Causes of recent changes in bill length in Crozet wandering albatross, a long-lived seabird

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Abstract

Phenotypes are changing in many wild populations, largely in response to environmental changes due to human activities. Phenotypic change can be driven by several mechanisms, with contrasted consequences for the persistence of populations. Identifying those mechanisms is key to understand current responses to human pressures and to predict the future fate of populations. Here we attempt to disentangle the causes of the increase in bill length observed in the population of wandering albatross breeding on La Possession Island, Crozet Archipelago, over the course of 60 years. Taking advantage of long-term monitoring, morphological and pedigree data, we build a model that estimate changes due to demographic structure, plastic responses to several key environments, selective disappearance within generations, and genetic change. We found that changes in sex-ratio caused a decline in bill length that opposes the phenotypic change and adds an extra ca. 25% of change to explain. Bill length was highly repeatable and was almost fixed after growth within an individual. However, bill length covaried with age among individuals, in part due to selective disappearance filtering out shorter bill lengths. Despite selective disappearance we did not identify a significant contribution of genetic change. In contrast, we identified an important contribution of phenotypic plasticity, in particular in response to the Southern Annular Mode, which relates to the distribution and strength of wind in oceanic regions used for foraging. In the end, we could explain about half the increase in bill length through demographic and plastic mechanisms. The demographic response is most likely transient and will not continue on the long-term, while the plastic response could be quickly reversed in parallel to environmental variables driving plastic changes. Phenotypic change accrued so far is likely not stable but is adaptive and given bill length high heritability, bill length has the potential to evolve adaptively in the future.

Introduction

Over the last decades, researchers have documented numerous shifts in the mean phenotypes of wild populations (Gardner et al., 2011; Hendry and Kinnison, 1999; Parmesan, 2006). For instance, many studies report recent changes in phenology (e.g., Barbraud and Weimerskirch, 2006; Charmantier and Gienapp, 2014; Dobson et al., 2017), or changes in body size (e.g., Boutin and Lane, 2014; Gardner et al., 2011). Recent phenotypic changes are often linked to environmental changes due to human activities, in particular to anthropogenic climate change (Merilä and Hendry, 2014; Parmesan, 2006; Pelletier and Coltman, 2018). Phenotypic change can mediate demographic responses to environmental change, but the relationship is heavily dependent on the mechanism causing phenotypic change (Chevin et al., 2010; Coulson and Tuljapurkar, 2008). In a majority of cases the mechanisms of phenotypic change are unknown (Merilä and Hendry, 2014), curtailing our ability to understand the consequences of phenotypic change and to predict the demographic responses to on-going environmental change. Broad categories of mechanisms are (i) changes in demographic structure, such as shifting sex-ratio or age-class frequencies; (ii) phenotypic plasticity; and (iii) genetic change, which include adaptive evolution in response to natural selection as well as genetic drift, inbreeding depression, and gene flow. In addition, one may consider selective disappearance within a generation as a separate mechanism, as it cause phenotypic change even in the absence of an evolutionary response to selection or even of a genetic basis for variation in the trait.

Phenotypic change due to phenotypic plasticity can be fast, especially when it occurs within individuals, and therefore allow a population to respond quickly to changes in its environment. However, phenotypic plasticity is often maladaptive if its expression is not itself shaped by selection (Ghalambor et al., 2007), and may be bounded. Demographic change does not have particular reasons to be adaptive or maladaptive, and in any case will always be transient, so it cannot offer a long-term response to on-going directional environmental change. Similarly, non-adaptive genetic change due to drift will usually not help a population sustain environmental change, or only in an idiosyncratic way, whereas gene flow may favour or hinder adaptation depending on the pattern of differences in local adaptation vs. direction of environmental change and the effect of admixture. Selective disappearance as a result of viability selection within generations provides only a short-term adaptive response, and carries a demographic costs as a direct function of the strength of selection, so it is a double-edged sword for population and does not allow a long-term response to on-going directional environmental change. In the end, only adaptive evolution in response to selection provides a response that tends to systematically help the population sustain directional environmental change on the long-term, although the change must not be too fast for too many generations (Kopp and Matuszewski, 2014). If we are to predict the persistence of wild populations to current environmental changes, it is crucial to disentangle the respective contributions of those various mechanisms. In this regard, it is particularly interesting to estimate simultaneously the respective contributions of different mechanisms that may drive phenotypic change (Bonnet et al., 2019; Strickland et al., 2024).

