Micro-evolutionary response of spring migration timing in a wild seabird

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ABSTRACT

Understanding the mechanisms by which populations can adapt to changing environmental conditions is crucial for predicting their viability. In the context of rapid climate change, phenological advance is a key adaptation for which evidence is accumulating across taxa. Among vertebrates, phenotypic plasticity is known to underlie most of this phenological change, while evidence for micro-evolution is very limited and challenging to infer. In this study, we quantified phenotypic and genetic trends in timing of spring migration using 8032 dates of arrival at the breeding grounds obtained from observations on 1715 individual common terns (*Sterna hirundo*) monitored across 27 years, and tested whether these trends were consistent with predictions of a micro-evolutionary response to selection. We observed a strong phenotypic advance in arrival date, with birds arriving on average 9.34 days earlier over the study period. This phenotypic trend translated into an advance in breeding values, which accounted for c. 7.4 % of the observed change in the population. The Breeder's equation and Robertson's Secondary Theorem of Selection predicted qualitatively similar evolutionary responses to selection, although the estimate from the latter was uncertain, and those theoretical predictions were largely consistent with observed genetic patterns. Overall, our study therefore provides rare evidence for micro-evolution to underlie (part of) an adaptive response to climate change in the wild, and illustrates how a combination of adaptive micro-evolution and phenotypic plasticity facilitated a shift towards earlier migration in this natural population of common terns.

IMPACT STATEMENT

Empirical evidence for evolutionary change underlying vertebrate adaptation to current global change is very rare. This may be due to phenotypic plasticity being the main mechanism underlying adaptation, or to challenges associated with the empirical testing of genetic changes in the wild, i.e., to data limitations. In this study, we tested whether an observed phenotypic advancement in the timing of spring migration in a wild seabird population was due to an evolutionary response (i.e., genetic change), and/or to phenotypic plasticity or other environmental (nongenetic) effects. To do so, we applied a series of "animal models" to a long-term dataset from a pedigreed population of common terns located at the North Sea coast of Germany and monitored over 27 years. We tested whether timing of migration underwent a genetic change towards earlier arrival of birds on the breeding grounds, in response to increasing temperatures at the wintering grounds in West Africa. We found an evolutionary response to selection favouring earlier arriving individuals. Additionally, we showed that two different theoretical approaches predicted a qualitatively similar evolutionary response, both in terms of direction and magnitude. As such, our study provides a rare empirical case where estimated and predicted evolutionary responses are in agreement and suggest an evolutionary response in the timing of avian spring migration. Our results further demonstrated that adaptive evolution likely played a smaller role than phenotypic plasticity, and overall, they highlight the importance of disentangling the relative contributions of plastic and evolutionary changes to better understand adaptive processes and predict responses to future changes.

INTRODUCTION

Phenotypic changes in response to climate change are common place across taxa (Parmesan and Yohe 2003; Parmesan 2006; Hendry et al. 2008; Chen et al. 2011; Bellard et al. 2012; Radchuk et al. 2019), but the mechanism(s) underlying these changes remain largely unknown (Lavergne et al. 2010; Salamin et al. 2010; Hoffmann and Sgrò 2011; Gienapp and Brommer 2014; Merilä and Hendry 2014). Where the mechanisms underlying the observed shifts have been explicitly investigated, they have often been attributed in vertebrates to phenotypic plasticity (i.e., genotypes express variable phenotypes under different environmental conditions), while evidence for micro-evolution (i.e., genotypes that have a higher fitness increase in frequency in the population) is still relatively rare (Hairston et al. 2005; Gienapp et al. 2008; Visser 2008; Hoffmann and Sgrò 2011; Vedder et al. 2013; Gienapp and Brommer 2014; Merilä and Hendry 2014).

Animal models (*sensu* Kruuk 2004) are useful statistical tools to test for genetic trends and rates of micro-evolutionary responses to selection by means of providing estimates of individual breeding values (i.e., the expected effect of the genes that an individual passes on to its offspring, Falconer and Mackay 1998; Lynch and Walsh 1998). The strength of this test, however, relies on properly accounting for uncertainty in breeding value predictions and environmental factors (Postma 2006; Hadfield et al. 2010). To our knowledge, there are only three long-term studies from natural vertebrate populations that have found evidence for a genetic change underlying phenotypic change (most likely) in response to climate change, while taking into account the uncertainty in the breeding value estimation and while controlling for a temporal trend in the phenotypic data (but see Merilä et al. 2001 and Walsh and Lynch 2018 for reviews on evolutionary stasis, where no micro-evolutionary change was observed). First, based on ten years of data on an alpine population of snow voles (*Chionomys nivalis*), Bonnet and colleagues (2017) showed a genetic change towards a reduced body mass as an adaptive response to viability selection, likely in response to a change in snowfall patterns. This genetic change represented a case of “cryptic evolution” where the population did evolve but there was no observed phenotypic change in body mass. Second, Evans and Gustafsson (2017) studied male plumage colouration in collared flycatchers (*Ficedula albicollis*) over 34 years and showed a marked phenotypic decline, which was mirrored by a decline in the mean breeding value of these males. This decline, which accounted for 11% of the total phenotypic change, was likely driven by viability selection acting on ornamentation being sensitive to the climatic conditions experienced at the breeding ground in the preceding year. And third, using data obtained from a wild population of red deer (*Cervus elaphus*), Bonnet and colleagues (2019) found that average parturition date had advanced by nearly two weeks over the 45-year study period, with warmer temperatures during the previous rut season tending to advance parturition date, and showed that a micro-evolutionary response accounted for 15% of the total change of -12.3 days (Bonnet et al. 2019).

