Climate change upends selection on ornamentation in a wild bird

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Secondary sexual traits have high heritabilities and are exposed to strong, environmentally sensitive selection, and so are expected to evolve rapidly in response to sustained environmental change. We examine the eco-evolutionary dynamics of ornament expression in a long-term study population of collared flycatchers, *Ficedula albicollis*, in which forehead patch size, which positively influences male reproductive success, declined markedly over 34 years. Annual fitness selection on forehead patch size switched from positive to negative during the study, a reversal that is accounted for by rising spring temperatures at the breeding site: highly ornamented males were selectively favoured following cold breeding seasons but selected against following warm breeding seasons. An 'individual animal model' describes a decline in the genetic values of breeding males during the study, which simulations showed was unlikely to result from drift alone. These results are thus consistent with adaptive evolution of a sexually selected trait in response to climate change.

Long-term population studies have provided many examples of traits undergoing substantial phenotypic change in response to climate change[1-3]. While these are seemingly indicative of contemporary evolution, robust demonstrations of adaptation are conspicuously rare, particularly in light of studies showing that phenotypic change does not equate to genetic change[4,5]. While direct demonstrations of shifts in allele frequencies in response to climate change have emerged[6,7], many phenotypes do not follow simple Mendelian patterns of inheritance and are instead influenced by innumerable loci, each of small effect, such that studying individual loci will provide little information about the evolutionary dynamics governing the trait. Quantitative genetics resolves this apparent impasse by providing an analytical framework that treats the summed contribution of all loci as the unit of interest, an approach that has proven highly successful in predicting the responses of domestic populations to artificial selection[8]. In particular, the 'individual animal model'[9] estimates the genetic value of each individual in the sample population, providing a robust methodology for quantifying evolutionary change in the wild[1,10,11]. However, published demonstrations of adaptive evolution of quantitative traits in response to climate change have been conspicuously absent since the realization that earlier applications are strongly anticonservative[10,12].

Research on the evolutionary impact of climate change in vertebrates has centred on phenological traits[1,3] yet selection on secondary sexual traits is highly environmentally sensitive[13], which, combined with their high heritabilities[14], would seem to make them ideal traits for observing evolutionary responses to climate change. However, while comparative analyses[15,16] support theoretical predictions that secondary sexual traits are evolutionarily labile[17], robust demonstrations of their contemporary evolution in the wild are scant, being limited to discrete traits[18] or populations exposed to severe artificial selection[19]. Indeed, the apparent evolutionary stasis of secondary sexual traits has been the subject of much speculation[20], despite the scarcity of demonstrations of contemporary evolution in the wild for quantitative traits in general[3,21].

We studied secondary sexual trait expression in a nestbox-breeding population of male collared flycatchers, *Ficedula albicollis*, from 1981 to 2014. The sex-limited, white forehead patch (Fig. 1) is an established ornamental trait: males expressing a large forehead patch have a competitive advantage over rival males[22,23]. Forehead patch size is heritable and the possibility that evolutionary change might underlie the decline in phenotypic expression (Fig. 2a) has been raised previously[24,25]. We therefore assessed selection on forehead patch size and used individual-level quantitative genetic modelling to infer the evolutionary change in ornamentation.

Results

Since forehead patch size exhibits delayed plumage maturation[26], altered population demographics could contribute to the decline in ornamentation. However, there is little support for a shift in the age structure of the male breeding population (slope estimate of linear regression of annual mean age (in years) on calendar year: $b = -0.0017 \pm 0.0044$ yr per yr, $t_{1,30} = -0.38$, $P = 0.708$), and the phenotypic decline is observed within age-classes (first years: $b = -0.231 \pm 0.072$ mm^2 yr^{-1}, $t_{1,32} = -3.22$, $P = 0.003$; adults: $b = -0.387 \pm 0.072$ mm^2 yr^{-1}, $t_{1,32} = -5.40$, $P < 0.001$; where b is the regression coefficient, P is the probability of wrongly rejecting the null hypothesis, and t is the t-statistic with associated degrees of freedom being indicated by subscripts).