Here we aim to decompose the mechanisms underlying an increase in bill length observed over 60 years as part of the monitoring of a wild population of wandering albatrosses. Bill length is an important trait in the biology of Procellariiformes, as it is linked to vocalization, olfaction, sexual selection, protection, feeding and territorial behaviour (Gémard et al., 2019; Pickering and Berrow, 2001; Tyler et al., 2023; Warham, 1996). In wandering albatross, bill size may play a specific role in courtship, and given the need to process carrion prey that are larger than the albatross (Tickell, 1968) bill length may influence the range of prey that can be consumed. Besides, the increase in bill length may be a reflection of the increase in the general size of individuals. Thus, bill length could be indirectly related to the benefits of a larger size, such as efficient use of winds, which is essential for reproductive success and foraging (Weimerskirch et al., 2012), or defence against predator (Dilley et al., 2013; Tickell, 1968).

A priori, plastic, demographic, and genetic mechanisms are all plausible explanations for phenotypic change in this population. Bird bills consist of bones covered in an outer layer of keratin, in the case of albatrosses made of several pieces (Hieronymus and Witmer, 2010; Piro, 2022). The bones develop during the chick growth until around fledging, and their length could be influenced by the quantity and quality of parent provisioning, as well as by aspects of the environment around the nest. The study population experienced important changes in its environment over the study period: climate change, fisheries, invasive species, and changes in population density (Weimerskirch, 2018). These changing conditions during the growth period, which is almost synchronous for all chicks born on a given year, may have caused among-individuals phenotypic plasticity structured by cohorts. The keratin pieces grow and erode continuously, which may produce age-structure in bill length (hence a potential for phenotypic change due to change in demographic structure), and may allow bill length to respond to various environmental variables by within individuals phenotypic plasticity. Further, the study population went through a sharp decline driven by adult, particularly female, mortality at the beginning of the monitoring, followed by a slow recovery. This change in population size probably coincided also with change in sex-ratio and age-structure, which could have driven changes in bill length. Given the importance of bills in avian ecology, even small differences in bill length with the population could be subject to natural selection. Selection could result directly in selective disappearance, which would change the average bill length within cohorts. In addition, selection could cause genetic change in response to selection across generations (hence, across cohorts). Although wandering albatrosses have a slow life-cycle, with a generation time of about 18 years, the monitoring spans 60 years, thus giving enough span for some genetic change to take place.

Methods

Species and population monitoring

The wandering albatross (*Diomedea exulans*, Procellariiformes: Diomedeidae) breeds in the Antarctic zone on different islands such as South Georgia, Prince Edward Islands, Kerguelen, Macquarie Island and on Crozet Archipelago (Brooke, 2004). This species has a slow life history, with reproduction beginning at around 10 years of age, high adult survival, and a lifespan sometimes exceeding 60 years (Bennett and Owens, 2002; Croxall et al., 1990). Their breeding season starts in November, and lasts for a full year. Successful breeding is usually followed by a full sabbatical year at sea, so they breed every two years only. They lay a single egg and care is bi-parental (Tickell, 1968). During sabbatical years wandering albatross travel long distances in the southern hemisphere, regularly circling around Antarctica (Weimerskirch, 1995; Weimerskirch et al., 2014; Weimerskirch and Wilson, 2000). Foraging areas during the breeding season depend on sex although this segregation is less marked during the sabbatical year (Ceia et al., 2012; Weimerskirch et al., 2014). However, birds are highly philopatric and will usually breed close to their birth colony (Charmantier et al., 2011; Inchausti and Weimerskirch, 2002).