Once genetic trends have been estimated, testing their consistency with predictions of a micro-evolutionary response to selection can inform us about the occurrence and magnitude of adaptive responses to selection, as well as our ability to model these responses. Traditionally, the per-generation evolutionary response to selection in a given trait, R, can be predicted by $R = h^2S$, also known as the Breeder’s equation, where h^2 represents the trait heritability, and S is the directional selection differential (Falconer and Mackay 1998; Lynch and Walsh 1998). This Breeder’s equation, however, tends to lead to biased predictions in studies from natural populations due to the occurrence of correlated selection as well as confounding environmental effects (i.e., when selection is acting on the environmental rather than genetic component of a trait, the Breeder’s equation will overestimate the trait’s response to selection) (Morrissey et al. 2010). It therefore has been argued that micro-evolutionary responses to selection in natural populations are better predicted by applying Robertson's Secondary Theorem of natural Selection (hereafter, STS) (Morrissey et al. 2010), which postulates that the additive genetic covariance between a trait and relative fitness is a direct measure of the expected per-generation evolutionary change in the mean trait value, *R* (Robertson 1966; Price 1970). While STS is a strictly genetic approach to predicting a response to selection, and therefore unbiased by unmeasured covariates, it is also agnostic regarding the selection processes underlying the micro-evolutionary responses. Moreover, the predictive power of STS can be hampered in the case of strong genetic drift or selection acting on a genetically correlated trait (Morrissey et al. 2010, 2012a; Walsh and Lynch 2018). Hence, a comprehensive understanding of the predicted evolutionary responses to selection will benefit from evaluating the predictions from both the Breeder's equation and the Robertson's Secondary Theorem of Selection, as both quantitative genetic models will provide complementary information.

Along with poleward shifts in geographic distributions, phenotypic changes in response to global warming are most apparent in phenology (Root et al. 2003; Menzel et al. 2006; Parmesan 2006; Thackeray et al. 2010; Poloczanska et al. 2013). As such, timing of migration, together with timing of breeding, is a trait of special interest in the context of current global and climate change (Parmesan and Yohe 2003; Charmantier and Gienapp 2014; Gienapp et al. 2014). Among birds, most studied populations have shifted their phenology to earlier migration and breeding (review: Lehikoinen et al. 2004; Gienapp et al. 2007; Gordo 2007; Charmantier and Gienapp 2014; meta-analysis: Radchuk et al. 2019), although not all bird species share the same adaptive potential (e.g., Keogan et al. 2018). For instance, some birds such as long-distance migrants might be constrained in their potential to keep track of changing environmental conditions by inherited circannual clocks and migratory behaviours (Åkesson et al. 2017) and by reduced correlation between climate on the wintering and the breeding grounds, making them more sensitive to rapid warming conditions. With respect to the timing of migration, the date of arrival at the breeding grounds has received most empirical attention, and an early arrival is expected to enable selection of high-quality breeding sites (Kokko et al. 2004) and mates (Coppack and Both 2002; Ludwigs and Becker 2005), and to favour an early initiation of breeding, which in turn provides offspring with additional developmental time before autumn migration. Besides often being under strong directional selection (favouring earlier arrival to the breeding sites), arrival date has also been found to harbour an important genetic component. For instance, arrival date heritabilities ranged from 0.11 to 0.32 in three different studies from bird populations: barn swallows (*Hirundo rustica*, Teplitsky et al. 2011), common terns (*Sterna hirundo*, Arnaud et al. 2013), and great reed warbler (*Acrocephalus arundinaceus*, Tarka et al. 2015), with collective evidence across four bird species revealing a mean heritability of 0.43 (Pulido 2007).

Even though the prerequisites for a micro-evolutionary response are often met (non-zero additive genetic variance and selection), to date we know of only two studies providing “indirect” evidence for a micro-evolutionary response of the timing of migration in natural bird populations. First, Teplitsky and colleagues (2011) used two long-term datasets on barn swallows from Spain and Denmark to show that, for the Spanish population, the Breeder’s equation and Robertson’s Secondary Theorem of Selection predicted qualitatively similar responses to selection (towards earlier arrival dates). Teplitsky and colleagues (2011) did not, however, further estimate whether their study population had undergone substantial phenotypic or genetic change across years, precluding the comparison between observed and predicted responses to selection in timing of migration. Second, Helm and colleagues (2019) replicated an experimental study of the annual cycle of a long-distance migratory species, the pied flycatcher (*Ficedula hypoleuca*), after 21 years of warming to show that migration timing had advanced by 9 days. This advance was also observed in a nearby natural population of flycatchers, such that, altogether, their results supported a role of micro-evolution in changing spring migration timing (Helm et al. 2019).