We estimated linear selection acting on forehead patch size via annual fitness[27]. A highly significant year-by-patch size effect on annual fitness ($b = -0.0036 \pm 0.0011$, $t_{1,9923} = -3.27$, $P = 0.001$; Supplementary Table 1) indicates that forehead patch size was subject to selection and that the selection regime underwent a long-term change over the study period. To better understand the temporality of the selection regime, we focus on annual-level variation, since this can be related to environmental change (collared flycatchers follow an annual breeding cycle, and the forehead patch is regrown every year[25]). Annual fitness selection on forehead patch size exhibited a reversal over the study period, from positive selection in the first decade (point estimates of selection gradients were positive for the first eight years of the study) to negative selection in the latter half of the study (negative point estimates in seven of the eight most recent years; Fig. 2b). This decline was mainly driven by the

Figure 1 | Male collared flycatcher with white forehead patch clearly displayed. Photo by Johan Träff.

individual survival component of annual fitness: the weighted linear regression of annual selection arising via (1) interannual survival of male breeders ($\beta = -0.0019 \pm 0.0006$, $t_{1,31} = -3.35$, $P = 0.002$) and (2) offspring recruitment (halved) ($\beta = -0.0012 \pm 0.0011$, $t_{1,31} = -1.11$, $P = 0.278$; where β represents the selection gradient).

When mean spring temperatures for both current and preceding breeding seasons (before and after the winter moult during which forehead patch feathers are regrown[25]) were included alongside year in a multiple regression model of annual fitness selection gradients, the year effect was marginal, while the mean temperature of the preceding spring was a strong negative predictor of annual fitness selection on forehead patch size (Table 1). This suggests that annual fitness selection on ornamentation is sensitive to the climatic conditions experienced in the breeding season preceding the annual regrowth of the trait, with small forehead patches being selectively favoured following warm springs (Fig. 3). Spring temperature at the breeding site increased by an estimated 1.5 °C from 1980 to 2012 (linear regression: $b = 0.048 \pm 0.022$ °C yr^{-1}, $t_{1,31} = 2.19$, $P = 0.037$), hence the observed long-term reversal in selection. While our analyses of the temperature dependence of annual fitness selection are necessarily based on correlational data, the ability of our climate index to account for the negative temporal trend in annual selection is consistent with climatic forcing of selection on ornamentation.

The influence of spring temperature on selection must be mediated via some ecological driver. Given the visual communication function of the trait and the social enforcement of expression costs[28], one possibility is that the population density of signal receivers modifies the cost–benefit equilibrium of ornament expression. Such a population-density-mediated effect would also account for the temporal lag (>12 months) between the period of environmental sensitivity and the selective episode. Alongside altered intraspecific signalling dynamics is the possibility that relaxed interspecific competition has reduced the selective benefit of a large forehead patch: in sympatry with the congeneric pied flycatcher, *Ficedula hypoleuca*, collared flycatchers exhibit larger forehead patches due to character displacement[29]. However, the competitively dominant collared flycatchers have increasingly displaced pied flycatchers from their preferred breeding habitat. This process of displacement has been linked to a warming climate at the breeding site[30], and over time it may have reduced interspecific competition. At our study site, the breeding densities of both flycatcher species declined (collared flycatcher: $b = -2.38 \pm 0.35$, $t_{1,31} = -6.79$, $P < 0.001$; pied flycatcher: $b = -0.00383 \pm 0.00039$, $t_{1,31} = -9.83$, $P < 0.001$; breeding densities measured on different scales), such that both intraspecific and interspecific competition were probably relaxed. However, neither explains the importance of spring temperature in determining the intensity of selection on forehead patch size (Table 2). The ecological
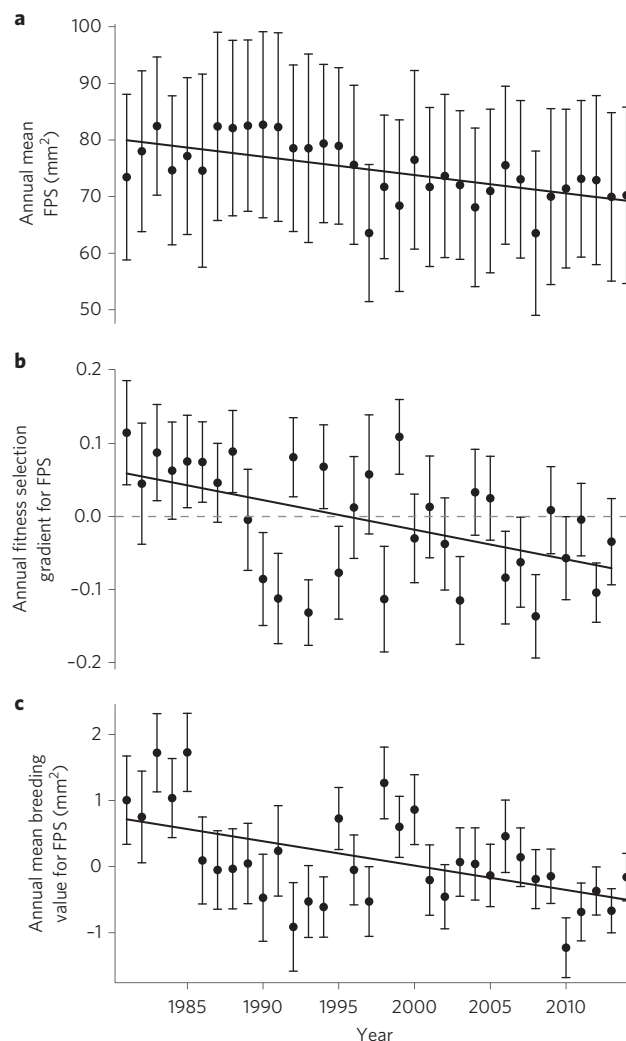