The population of wandering albatross on Possession Island, Crozet Archipelago (46°S, 51°E) has been monitored annually since 1958 as part of programs carried out by the French Polar Institute (IPEV). Between 1961 and 1990, wandering albatross populations underwent a major decline, likely as a consequence of by-catch due to the development of longline fishing (Croxall, 1979; Croxall et al., 1990; Tomkins, 1985; Weimerskirch and Jouventin, 1987). On Possession Island, the annual rate of decline was around 4.9% between 1969 and 1985 (Weimerskirch and Jouventin, 1987). Most populations, including Possession Island, then gradually recovered possible due to changes in exposure to by-catch (Inchausti and Weimerskirch, 2002; Weimerskirch et al., 2018).

At the beginning of monitoring only adults were banded. From 1965 on, each chick was banded with a stainless steel band before fledging. Every year, starting from early to mid-December, checks on pre-breeding adults were conducted across the entire island. From mid-January to mid-February, visits were made every 10 days to identify the two members of each breeding pair and determine their breeding status. Any individuals without bands were equipped with uniquely numbered stainless steel bands. In mid-April, June, and August, nests were inspected and the status of the chicks was recorded (alive or dead). From mid-September to mid-October fledglings were measured and banded. Here we use data collected up to 2018, newer data having not been fully incorporated into the database yet.

Wandering albatrosses are socially monogamous, so we constructed a social pedigree by matching each ringed chick to the adults identified at the nest. Extra pair mating have been reported and may concern 10% of the chicks based on a small sample (Jouventin et al., 2007). This introduces errors in the pedigree which probably lowers slightly the precision of quantitative genetic parameter estimation (Charmantier and Réale, 2005). pedigree. We computed pedigree properties using the R-package pedantics (Morrissey and Wilson, 2010). The pedigree contains 11232 individuals. Both parents are missing for 2673 of them. The pedigree has a maximal depth of five generations, reached for 31 individuals, and an average depth of 1.37 generations.

We measured several biometric variables for most ringed chicks, as well as for adults according to opportunities. Firstly, we measured the length of the bill as well as the maximum height of the hook using a caliper with 0.1 millimetre accuracy. The measurements are likely very accurate given the long bill of wandering albatrosses. In museum conditions, the measurement error variance for bill around 160 mm long, and measured with similar equipment, is approximately 0.1 mm^2, corresponding to an error standard deviation of around 0.3 mm and a within sample measurement repeatability of over 99% (Subasinghe et al., 2021). We measured tarsus length with callipers as for bill length and wing length using a millimetre precision ruler. In addition, we measured body mass, with a precision of 5 grams. Individuals, both chicks and adults, were sometimes caught several times during the same year and across years in the case of individuals that survived to recruitment. Before any filtering process the biometric dataset of individuals ringed as chicks consisted of 2 849 observations of 1 861 individuals and the biometric dataset of individuals ringed adults was composed of 396 observations of 275 individuals (Table 1).

Wandering albatrosses are somewhat sexually dimorphic and we therefore accounted for sex, and filtered the data in order to avoid biases due to missing sex data in each analysis. Adult sex determination was initially based on field observations such as size and plumage dimorphism, mating behaviour. Chicks cannot be sexed visually. Starting from 1990, genetic analyses were also used and became more regular after 1999. Between 1999 and 2018, an average of 45 chicks were sexed every year. Individuals not sexed genetically as chicks were sexed visually or genetically if they returned to the colony as breeders.

Some morphological measurements were done during growth. Since we do not know the exact age of chicks (i.e. hatching date) we could not easily model growth to correct for it. Because measurements tended to be done at earlier dates in recent years, there was an artefactual trend

	Observations	Individuals
Pedigree	-	11196
Raw bill length data	3245	2136
Filtered data	1265	815
Juvenile survival	639	639
Adult survival	1568	96

Table 1: Sample sizes in the study. Filtered data are those used in the animal model, used to estimate all contributions except selective disappearance.

towards shorter bill lengths among juveniles. This trend becomes more positive as we discard earlier measurements and thus increase the proportion of measurements that are done after growth is completed, although the proportion is unknown. In a sensitivity analysis we computed the trend in phenotypic change over years using different cut-off dates. We found that the trend among years was stable when we discarded measurements done before October 1st, or before later dates. We found that the trend among cohorts was stable when we discarded measurements done before November 25th (whereas the trend was underestimated by around 30% using the October 1st cut-off.) We consider and try to explain both change in bill size among cohorts and among measurement years.