In this study, we applied a series of univariate and bivariate animal models to test for the existence and magnitude of a micro-evolutionary response in the timing of spring arrival in a long-distance migratory bird. We used 27 years of data from a natural, pedigreed population of common terns (*Sterna hirundo*). We had two main objectives: (1) to quantify whether there was a detectable genetic change in arrival date (i.e., a temporal trend in individual breeding values), and (2) to test whether this trend was consistent with predictions of micro-evolutionary responses to selection based on both the Breeder's equation and Robertson's Secondary Theorem of natural Selection. Previous studies from the same study population found that arrival date was heritable (Arnaud et al. 2013; Moiron et al. 2020) and under directional selection, with earlier arrival being associated with a higher annual number of fledglings (Arnaud et al. 2013, but see Ezard et al. 2007) and a higher probability of survival (Zhang et al. 2015b). Hence, although we acknowledge that evolutionary stasis often occurs, even when these prerequisites are met (Merilä et al. 2001; Walsh and Lynch 2018), we expected a micro-evolutionary response towards earlier arrival dates from the wintering grounds. Finally, earlier work found evidence for individual, and, to a lesser extent, additive genetic variance in plasticity of arrival date in response to sea surface temperature at the main wintering areas (Moiron et al. *in revision,* see Dobson et al. 2017 for analyses on breeding timing), highlighting the potential for multiple, non-mutually exclusive adaptive responses to be in action in this population of common terns.

METHODS

STUDY SYSTEM AND DATA COLLECTION

The data were collected as part of a long-term study of a common tern population located at the Banter See on the German North Sea coast (53°36´N, 08°06´E). The colony consists of six concrete islands, each of which is surrounded by a 60 cm wall. An individual-based study was initiated in 1992, when 101 adult birds were caught and marked with individually numbered subcutaneously injected transponders. Since 1992, all locally hatched birds have similarly been marked with a transponder shortly prior to fledging and the presence and reproductive performance of marked individuals has been monitored with the help of antennae and following a standard protocol (Becker and Wendeln 1997). Thanks to the automatic antenna system, affixed to the walls of the colony site since 1994, it is possible to record the arrival date from the wintering grounds of every marked bird in the population. From this, and confirmed by a tracking study, it is known that the common terns of this population show highly repeatable migratory behaviour (Kürten et al. 2022).

As part of the standard protocol, breeding birds are identified using portable antennae placed around each nest for 1–2 days during incubation, which is shared by both partners. Pairs can rear up to three chicks per brood and produce replacement clutches after loss of eggs or chicks. True second clutches are extremely rare (Becker and Zhang 2011). Chicks are ringed at hatching and checked every 2–3 days throughout the breeding season until they fledge (at about 26 days; Becker and Wink 2003) or perish.

DATA SELECTION

The phenotypic and fitness data used in this study were collected between 1994 and 2020. We focused on arrival date at the breeding area from the wintering grounds in West Africa (Becker et al. 2016; Kürten et al. 2022), a phenological trait that captures variation in the timing of spring migration and that is defined as the day of first return to the breeding grounds (January 1st =1) (Zhang et al. 2015a). Because no breeding can occur before a bird has arrived at the colony and recovered from migration, we removed those observations of arrival date that were not at least 10 days earlier than the egg laying date (n = 696 observations from 390 birds). The resulting dataset included 8032 observations of arrival date from 1715 individuals of known sex and age (mean number of observations per individual = 4.68, range = 1–21). The overall mean (±SD) arrival date across the 27 years (1994 - 2020) included in our dataset was 118 ± 12.63 (~April 28).

We used Adult Lifetime Reproductive Success (adult LRS) as our fitness measure, and quantified it as the total number of fledglings locally produced in the lifetime of an adult individual (Fig. S1). Although we cannot directly observe an individual's death, we can reliably assume it, because breeders at the Banter See are highly site-faithful, evidenced by the resighting probability of adult individuals that bred at least once being close to one (Szostek and Becker 2012), and 96% of breeders not skipping recording by the antenna system for two or more consecutive years after first reproduction (Bouwhuis et al. 2015; Zhang et al. 2015a). Based on this knowledge, we removed birds that were observed in 2019 and/or 2020 because they are known to not be, or cannot yet be assumed to be, dead. In addition to using data from individuals assumed to be dead (n = 946 individuals), however, we also included fitness data from those individuals that were still alive but older than 10 years (n = 121) to avoid "cohort truncation" (i.e., to avoid excluding individuals "not at random" with respect to fitness, Hadfield 2008; Morrissey et al. 2012). We chose this threshold because the cumulative reproductive success of known dead birds at ages older than 10 and their lifetime reproductive success is known to be highly correlated (r>0.8, Moiron et al. 2021). This age threshold also matches the biology of the population, as the mean lifespan is ~10 years

(Szostek and Becker 2012). The dataset for the analyses with adult LRS consisted of 7000 observations from 1067 individuals of known age and sex. Relevant details of the social pedigree used in the study are in the Supplementary Material.

STATISTICAL ANALYSES

Phenotypic trend and sources of phenotypic variation in arrival date

We used annual mean arrival dates to test for a temporal (inter-annual) trend in phenology between 1994 and 2020. The model was run as a linear model with arrival date as a response variable modelled assuming a Gaussian error distribution and year as a continuous fixed effect.