Figure 2 | Annual estimates of phenotypic expression, selection and genetic value for forehead patch size (FPS) in a breeding population of male collared flycatchers. a, Annual mean FPS (1981–2014). The line represents the best-fit equation from a weighted linear regression ($b = -0.324 \pm 0.071$ mm^2 yr^{-1}, $t_{1,32} = -4.58$, $P < 0.001$). **b**, Annual fitness selection gradients for FPS (1981–2013). The best-fit line from a weighted linear regression is plotted ($b = -0.00406 \pm 0.00126$, $t_{1,31} = -3.22$, $P = 0.003$). **c**, Annual mean breeding value of FPS (1981–2014). The line represents the best-fit equation from a weighted linear regression model. In all panels, error bars represent the standard error.

mechanism linking spring temperature to the ornamentation-dependent fitness of males thus remains undetermined, a situation that is not uncommon for examples of climatic forcing[31].

Given that forehead patch size is heritable (Supplementary Table 2), we may expect an evolutionary response to the altered selection regime (a decline in forehead patch size at the genetic level), although non-genetic (environmental) sources of variation can also facilitate phenotypic change[2,4,5]. We used a Bayesian linear mixed effects model incorporating relatedness information from a social pedigree[10] (an 'individual animal model'[9]) to partition phenotypic variance in forehead patch size (conditioned on age-class) into additive genetic and various environmental (permanent environment, annual and residual) components. The individual animal model assigns each individual in the sample population an estimated breeding (genetic) value, which allows us to examine how breeding values have changed in the breeding population over time, and thus to infer the evolutionary change[10,32]. Our model indicates a decline

Table 1 | Weighted linear regression model of annual selection on forehead patch size.

Variable	Estimate $\pm$ s.e.	t	P
Year	-0.0021 ± 0.0012	-1.73	0.095
Current spring temperature	-0.0078 ± 0.0085	-0.92	0.368
Preceding spring temperature	-0.0332 ± 0.0085	-3.90	0.001

Results are from a breeding population of male collared flycatchers that was monitored over 33 years and include year (as a continuous variable) and mean spring temperature for the focal and preceding years. s.e., standard error. t, t-statistic.

in the annual mean breeding value of males between 1981 and 2014 ($b = -0.037$ mm^2 yr^{-1}, 95% highest posterior probability density interval: -0.067 to -0.009, $P = 0.005$; Fig. 2c). Simulations based on neutral sampling from the pedigree[10] show that genetic drift alone is unlikely to account for an evolutionary decline of this magnitude ($P = 0.054$; Supplementary Figure 1). The inferred genetic change represents 11% of the observed phenotypic decline in forehead patch size, indicating that phenotypic plasticity underlies the majority of the observed reduction in ornamentation, congruent with the general pattern that phenotypic responses to climate change are facilitated by phenotypic plasticity[1,3]. However, the estimate of genetic change is probably conservative: in an open population such as ours, known relatives will be temporally clustered, such that real additive genetic sources of phenotypic variance will be attributed to annual, that is, environmental, variance[12].