Environmental predictors

Previous research in this population and other wandering albatross population has shown it was difficult to relate most aspects of the species biology to environmental variables. One reason may be the extensive and heterogeneous movements of the species around the Antarctic continent, exposing different individuals to different environments at different times. One exception, is the Southern annular mode, which correlates with patterns of wind strength at different latitudes and is related to changes in life-history in the population (Cornioley et al., 2016; Fay et al., 2015; Weimerskirch et al., 2012). Given that bill length is highly repeatable and there is little evidence that the trait changes with age after fledging (see results), we used SAM averaged during the birth year, as a proxy for chick feeding quality, which may influence bill length. In addition, we made the hypothesis that population density, measured as the number of breeding pairs at the island, could impact bill length growth, due to effects of competition or stress. Finally, in an attempt to capture variation in other dimensions of environmental quality, we included annual reproductive success (number of fledged birds divided by the number of eggs laid) as an environmental variable in models.

Statistical analyses

All statistical analyses were carried out using the R statistical program, version 4.4.12 (2024-06-14).

Phenotypic change

To estimate the change in bill length over years, we fitted linear regressions with year as a predictor and individual identity as a random intercept. For year, we used both year of measurement, and cohort (i.e., birth year). In one set of regressions we filtered data to keep only measurements taken on birds that are 5 years old or older. Birds are never seen at the colony between fledging and at least 5 years old. This filters out completely juvenile measurements, which may be influenced by growth, to focus on birds that are back to the colony as sub-adults or adults. In another set of regression, we retained juveniles measurements that were done after some threshold dates, to reduce the influence of growth on the estimation. We determined the thresholds with a sensitivity analysis, computing the rate of phenotytpic change for every threshold date to identify above which date the trends stabilized. We obtained thresholds of the 330th Julian day for the cohort trend and 275th Julian day for the measurement year trend.

Model of source of variation in bill length among cohorts

We started by developing models that captured different aspects of variation in bill length: demographic structure, environmental variables, genetic change. In the end we converged to a single model that captures all those aspects, which lets us account for correlations between all those predictors. The model may be written as

$$z_{ij} = \mu + \boldsymbol{X^T b} + a_i + p_i + m_i + c_i + y_j + r_{ij} \tag{1}$$

, where z_{ij} is the bill length of individual i at time j. Then, μ is an intercept. $\boldsymbol{X^T\beta}$ is a matrix expression of all fixed effects, which included: Sex as the species is sexually dimorphic; Cohort to capture residual linear change that would remain unexplained; the three environmental variables presented above (number of breeding pairs, annual reproductive success, and SAM); the mean age of each individual in the dataset; and the difference between the mean age of each individual and their age at measurement. This last pair of fixed effects correspond to the technique of mean-centring, which allows to partition an effect into within-individual and between-individual components (van de Pol and Wright, 2009). For later computation of repeatability and heritability, we computed variances due to some fixed effects as the variance in partial predictions following (de Villemereuil et al., 2018). We computed the within-individual variance due to fixed effects (V_w), which included only the effect of age-difference to the mean age; and the between-individual, within-sex, variance due to fixed effects (V_b), which included the effect of environmental variables, age, cohort, but not sex (as we aimed to estimate within-sex repeatability and heritability).