To estimate sources of phenotypic variation in arrival date and test for a temporal trend in breeding values, we built a univariate animal model that decomposed the total phenotypic variance of arrival date (V_P) into additive genetic (V_A), permanent environmental (V_{PE}), year of breeding (V_{YR}), year of hatching (V_{COHORT}) and residual (V_R) variances. We fitted arrival date as the response variable, and modelled it assuming a Gaussian error distribution. We fitted random intercepts for year of breeding (to control for temporal variation over and above the linear trend modelled in the fixed effect structure), year of hatching (to control for differences among cohorts), individual identity linked to the relatedness matrix (to quantify additive genetic effects), and individual identity not linked to the relatedness matrix (to control for repeated measures of individuals across years and model permanent environmental effects). We did not fit parental or maternal identity as random effects because 61.22% of individuals have an unknown mother, and 62.27% an unknown father, such that doing so would reduce the dataset (see Supplementary Material for detailed information on the pedigree structure). As fixed effects, we fitted the linear and quadratic effects of age (continuous variable measured in years, Ezard et al. 2007; Zhang et al. 2015), sex (categorical variable), the linear effect of year of breeding (continuous variable, to control for the linear temporal trend in phenology), and sea surface temperature at the main wintering area (Kürten et al. 2022) (continuous variable) both as a main effect and in interaction with the linear and quadratic effects of age. We used data of sea surface temperature between June 23 and July 27 the year prior to arrival at the coast of Guinea and Sierra Leone, determined based on the approach developed by Haest and colleagues (2018, 2019, 2020) (Bouwhuis et al. *in prep*). All continuous fixed effects (except age) were mean centred and variance standardized. We estimated the heritability (h^2) conditional to the variance explained by fixed effects as the proportion of the total phenotypic variance explained by the additive genetic variance.

Testing for observed micro-evolutionary change and genetic drift

We used the univariate animal model described above to extract the best linear unbiased predictors (BLUPs) of breeding values for each individual and test for a temporal change in breeding values in arrival date. To avoid biasing the estimate of the temporal trend in breeding values towards the trend in the phenotypes (due to the environmental structure not being explicitly modelled, Postma 2006), we fitted year of breeding both as a random and fixed effect in our univariate animal model following Bonnet and colleagues (2019), rather than as either a fixed effect as *per* Hadfield and colleagues (2010), or a random effect as *per* Postma (2006). Fitting year of breeding as a covariate in the univariate animal model used to obtain BLUPs is, however, a conservative approach because it likely underestimates the rate of change in breeding values (Postma 2006; Hadfield et al. 2010). Hence, we also fitted a univariate animal model with the same fixed and random effect structure as detailed above but without year of breeding (linear and quadratic components) as a fixed effect and extracted the BLUPs to test for a temporal change in breeding values in arrival date (see Table S1).

To calculate the probability that the observed change in breeding values differed from a scenario resulting from genetic drift, we simulated random breeding values for arrival date as *per* Hadfield et al. (2010), and fitted a linear regression to these random breeding values to obtain the temporal slopes due to drift for each posterior sample. Because the distribution of temporal slopes due to random drift is expected to be centred at zero (sampling was neutral), we could then calculate the proportion of the posterior distribution of these drift slopes that returned a regression value more negative than the posterior mode of the observed temporal slopes.

Finally, the annual estimate of a micro-evolutionary response was converted to a per-generation rate by multiplying by the population's generation time of ~7.95 years. We estimated this generation time for common terns in our dataset as the mean age of parents of nestlings that later recruit in the population (Charlesworth 1994), eight years being in line with the generation time known for common terns (Nisbet et al. 2020). We also converted the annual estimate of micro-evolution to units of standard deviation per generation by multiplying by generation time and dividing by phenotypic standard deviations. This way, the unit for evolutionary change was equivalent to a change measured in Haldanes (Hendry and Kinnison 1999).

Predicting micro-evolutionary change

To test for a micro-evolutionary response in arrival date, we fitted a bivariate animal model with arrival date and adult LRS as response variables to estimate (1) the additive genetic covariance between the two traits (direct test of Robertson's Secondary Theorem of Selection), and (2) the individual covariance between adult LRS and arrival date (i.e., selection differential). Arrival date was modelled assuming a Gaussian error distribution, while adult LRS was modelled assuming an overdispersed Poisson error distribution with log-link function (Fig. S1). Because our fitness measure follows a log-normal distribution, variance estimates for absolute fitness on the latent scale data are equivalent to variance estimates directly on the data scale for relative fitness (de Villemereuil et al. 2016; Bonnet et al. 2019; Morrissey and Bonnet 2019). The bivariate animal model included random intercepts for individual identity linked to the relatedness matrix (V_A), for individual identity not linked to the pedigree to account for repeated measures (V_{PE}), and for among-cohort variation (V_{COHORT}) within an unstructured variance–covariance matrix allowing the estimation of additive genetic, permanent environmental and cohort covariances (COV_A, COV_{PE} and COV_{COHORT}, respectively). We also fitted year of breeding as a random effect associated only with arrival date. Additionally, adult LRS is only measured once per individual, unlike the repeated annual measures on arrival date, and hence, V_{PE} and V_R in adult LRS are not separable. To accommodate this difference in replication between the two traits, we fixed the residual variance of LRS to a very small value (i.e., 0.001), allowing us to effectively model the additive genetic and permanent environmental covariances between LRS and arrival date. We modelled the same fixed effect structure as described for the univariate animal model.