Discussion

The long-term reversal in selection on ornament expression that we report was mainly driven by the individual survival component of annual fitness, paralleling observations from another European collared flycatcher population where selection on forehead patch size via individual survival became increasingly negative over time[24]. Trade-offs between investment in sexually selected traits and investment in survival are well documented and often invoked to explain evolutionary stasis[33]. Here, we describe a dramatic reversal in the selection acting on a sexually selected trait, suggesting that the balance of this ornamentation–survival trade-off was fundamentally altered over the study period. The forehead patch is one component of a breeding behavioural syndrome—a suite of traits associated with reproduction that are correlated at the individual level— that includes a negative correlation between forehead patch size and parental provisioning[28]. If genetic correlations underpin this behavioural syndrome, then this would provide indirect routes for environmental changes to alter the selective regime on male ornamentation.

Our results are consistent with the theoretical expectation that sexually selected traits exhibit rapid adaptation in response to changes in selection[17], and they highlight the value of long-term population studies for elucidating the biological impact of climate change[34]. The rates of change in selection and phenotypic expression we report are of a similar magnitude to those reported for a more recently established collared flycatcher study population in Hungary[24], suggesting that our results are representative of continent-wide changes to ornamentation in this species. Based on this, we posit that climate change could similarly be impacting the eco-evolutionary dynamics of signalling in other species. However, documenting adaptive evolution is likely to remain challenging: despite a study spanning more than three decades and with annual sample sizes in the hundreds, support for deterministic genetic change was marginal. Nonetheless, the reversal in selection that we report means that understanding of this model system for studying sexual selection in the wild has become wholly outdated within the timespan of an individual research career[35], highlighting just how rapidly evolutionary dynamics can potentially be altered by climate change,
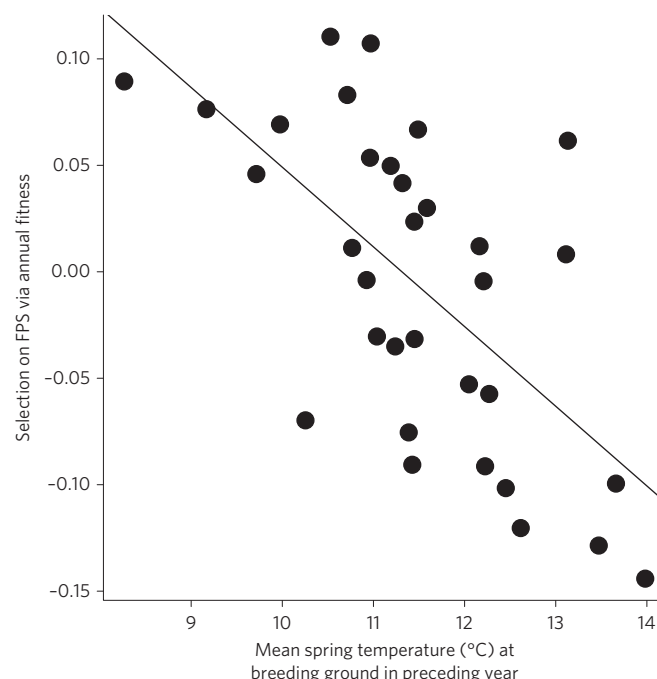

Figure 3 | Relationship between annual fitness selection gradients on forehead patch size (FPS) and spring (May–June) temperature at the breeding site the previous year. The line represents the best-fit equation from a weighted linear regression ($b = -0.039 \pm 0.008$, $t_{1,31} = -4.67$, $P < 0.001$).

not only through a change in the magnitude of selection[24] but by a complete reversal in its direction.

Methods

Study system. The collared flycatcher is a small (weight, ~13 g), hole-nesting passerine that breeds in Europe and overwinters in sub-Saharan Africa, and which readily adopts nestboxes as nesting sites. Phenotypic data were collected from a breeding population of collared flycatchers on the Baltic island of Gotland (57.2 °N, 18.2 °E) between 1981 and 2014 (population monitoring began in 1980 and contributes to pedigree information). Between-year breeding site fidelity is high and natal dispersal distances (natal site to breeding site) are limited, so individuals can be monitored throughout their reproductive lives and their realized productivity (recruitment of offspring) can be quantified. Breeders were caught at their nestbox during the breeding season: females mainly during clutch incubation, males when provisioning chicks. All individuals (including chicks) were fitted with a uniquely numbered, aluminium leg-ring. Collared flycatchers are sexually dimorphic at maturity so breeders were reliably sexed based on plumage. Previously unringed males were aged (first-year or adult) based on the colour of their flight feathers[36].