As random effects, we included: An individual additive genetic effect or 'breeding value' (a_i, which allows the estimation of heritability and genetic change), with effects correlated according to the pairwise relatedness matrix; A permanent environmental effect (p_i), which is the individual identity but is not linked to the relatedness matrix, and allows to account for replicated measurements and avoid biases in the estimation of genetic effects (Kruuk, 2004); The mother identity (m_i), which may avoid over-estimation of genetic effects due to confounding parental environment (Kruuk, 2004); Cohort (c_i), to account for non-independence due to environments experienced by birds born on the same year and not accounted for elsewhere; Year of measurement (y_j), which may capture non-independence due to year-specific measurement error as most of the measurements were made by teams of researchers that coincide with civil years, or within-year within-individual plasticity. The model included residuals assumed to be Gaussian (r_{ij}). We write the variance in $\boldsymbol{a}$ as V_A, that in $\boldsymbol{p}$ as V_{PE}, that in $\boldsymbol{m}$ as V_M, that in $\boldsymbol{c}$ as V_C, that in $\boldsymbol{y}$ as V_Y, that in $\boldsymbol{r}$ as V_R.

We filtered out data with missing values in predictors, and with measurements taken before the 330th day of the year in juveniles (to avoid biases due to growth, see above). We run the model in the R-package MCMCglmm (Hadfield, 2010). We assumed a Gaussian family. We run the model for 250000 iterations, with a burnin of 50000, and thinning of 200 (computation time of secondary calculations). We checked convergence by visual inspection of the trace for all parameters, and by running the model three times. We used default normal broad priors for fixed effects, and parameter-expanded priors for random effects (with parameter V=1, nu=1, alpha.mu=0, alpha.V=1000). We recorded Best Linear Predictors (BLUPs) to run derived calculations of predicted breeding values (using the option "pr=TRUE"). All derived calculations were integrated over the full posterior distribution to propagate uncertainty.

Repeatability and heritability

We computed repeatability in two ways. First,

$$R_1 = \frac{V_A + V_{PE} + V_M + V_C + V_b}{V_A + V_{PE} + V_M + V_C + V_Y + V_R + V_b + V_w} \tag{2}$$

We note that V_Y is likely to capture measurement error, due to fieldworkers misusing callipers on some years, and as such it should be excluded from the calculation (Ponzi et al., 2018). There may be genuine biological effects captured by V_Y, however, so we keep it in the calculation. V_Y was small anyway, and our decision does not affect the result significantly. With R_1 we estimate how correlated measurements of a given individuals would be, given the environment experienced by each individual on their birth year. We therefore included V_C and V_b in the numerator. Second,

$$R_2 = \frac{V_A + V_{PE} + V_M}{V_A + V_{PE} + V_M + V_Y + V_R + V_w} \tag{3}$$

, in which we excluded V_C and V_b. With R_2 we estimate how correlated an individual measurements would be within a particular birth year, on average.

We computed heritability as

$$h^2 = \frac{V_A}{V_A + V_{PE} + V_M + V_C + V_Y + V_R + V_w + V_b} \tag{4}$$

In contrast to the calculation of repeatability, here we also included V_C and V_b, as heritability may be thought of as the proportion of additive genetic variance across environments experienced by all individuals.

Estimated contributions of environmental and demographic variables

We estimated the contribution of each environmental and demographic variable fitted as a fixed effect using the Geber method (Ellner et al., 2011). For a predictor x, we calculated the mean of x every year ($\bar{x_t}$). We the multiplied $\bar{x_t}$ by the estimated effect of x on bill length in our main model (β_x), to obtain partial predictions due solely to the effect of x, with arbitrary baseline, but comparable scales across years. We visualised those $\bar{x_t}\beta_x$ to identify potential major non-linear changes. We regressed $\bar{x_t}\beta_x$ on year, and then multiplied the regression coefficient by the duration of the study to estimate the average contribution of x over the study period (Bonnet et al., 2019).

Genetic change

We estimated genetic change for bill length by fitting a linear regression with the response variable being the mean of breeding values per cohort and the explanatory variable being cohort. We fitted the linear regression for every of the 1000 MCMC posterior samples so as to incorporate the uncertainty in each individual breeding value into the estimation of genetic change (Hadfield, 2010). To quantify the rate of genetic change possible without selection, we also simulated genetic change under a null model of genetic drift, conditional on the population pedigree. For each posterior sample of additive genetic variance, we simulated a set of breeding values for each individual, using draws according to an infinitesimal model of inheritance down the pedigree (Hadfield, 2010). This generated a distribution of possible rates of genetic changes due to drift, hence centred on zero.