We predicted the expected per-generation rate of micro-evolutionary change of arrival date by first applying the univariate Breeder's Equation (i.e., $R = h^2S$). The selection differential or phenotypic covariance between focal trait and fitness, S, reported in the main text was calculated as the sum of the additive genetic and permanent environmental covariances between arrival date and adult LRS (but see Table S2 for a direct estimate of individual-level covariance between arrival date and adult LRS, as opposed to the sum of the two covariance components). To obtain the full posterior distribution for the evolutionary response to selection (R) and hence account for the uncertainty in all estimated parameters, we multiplied the associated posterior distributions of h^2 and S instead of the point estimates. Second, Robertson's Secondary Theorem of natural Selection states that the additive genetic covariance between a trait and relative fitness represents a direct measure of the expected per-generation evolutionary change R in that trait (Robertson 1966; Price 1970). Both estimates of evolutionary response to selection (R) were reported as the posterior mode and 95% Credible Intervals.

Statistical model implementation

We fitted all models using a Bayesian framework implemented in the statistical software R (v. 4.0.5, R Core Team 2021) using the R-package *MCMCglmm* (Hadfield 2010). We fitted parameter-expanded priors (see Text S2). The number of iterations and thinning intervals for each model were chosen so as to ensure that the minimum MCMC effective sample size for all parameters was 1000. Burn-in was set to a minimum of 2000 iterations. The retained effective sample sizes yielded absolute autocorrelation values lower than 0.1 and satisfied convergence criteria based on the Heidelberger and Welch convergence diagnostic (Heidelberger and Welch 1981). We drew inferences from the posterior mode and 95% Credible Intervals (95% CI).

RESULTS

Temporal trend in arrival date

Between 1994 and 2020, annual mean arrival date advanced at a rate of 0.36 days per year (overall change: -9.34 days, 95% CI: -10.43, -8.24; Fig. 1A), as did the individual's mean arrival date regressed over their mean breeding year, with a rate of 0.09 days per year (overall change: -2.45 days, 95% CI: -4.51, -0.38).

Sources of phenotypic variation in arrival date

The mean population age increased steadily over the first 19 years of study, with a flattening-out phase in the latter years (Fig. S2), and the linear and quadratic effect of age influenced the population's arrival date (Table 1). Arrival date was also influenced by the sex of individuals, as well as by sea surface temperature at the main wintering area and year of breeding in interaction with age (Table 1).

Interpreting the variance components, common terns showed strong heritable differences in arrival date: additive genetic effects accounted for 20.6% of the total phenotypic variance, while permanent environmental effects accounted for an additional 10.6% (Table 1). Arrival date also harboured important variance among years of breeding (7.6%) and cohorts (0.5%) (Table 1).

Testing for observed micro-evolutionary change and genetic drift

The best linear unbiased predictors (BLUPs) for breeding values of arrival date extracted from the univariate animal model described above were tested for a trend over time (i.e., over an individual's mean breeding year). The slope of the linear regression was estimated at -0.026 days per year of breeding (95% CI: -0.062, 0.005), indicating that breeding values advanced a total of ~0.687 days across the 27-year study (Fig. 1B). While the lower 95% CI of the annual estimate was slightly overlapping zero, the fraction of the posterior distribution of the genetic slopes that was greater than zero was only 3.3%. Re-expressed in units of phenotypic standard deviations per generation, the estimated rate of micro-evolution corresponded to an observed evolutionary change of -0.017 Haldanes (95% CI: −0.040, 0.003), equivalent to -0.211 days per generation (95% CI: -0.500, 0.036).

Using a potentially less conservative approach to estimate breeding values for arrival date, i.e., using BLUPs from a univariate animal model that did not include year of breeding as a fixed effect (Table S1), the observed rate of evolution was of -0.035 days per year (95% CI: -0.072, 0.000). This estimate was of similar magnitude as that obtained using the more conservative approach (Table 1). Finally, only 4.5% of the simulations of random drift generated an advance as large as, or larger than, the change estimated from the linear regression of genetic change (Fig. S3).

Predicting micro-evolutionary change

The phenotypic selection differential for arrival date quantified as the sum of additive genetic and permanent environmental covariances from our bivariate animal model was negative and the associated 95% credible intervals did not overlap zero ($S_{\text{bivariate animal model}}$ = -1.232, 95% CI: -1.592, -0.788), indicating that individuals with earlier arrival dates obtained, on average, higher adult Lifetime Reproductive Success. We also estimated the selection differential for arrival date directly as the individual-level covariance between arrival date and adult LRS from a bivariate phenotypic model, instead of the sum of additive genetic and permanent environmental covariances from a bivariate animal model. We did so because additive genetic (co)variances involving fitness are notoriously difficult to estimate with high precision and accuracy. Reassuringly, both estimates were similar in magnitude and direction ($S_{\text{bivariate phenotypic model}}$ = -1.234, 95% CI: -1.618, -0.805, Table S2).

Given that arrival date was heritable and under directional selection (Table S3), the Breeder's equation predicted a rate of evolutionary change in arrival date of -0.030 days per year (95% CI: -0.052, -0.018), equivalent to a total change of -0.788 days across the 27 years of study

(95% CI: -1.360, -0.469, Fig. 2), and translating into a response rate of -0.243 days per generation (95% CI: -0.418, -0.144) and -0.019 Haldanes (95% CI: -0.032, -0.011).