The white forehead patch of males is grown during the partial moult in the African overwintering grounds[37] and consists of an approximately square area of unpigmented feathers surrounded by dark, melanic plumage (Fig. 1). Forehead patch size was calculated as the product of patch height and patch width. Forehead patch size is only weakly correlated with tarsus length and body weight[25] so we did not control for body size in our analyses. Various experiments were conducted during the study period: individual males involved

Table 2 | Weighted linear regression model of annual selection on forehead patch size.

Variable	Estimate $\pm$ s.e.	t	P
Preceding spring temperature	-0.032 ± 0.009	-3.58	0.001
Collared flycatcher population density	0.001 ± 0.000	1.32	0.196
Pied flycatcher population density	0.182 ± 0.308	0.59	0.558

Results are from a breeding population of male collared flycatchers that was monitored over 33 years and include the mean spring temperature (°C) for the preceding year and estimates of the population densities of collared and pied flycatchers in the focal year. s.e., standard error. t, t-statistic.

in experiments with a recognized potential to influence future forehead patch size (for example, brood size manipulations[35]) were excluded. After these exclusions, our dataset consisted of 12,525 samples representing 7,906 individuals. Analyses were conducted using R version 3.3.1[38]. Fixed-effects regression models used the lm() function and mixed-effects regression models used the lme() function from the R package, nlme[39].

When assessing the demographic stability of the male breeding population with respect to age composition, we excluded all males first caught as adults, that is, those whose exact age was unknown. We also excluded the first two years of the study period because the large proportion of adults of unknown age is likely to be an artefact of the study design.

Given the timespan of our study and the inevitable turnover of fieldworkers, consistent differences between measures by individual fieldworkers could conceivably bias the phenotypic measures. To explore the possibility that such an effect drove the phenotypic decline we observed, we plotted the annual means for the four nestbox plots for which breeding attempts were monitored continuously (without interruption) for at least 33 years (Supplementary Figure 2)—responsibility for catching adults was usually allocated spatially among the available fieldworkers that breeding season. Although between-plot heterogeneity was discernible, the consistent temporal changes we observed in spatially distinct nestbox plots suggests that the interannual changes in the mean forehead patch size for the overall population are representative of a population-level process rather than being a methodological artefact driven by spatial heterogeneity combined with differential sampling. Further support for this conclusion can be derived from the fact that a contemporaneous decline in forehead patch size was observed in a population of collared flycatchers breeding elsewhere in Europe[24].

Selection via annual fitness. We combined interannual survival of the focal male (whether he was recorded in future years) and recruitment of offspring from his nest to estimate individual-level 'annual fitness'; this is an estimate of the relative genetic contribution of each male to the future breeding population. The individual genetic contribution was calculated as the interannual survival outcome (1 or 0) plus half the number of recruited offspring[27]. This was converted to an estimate of relative fitness by dividing by the annual mean. In an open population such as ours, this approach may yield biased fitness estimates because of emigration from the study site but it ensures that each fitness component is assigned to only one individual[40], and provides a simple means of estimating the intensity of natural selection at the annual scale that can then be linked to interannual variation in the environment. If a study plot was not monitored continuously over the study period, we excluded the year immediately preceding any missing years, since survival cannot be estimated for these males. We also excluded data from nestbox plots with very low representation per year (<~10 individuals). The selection dataset thus includes 9,927 records of 6,187 individual males collected between 1981 and 2013.

Initial models found little support for non-linear selection on forehead patch size (for example, in year-wise analyses, the quadratic term was significant in only three years (1999, 2002, 2012), with no support for a temporal trend in the quadratic coefficient), so we focused on linear selection. To first determine whether forehead patch size was subject to selection via annual fitness, we fitted a mixed-effects model of annual fitness, with forehead patch size, year (as a continuous variable) and their interaction included as fixed effects, and individual identity and year (as a categorical variable) included as random effects. Forehead patch size estimates were converted to z-scores (mean $= 0$, standard deviation $= 1$) to aid comparison of our selection gradients with those of other studies[41]. The interaction term indicates whether there has been a long-term change in directional selection over the study period. This is particularly pertinent in our study, given that the model indicates a reversal in the direction of selection occurring approximately midway through the study period (Fig. 2b, Supplementary Table 1), such that forehead patch size does not predict annual fitness when considered in isolation (univariate mixed-effects model: $\beta = -0.015 \pm 0.010$, $t_{1,9893} = -1.53$, $P = 0.126$). Thereafter we focused on interannual variation in selection by calculating year-wise linear selection gradients on forehead patch size using standard methods[41]: annual selection gradients were defined as the slope of a linear regression of annual fitness on forehead patch size.