Selection

To estimate selection on bill length between fledging and the return to the colony, from around 5 years old (Tickell, 1968; Weimerskirch et al., 2014), we retained only measurements taken on juveniles. We retained only measurements taken after the 275th Julian day, because there is no correlation between measurement day and survival after that point, and because the growth of bill length is almost complete at this time (mean bill size between 275th and 285th day: 166.6mm, vs. mean bill size among birds above 5 years old: 166.9mm). We discarded individuals born after 2012, as those cohorts had just started, or not started at all, to come back to the colony and we do not know which individuals survived yet. We retained a single measurement per individual, the last one before fledging.

We fitted a model of survival, defined as a binary variable indicating whether a juvenile was seen again as a sub-adult/adult. As fixed effects we used bill length, and Julian date, and as random effect we used cohort. We assumed a Bernoulli distribution with a logit link-function. We run a second version of the model also including sex in the fixed effects, and therefore discarding data for which sex is unknown. This decreased our sample size but let us account for sexual dimorphism in bill length. However, because survival probability did not differ much between sexes, the results for the effect of bill length were similar between the two models.

Results

Phenotypic change

Bill length increased over the study period, both considering years of measurements or cohort (i.e., birth year). Predicted change was higher when considering change over measurement years rather than cohorts, and higher when censoring more of the juvenile data (table 2). Estimates of changes among birds that are sub-adults or adults range from 3.67 to 4.39 mm. When also considering juveniles estimates of change range from 2.68 to 4.23 mm. The different estimates of change represent 2 to 3% of the mean bill length (ca. 167 mm), but 47 to 77% of the standard deviation in bill length (ca. 5.7 mm).

Sources of variation in bill length

Males had longer bills than females (difference = 6.11 mm, $p_{MCMC} < 0.001$). Bill length was not correlated with age, but our model revealed that the lack of correlation masked a significant

Censoring	trend	slope	SE	sample size	change (mm)	change/sd	change/mean
> 5 years	Cohort	0.06	0.02	771	3.67	0.64	0.02
> 5 years	Measurement year	0.15	0.02	771	4.39	0.77	0.03
> 330 days	Cohort	0.04	0.02	875	2.68	0.47	0.02
> 275 days	Measurement year	0.14	0.02	1088	4.23	0.73	0.03

Table 2: Estimations of phenotypic change over the study period. Censoring indicates the left date threshold to filter measurements, SE is the standard error of the slope, change is the total phenotypic change predicted over the study period, change/sd, respectively change/mean, is the change divided by the standard deviation, or mean respectively, of bill length in the sample

age effects among individuals. Thus, among-individual age had a significant positive effect of 0.14 (95%CI [0.05;0.24]). The effect of age within individuals tended to be positive but was not clear ($\beta = 0.05$, 95%CI [-0.03;0.13]). The effect of number of breeding pairs at birth was not significant, and neither was the effect of the reproductive success rate on the birth year (Table 4). SAM during the birth year had a positive effect on bill length (0.26, 95%CI[0.05; 0.44]).

Bill-length was highly repeatable, with similar estimates for our two definitions of repeatability (R_1=0.84; 95%CI [0.75;0.88], and $R_2 = 0.84$; 95% [0.73;0.87]), even though we did not account for measurement error and therefore underestimate the biological repeatability (Ponzi et al., 2018).