The bivariate animal model of adult Lifetime Reproductive Success and arrival date revealed a negative additive genetic covariance between arrival date and adult LRS (COV_A = -0.474, 95% CI: -1.015, 0.247, Table S3), corresponding to a total evolutionary change in arrival date of -1.541 days across the 27-year study period (95% CI: -3.298, 0.803; Fig. 2), or a predicted evolutionary rate of -0.059 days per year (95% CI: -0.127, 0.031) and -0.037 Haldanes (95% CI: -0.079, 0.019). While Robertson's Secondary Theorem of natural Selection also predicted a clear advance in arrival date, the 95% CI of the evolutionary response estimate was wide and the lower 95% CI limit overlapped with zero (Table S3). Nevertheless, 89.3% of the posterior samples were below zero, suggesting the additive genetic covariance between arrival date and adult LRS to be very likely negative, but we might lack the statistical power to detect it with more certainty. Additionally, this bivariate animal model showed the additive genetic variance in adult LRS to be close to or not significantly different from zero (Table S3). While this is a pattern commonly observed in fitness and fitness components (reviewed by Hendry et al. 2018), the close to zero estimate might be due to either a true absence of additive genetic variance in fitness or a lack of power to detect it with higher precision, being the latter case true for several fitness components in this population (Moiron et al. 2021).

DISCUSSION

In this study, we investigated a case of expected evolutionary change in the timing of spring migration of a seabird to further our understanding of the evolutionary dynamics of phenology in natural populations, whilst also unravelling the selection pressures that underlie micro-evolutionary changes. We did so by using long-term phenotypic data from a natural population of common terns located at the North Sea coast of Germany and applying a series of quantitative genetic models that allowed incorporating relatedness information from a social pedigree.

Previous studies from the common tern population at the Banter See found that the timing of migration from the wintering grounds was heritable ($h^2 = 0.06 \pm 0.03$, Arnaud et al. 2013), and under directional selection (Arnaud et al. 2013, but Ezard et al. 2007). In the current study we corroborated those earlier findings using a considerably longer and larger dataset, finding a heritability of 20.6% and a phenotypic selection differential of -1.2. Given that the requisites for a potential evolutionary change were therefore met, we expected an evolutionary response to selection with advanced arrival dates from the wintering grounds, i.e., a change in mean phenotype towards earlier arrival dates at the genetic level, although evolutionary stasis is widespread (see Table 1 in Merilä et al. 2001 and Table 20.3 in Walsh and Lynch 2018), and phenotypic plasticity and/or other sources of environmental (non-genetic) variation might also lead to phenotypic divergence (e.g., Gienapp et al. 2008; Gienapp and Merilä 2014; Bonnet et al. 2017, 2019). Indeed, a previous study from this population of common terns has found support for individual, and, to a lesser extent, additive genetic variance in plasticity of arrival date in response to an important climatic factor at the main wintering areas (Moiron et al. *in revision*), although that was not the case for timing of breeding (Dobson et al. 2017).

We found average arrival dates to have advanced 9.34 days across the 1994 to 2020 study period (95% CI ranged from -10.43 to -8.24, Fig. 1A). Likewise, there was a genetic trend in the average breeding values for arrival date (Fig. 1B). Taking into account the parameter uncertainty and early criticisms on the use of predicted breeding values (Postma 2006; Hadfield et al. 2010), we found that the expected selection response ranged from -0.062 to 0.005 days per year. Whereas the 95% credible intervals of the observed genetic change slightly overlapped with zero, the posterior probability of this trend being greater than zero was only 3.3% (Fig. 2). Additionally, the probability of random genetic drift to generate a trend in breeding values as strong as, or stronger than, the observed genetic trend was only 4.5%, indicating that an evolutionary response to selection was a much more likely explanation for the observed temporal change in arrival date than genetic drift. Translating the estimated annual rate of evolution to Haldanes (in units of phenotypic standard deviations per generation), the estimated response corresponds to an evolutionary rate of -0.017 Haldanes (95% CI: −0.040, 0.003), being this estimate slightly lower than both the median rate of 0.035 Haldanes reported by Kinnison and Hendry (2001) for studies of less than 80 generations, and the average rate of -0.066 Haldanes reported by Gienapp and colleagues (Gienapp et al. 2007) for several traits related to the timing of migration in birds.

Theoretical predictions of evolutionary change

Because we estimated all parameters associated with the Breeder's equation and Robertson's Secondary Theorem of Selection, e.g., heritability, selection differential, and genetic covariance of phenotype and relative fitness, using a single Bayesian animal model, our approach allows for a quantitative comparison of both evolutionary change predictions, while also taking forward the uncertainties in the estimated parameters and subsequent calculations. The predicted rate of evolutionary change in arrival date based on the Breeder's equation was -0.019 Haldanes (95% CI: -0.032, -0.011), indicating that common terns were expected to advance the timing of their spring migration over time. The predicted rate of evolutionary change in arrival date based on the STS was -0.037 Haldanes, similarly indicating a response to selection towards earlier spring migration dates, although the associated 95% credible intervals for this estimate were partially overlapping zero (95% CI: -0.079, 0.019).

