	1692.94	30.29	0.00
Phi (~MFAst * Site + Time) p(~1)	6	1693.00	30.35	0.00

Phi (~Age + MFAst + Time) p(~Site + time + Sampling effort)	26	1693.16	30.51	0.00
Phi (~Age + Site + MFAst + Time + Site:Age + Site:Time + Age:Time + MFAst:Site + MFAst:Age) p(~Site + time)	34	1693.42	30.76	0.00
Phi (~Age + MFAst) p(~time)	23	1693.44	30.78	0.00
Phi (~MFAst * Age + Time) p(~Site + time)	27	1693.78	31.13	0.00
Phi (~MFAst * Site + Time) p(~Sampling effort)	7	1693.99	31.34	0.00
Phi (~Site + MFAst) p(~Site)	5	1694.11	31.46	0.00
Phi (~MFAst * Site) p(~1)	5	1694.15	31.50	0.00
Phi (~Site * Time + MFAst) p(~Sampling effort)	7	1694.16	31.50	0.00
Phi (~Site + MFAst) p(~Sampling effort)	5	1694.20	31.55	0.00
Phi (~Age * Time + MFAst) p(~time)	26	1694.21	31.56	0.00
Phi (~Age + MFAst + Time) p(~time)	24	1694.47	31.82	0.00
Phi (~MFAst * Age) p(~Site + time + Sampling effort)	27	1694.72	32.07	0.00
Phi (~Site * Time + MFAst) p(~Site)	7	1694.79	32.13	0.00
Phi (~MFAst * Site + Time) p(~Site)	7	1694.87	32.22	0.00
Phi (~Age + Site + MFAst + Time + Site:Age + Site:Time + Age:Time + MFAst:Site + MFAst:Age) p(~Site + time + Sampling effort)	35	1695.54	32.89	0.00
Phi (~MFAst * Age + Time) p(~Site + time + Sampling effort)	28	1695.80	33.15	0.00
Phi (~MFAst * Site) p(~Site)	6	1696.06	33.40	0.00
Phi (~MFAst * Age) p(~time)	25	1696.08	33.42	0.00
Phi (~MFAst * Site) p(~Sampling effort)	6	1696.13	33.48	0.00
Phi (~MFAst * Age + Time) p(~time)	26	1697.13	34.48	0.00
Phi (~Time) p(~Site)	4	1697.24	34.59	0.00
Phi (~Time) p(~Sampling effort)	4	1697.38	34.73	0.00
Phi (~1) p(~Site)	3	1698.05	35.40	0.00
Phi (~Time) p(~1)	3	1698.91	36.26	0.00
Phi (~MFAst + Time) p(~Site)	5	1699.26	36.61	0.00
Phi (~MFAst + Time) p(~Sampling effort)	5	1699.40	36.75	0.00
Phi (~1) p(~1)	2	1699.70	37.05	0.00
Phi (~MFAst) p(~Site)	4	1699.88	37.23	0.00
Phi (~1) p(~Sampling effort)	3	1700.50	37.85	0.00
Phi (~MFAst + Time) p(~1)	4	1700.93	38.28	0.00
Phi (~MFAst) p(~1)	3	1701.57	38.92	0.00
Phi (~MFAst) p(~Sampling effort)	4	1702.27	39.62	0.00
Phi (~Site + Time) p(~time)	22	1704.08	41.43	0.00
Phi (~Site) p(~time)	21	1704.28	41.63	0.00
Phi (~Site + Time) p(~Site + time)	23	1706.08	43.43	0.00
Phi (~Site * Time) p(~time)	23	1706.16	43.51	0.00
Phi (~MFAst + Time + Site) p(~time)	23	1706.17	43.52	0.00

Phi (~Site) p(~Site + time)	22	1706.20	43.55	0.00
Phi (~Site + MFAst) p(~time)	22	1706.26	43.61	0.00
Phi (~MFAst * Site + Time) p(~time)	24	1707.98	45.33	0.00
Phi (~MFAst * Site) p(~time)	23	1708.10	45.45	0.00
Phi (~Site + Time) p(~Site + time + Sampling effort)	24	1708.17	45.52	0.00
Phi (~Site * Time) p(~Site + time)	24	1708.17	45.52	0.00
Phi (~MFAst + Time + Site) p(~Site + time)	24	1708.17	45.52	0.00
Phi (~Site + MFAst) p(~Site + time)	23	1708.19	45.54	0.00
Phi (~Site * Time + MFAst) p(~time)	24	1708.25	45.60	0.00
Phi (~Site) p(~Site + time + Sampling effort)	23	1708.27	45.61	0.00
Phi (~1) p(~Site + time)	21	1709.67	47.02	0.00
Phi (~MFAst * Site + Time) p(~Site + time)	25	1709.97	47.32	0.00
Phi (~MFAst * Site) p(~Site + time)	24	1710.00	47.35	0.00
Phi (~Time) p(~Site + time)	22	1710.26	47.61	0.00
Phi (~MFAst + Time + Site) p(~Site + time + Sampling effort)	25	1710.26	47.61	0.00
Phi (~Site + MFAst) p(~Site + time + Sampling effort)	24	1710.26	47.61	0.00
Phi (~Site * Time) p(~Site + time + Sampling effort)	25	1710.26	47.61	0.00
Phi (~Site * Time + MFAst) p(~Site + time)	25	1710.26	47.61	0.00
Phi (~1) p(~Site + time + Sampling effort)	22	1711.66	49.01	0.00
Phi (~MFAst) p(~Site + time)	22	1711.72	49.07	0.00
Phi (~MFAst * Site + Time) p(~Site + time + Sampling effort)	26	1712.05	49.40	0.00
Phi (~MFAst * Site) p(~Site + time + Sampling effort)	25	1712.05	49.40	0.00
Phi (~Time) p(~Site + time + Sampling effort)	23	1712.26	49.61	0.00
Phi (~MFAst + Time) p(~Site + time)	23	1712.35	49.70	0.00
Phi (~Site * Time + MFAst) p(~Site + time + Sampling effort)	26	1712.36	49.71	0.00
Phi (~MFAst) p(~Site + time + Sampling effort)	23	1713.70	51.05	0.00
Phi (~1) p(~time)	20	1714.10	51.45	0.00
Phi (~MFAst + Time) p(~Site + time + Sampling effort)	24	1714.35	51.70	0.00
Phi (~Time) p(~time)	21	1714.73	52.07	0.00
Phi (~MFAst) p(~time)	21	1716.16	53.51	0.00
Phi (~MFAst + Time) p(~time)	22	1716.80	54.15	0.00