Local temperature. Daily temperature records from the meteorological station at Hoburg (56.92 °N, 18.15 °E; approximately 10 km from main study areas) were accessed via the website of the Swedish Meteorological and Hydrological Institute (http://opendata-download-metobs.smhi.se/explore/?parameter=3). We defined 'spring temperature' as the mean daily air temperature during May and June, the period when collared flycatchers breed. The location of the thermometer was changed in the final years of the study (from 1 September 2012). However, this was preceded by 39 months of temperature recordings at both locations; although closely consistent (Pearson product-moment correlation $r > 0.999$; $n = 1,188$), measurements were not identical and we used the best-fit equation from a linear regression to estimate temperature at the former location for 2013 and 2014.

Population density measures. Annual population density of collared flycatchers was estimated as the number of males caught in the three nestbox plots for which the number of nestboxes had remained constant and for which breeding attempts

were monitored every year (Faludden, Fide Prästäng, Öja). The annual population density of pied flycatchers, *F. hypoleuca*, was relative rather than absolute, and estimated as the proportion of flycatcher breeding attempts (for the two species combined) across all monitored nestbox plots for that year.

Individual animal model. Recent quantitative genetic analyses of long-term population studies have demonstrated that phenotypic trends seemingly suggestive of evolution are often facilitated by phenotypic plasticity rather than evolutionary change[2,5,10], so demonstrating an evolutionary response to selection necessitates an assessment of genetic change. For quantitative traits, this can be inferred by combining phenotypic measurements with a pedigree describing the relatedness of phenotyped individuals, based on the individual animal modelling framework[32]. The 'individual animal model'[9] (usually abbreviated to the 'animal model') is a mixed-effects model in which a relatedness matrix describing the relatedness-by-descent of all individuals in the sample population is used to infer the contribution of additive genetic variance to the phenotypic variance. The relatedness matrix is based on the population's pedigree information—a pedigree file details the father (sire) and mother (dam) of each individual. In our study, this pedigree was based on behavioural observations of individuals caught at nestboxes. Extra-pair paternity occurs in the population (~15% of nestlings[42]) but the potential for it to bias estimates of additive genetic variance is expected to be limited[43]. Individuals that were moved between nests as part of cross-fostering experiments were assigned parents based on their original nest. For nests where a parent was unidentified, a dummy code was used to represent the missing parent so that sibship information is retained. Individuals ringed post-fledging were assigned unknown parental identities. Pruning non-informative individuals[44] yielded an informative pedigree with a maximum depth of 15 generations and containing 10,842 individuals, with 3,578 maternities and paternities, 801 full sibships and mean maternal and paternal sibship sizes of 1.42 and 1.41, respectively.

Forehead patch size is age-dependent[26] so age-class was included as a fixed effect. After conditioning on this categorical age effect, the phenotypic variance in forehead patch size was partitioned among four random effects (Supplementary Table 2), including one representing additive genetic variance. A permanent environment effect was included because many individuals are sampled in multiple years, while a random effect defined by calendar year accounts for non-independence of measures from a single breeding season. Remaining deviance from the population mean is attributed to residual variance. These analyses used the MCMCglmm package[45], with a total of 13,000,000 iterations, including a burn-in period of 500,000 iterations and a thinning interval of 2,500 iterations. The results we present are based on a model assuming forehead patch size follows a Gaussian distribution and using parameter-expanded priors; alternative prior structures ('flat' priors) yielded near-identical results.

The rate of evolutionary change in forehead patch size was estimated by regressing the mean breeding value of male breeders in each year against time (the temporal change in the annual mean breeding value) for each of the 5,000 sampled iterations[10]; the distribution of regression coefficients was taken to be the posterior distribution of the genetic change[46]. The contribution of random genetic drift was estimated using repeated ($\times 5{,}000$) neutral sampling from the pedigree; since sampling was neutral, *a priori* the distribution of slopes is expected to be centred at 0. The proportion of iterations returning a regression value more negative than the observed slope was taken as the probability that genetic drift alone was responsible for the observed evolutionary decline.

Data availability. The data and code required to replicate the results are archived in the Dryad Digital Depository[47].

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Author contributions

This study was conceived jointly by the authors. L.G. secured all funding for the fieldwork and was responsible for collating data. S.R.E. conducted all analyses and drafted the manuscript.

Additional information

Supplementary information is available for this paper.

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Competing interests

The authors declare no competing financial interests.