Altogether, the theoretical predictions of evolutionary change based on Breeder's equation and Robertson's Secondary Theorem of Selection were largely concordant, both in direction and strength, although the STS estimate was associated with substantial statistical uncertainty. In addition, these two theoretical predictions of evolutionary change were qualitatively similar to the estimated genetic change (i.e., the posterior distributions for the three parameters largely overlapped, Fig. 2), and in line with the observed temporal trend in mean phenotype (Fig. 1A). As such, our results provide a rare case of consistency in theoretical predictions of evolutionary change, that are additionally consistent with observed genetic patterns.

Additionally, and given that we found the evolutionary predictions from the Breeder's equation and STS to be in substantial agreement, our finding implies that the Breeder's equation might be a good predictor of evolutionary change in our study system, where the assumption of causality most likely holds, at least, when assuming a static environment (Queller 1992; Rausher 1992; Kruuk et al. 2002, 2003; Morrissey et al. 2010, 2012a). It also implies that our selection estimate might be mostly unbiased (i.e., the individual-level covariance between arrival date and relative fitness is mostly caused by arrival date, and there are no "missing traits", Queller 1992; Hadfield 2008; Morrissey et al. 2010, 2012b), shedding light on the true form of natural selection acting on spring migration timing and suggesting a lack of genetic constraints that might interfere with an evolutionary responses to selection. However, it is important to note that, while our three estimates of evolutionary response largely agreed, conclusions must be drawn with care as we cannot readily neglect the potential for the apparent agreement in evolutionary predictions to be coincidental. Multiple factors can potentially bias evolution estimates (e.g., "missing fraction" in fitness estimate or indirect selection from genetically-correlated traits), most often affecting evolutionary predictions based on the Breeder's equation, but also on STS (Merilä et al. 2001; Kruuk et al. 2002, 2003; Morrissey et al. 2012a; Walsh and Lynch 2018).

Global warming as underlying driver of phenotypic change

Temperatures in the wintering grounds of the studied population have significantly increased since 1994 (sea surface temperature change in West Africa between 1994 to 2020: $\beta = 0.66$, 95% CI: 0.16, 1.16), and such warming has been associated with earlier spring phenological events (Dobson et al. 2017), making climate change-related warming an obvious mechanism underlying the population's change in migration timing. However, given the observational nature of our study and the complex life cycle of long-distance migratory species experiencing environmental conditions in both hemispheres, we cannot test this hypothesis directly and identify the true biological cue. We can, however, speculate about the potential benefits of earlier arrival from the wintering grounds. Such early arrival could facilitate access to higher-quality breeding sites (Kokko et al. 2004) and mates (Coppack and Both 2002; Ludwigs and Becker 2005), and an early initiation of breeding. Early breeding, in turn, would allow for the production of replacement clutches in cases of predation, accidental egg or chick loss, or poor food availability for rearing offspring early in the season, and such replacement clutches indeed are known to significantly contribute to lifetime reproductive success (Becker and Zhang 2011). As such, selection for earlier timing of breeding may translate into selection for earlier timing of spring migration, by penalizing late breeders. Additionally, evolutionary responses in arrival date likely are aided by assortative mating for migration timing (Bearhop et al. 2005; see also Moiron et al. 2020).

Relative contributions of evolutionary and plastic responses to phenotypic change

The genetic change in response to selection as estimated from the breeding values trend and as predicted by the Breeder's equation and Robertson's STS (ranging from -1.541 to -0.687 days over the 27 years of study), was much smaller than the observed change in the population's phenotype (change = -9.34 days over the study period). This disagreement is somewhat expected because phenotypic divergence can arise from several mechanisms of both genetic and environmental (nongenetic) nature.

The estimated genetic change in the timing of spring migration represented c. 7.4% of the population's phenotypic change, subsequently indicating that the observed advance in migration timing was mostly underpinned by other sources of environmental (nongenetic) variation, such as phenotypic plasticity. Indeed, a recent study identified a plastic response of arrival date to climate change, with birds arriving earlier at the breeding ground following warmer years at the main wintering area (Moiron et al. *in revision*). Altogether, our findings therefore are fully in line with general reports of phenotypic plasticity underlying the vast majority of phenotypic responses to climate change (Parmesan 2006 and references therein; Vedder et al. 2013; Charmantier and Gienapp 2014; Merilä and Hendry 2014), but also highlight that the existence of phenotypic plasticity does not readily imply a lack of a micro-evolutionary response (or preclude their simultaneous existence) (e.g., Bonnet et al. 2019).

Concluding remarks

Altogether, our study not only provides evidence for an advance in spring migration which matched the widely reported phenotypic shifts in phenology in response to climate change found in multiple vertebrate groups, including other migratory bird species (e.g., Root et al. 2003; Menzel et al. 2006; Parmesan 2006; Thackeray et al. 2010; Poloczanska et al. 2013; Haest et al. 2021, meta-analysis: Radchuk et al. 2019, but see Keogan et al. 2018), but also adds to the slowly growing evidence of micro-evolutionary responses of spring phenology to climate change in natural animal populations (Bonnet et al. 2019; Helm et al. 2019).

While plastic responses to climate change are widely reported across taxonomic groups, evidence of micro-evolutionary responses to selection is still uncommon and considerably more challenging to accrue, mostly because the data collection for documenting micro-evolution in the wild remains a long-term daunting task. In this study, we provided rare evidence of an evolutionary change in spring phenology, likely in response to global warming, while also illustrating how both plastic and genetic changes can simultaneously facilitate phenotypic divergence in natural populations. Our work further emphasizes the importance of maintaining long-term individual-based studies of natural populations to unravel the diversity of biological responses to climate change, and, generally, to understand selective patterns and evolutionary dynamics of phenotypic traits in the wild.

AUTHOR CONTRIBUTIONS

M.M. conceived the study with input from S.B., A.C. and C.T. M.M. designed and conducted the statistical analyses, and wrote the manuscript. S.B. manages the tern data and collated the phenotypic dataset. B.H. contributed the sea surface temperature dataset. All authors contributed to discussions and editing of the final paper.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA ARCHIVING

Data will be archived in the Dryad Digital Repository upon acceptance of the manuscript.

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TABLES

Table 1. Estimates from a univariate animal model used to investigate sources of phenotypic variation in arrival date in a natural population of common terns. All fixed effects, except age, were mean centred and variance standardized. Estimates represent posterior modes with associated 95% Credible Intervals.

Fixed effects	**β (95% CI)**	
Intercept	156.856	[155.578 , 158.93]
Sex [female]	-1.621	[-2.243 , -0.987]
Age [linear]	-8.51	[-8.765 , -8.21]
Age [quadratic]	0.373	[0.354 , 0.389]
Sea surface temperature	-1.278	[-2.731 , 0.368]
Sea surface temperature x age [linear]	0.16	[-0.043 , 0.366]
Sea surface temperature x age [quadratic]	-0.011	[-0.022 , -0.001]
Year	-3.89	[-5.427 , -2.483]
Year x age [linear]	1.299	[1.096 , 1.606]
Year x age [quadratic]	-0.108	[-0.123 , -0.095]

Random effects	**σ2 (95% CI)**	
Additive genetic	19.918	[14.396 , 27.284]
Permanent environment	8.266	[2.766 , 13.558]
Cohort	0.474	[0.129 , 1.699]
Year	6.922	[3.68 , 13.552]
Residuals	52.782	[50.67 , 54.354]
Heritability	0.206	[0.163 , 0.301]

FIGURES

Figure 1. Temporal phenotypic trend in mean arrival date across years (A) and in individual breeding values in arrival date across an individual's mean breeding year (B) measured in days. Breeding values were extracted from the univariate animal model of arrival date (Table 1). In (A), large silver dots represent annual means, small grey dots individual observations, and silver lines the slope and associated 95% confidence interval of the phenotypic trend across the 27 years of study. In (B), grey dots represent individual breeding values of arrival date; silver lines are the slope and associated 95% confidence interval of the temporal trend in breeding values.

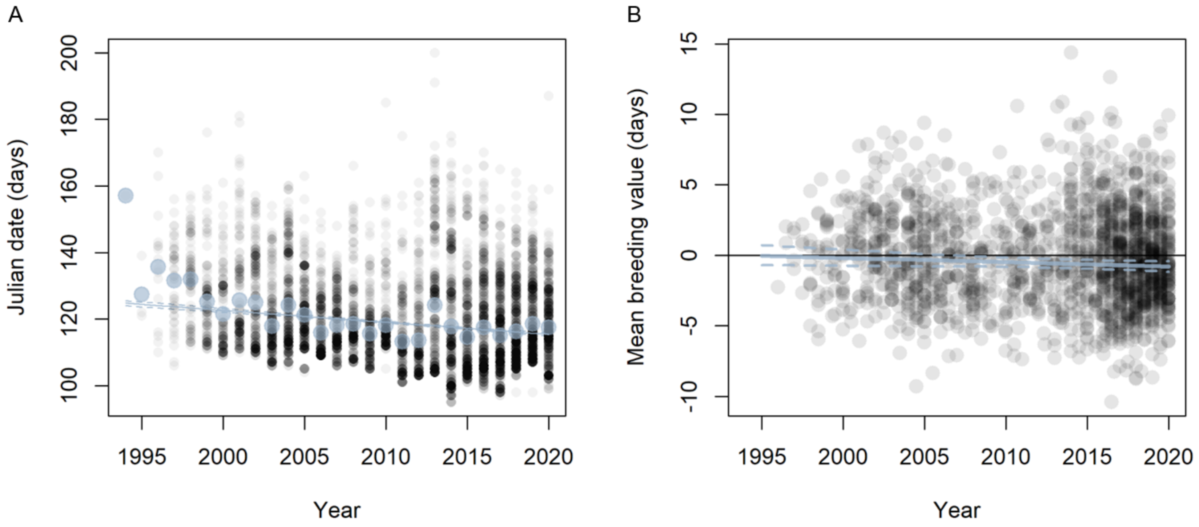

Figure 2. Posterior distributions for the estimated and predicted evolutionary response of arrival date over the 27-year study period. From top to bottom, “genetic change” was measured as the temporal change in individual breeding values for arrival date across the 27-year study period, the evolution estimate from the “Breeder’s equation” was quantified using a bivariate animal model from which we extracted the estimates of selection differential (individual-level covariance between arrival date and adult lifetime reproductive success) and heritability of arrival date, and the evolution estimate from “Robertson’s Secondary Theorem of Selection” was estimated as the additive genetic covariance between arrival date and adult lifetime reproductive success. All estimates presented here were converted to an evolutionary change (“evolution”) measured in days of change over the 27-years study period. Parameter estimates are summarized in the main text. All distributions have the same area and axes scales.