The additive genetic variance for bill length was estimated to 15.32 mm^2 (95%CI [10.22; 18.67]), corresponding to a heritability of 0.62 (95%CI [0.44;0.74]). The evolvability of bill length, expressed as V_A divided by the square of the trait mean was 0.6%. Maternal identity and the random effect of cohort accounted for almost no variance (Table 3).

	mode	lower-95% CI	upper-95% CI
Additive genetic (V_A)	15.32	10.22	18.67
Permanent environment (V_{PE})	3.66	1.19	7.58
Maternal identity (V_M)	0.0005	10^{-7}	0.17
Cohort (V_C)	0.002	10^{-6}	0.46
Measurement year (V_y)	2.40	1.19	5.02
Residual (V_R)	1.62	1.38	1.82
Within-individuals fixed (V_w)	0.001	10^{-9}	0.25
Between-individuals fixed (V_b)	0.68	0.17	2.67

Table 3: Random effect variance estimates, and variance ascribed to fixed effects, from the animal model.

	post.mean	lower-95% CI	upper-95% CI	p_{MCMC}
Intercept	160.74	158.94	163.37	< 0.001
Sex (Male)	6.18	5.49	6.68	< 0.001
Cohort (standardized)	0.48	-0.41	1.57	0.178
Individual centred age	0.05	-0.03	0.13	0.208
Individual mean age	0.11	0.05	0.24	0.004
Breeding pairs	-0.003	-0.007	0.002	0.192
Annual reproductive success	0.86	-0.18	2.96	0.110
Southern annular mode	0.26	0.05	0.44	0.014

Table 4: Fixed effect estimates from the animal model.

Demographic structure

Early in the monitoring the sex ratio tended to be male biased, but it became about balanced from 1975, and then rather female-biased after 2000. Thus, the proportion of males decreased during the study period. Since males have longer bills than female, the change in sex ratio was predicted to have changed mean bill length by -0.92 mm (95%CI -1.01; -0.83]). The effect of within-individual age variation was not clear, but tended to be positive. Over years, we tended to measure older birds on average, which predicts a contribution of +0.30 mm over the study period (95%CI [-0.18;0.76]). The effect of mean age was clearly positive. Since most of our sample consisted of birds first measured as juveniles, the average mean age tended to increased in our sample (although this may not reflect the true dynamic of age structure in the population). Therefore, our model predicts a positive contribution of mean age of + 0.60 mm over the study period (95%CI [0.27;1.28]). The sum of sex contribution and age contributions largely cancel out to a net demographic contribution of +0.10 mm over the study period (95%CI [-0.88;1.03]).

Plastic responses

Only the effect of the Southern annular mode (SAM) was clear in the model (Table 4), but all three environmental variables were predicted to have more positive contributions across cohorts, and the sum of their contributions was positive and large (Fig. 1). SAM had a positive estimated effect on bill length, and SAM tended to become more positive through time, giving an estimated change in its contribution of 0.85 mm over the study period (95%CI [0.16;1.43]). The number of breeding pairs had a non-significant negative effect on bill length, and since the number of breeding pairs decreased overall despite a recent recovery, its contribution tended to be positive with +0.22 mm (95%CI [-0.19;0.73]) over the study period. Annual reproductive success had a non significant positive effect on bill length, and since it increased over the study period, it tended to contribute to an increase in bill length of +0.21 mm (95%CI [-0.045;0.73]). Summing the three environmental variables, the total contributions of plasticity in response to the environment across cohorts was estimated to +1.34 mm (95%CI [0.33;2.33]).

Genetic change

Average breeding values tended to increase between 1958 and 2018, but the change was not statistically significant (slope=0.00236; p_{MCMC}=0.223). The total predicted change over the study period of was 0.142 mm ; 95% CI [-0.0034 ; 0.0089], which represents 3.87% of the phenotypic change estimated across cohorts. The estimated genetic change represents 3.6% of the additive genetic standard deviation (i.e., square-root of V_A). Simulations of genetic drift produced greater rates of evolution in 26.6% of replicates.

Explained and unexplained changes

The estimated effect of cohort, as fixed effect, in our animal model is meant to capture the change in bill length left unexplained by other predictors. Since cohort is correlated to other predictors, there should be large uncertainty in the estimation of this effect. Indeed, the unexplained change over the study period was estimated to +2.32 mm, with 95%CI [-1.96;7.51]. The change explained by contributions of sex, age, environment and genetic change added up to +1.67 mm (95%CI [0.10;2.88]).

Selective disappearance

The positive effect of mean age could be in part driven by selective disappearance. We explored this possibility outside our animal model, using models of viability selection. Bill length covaried

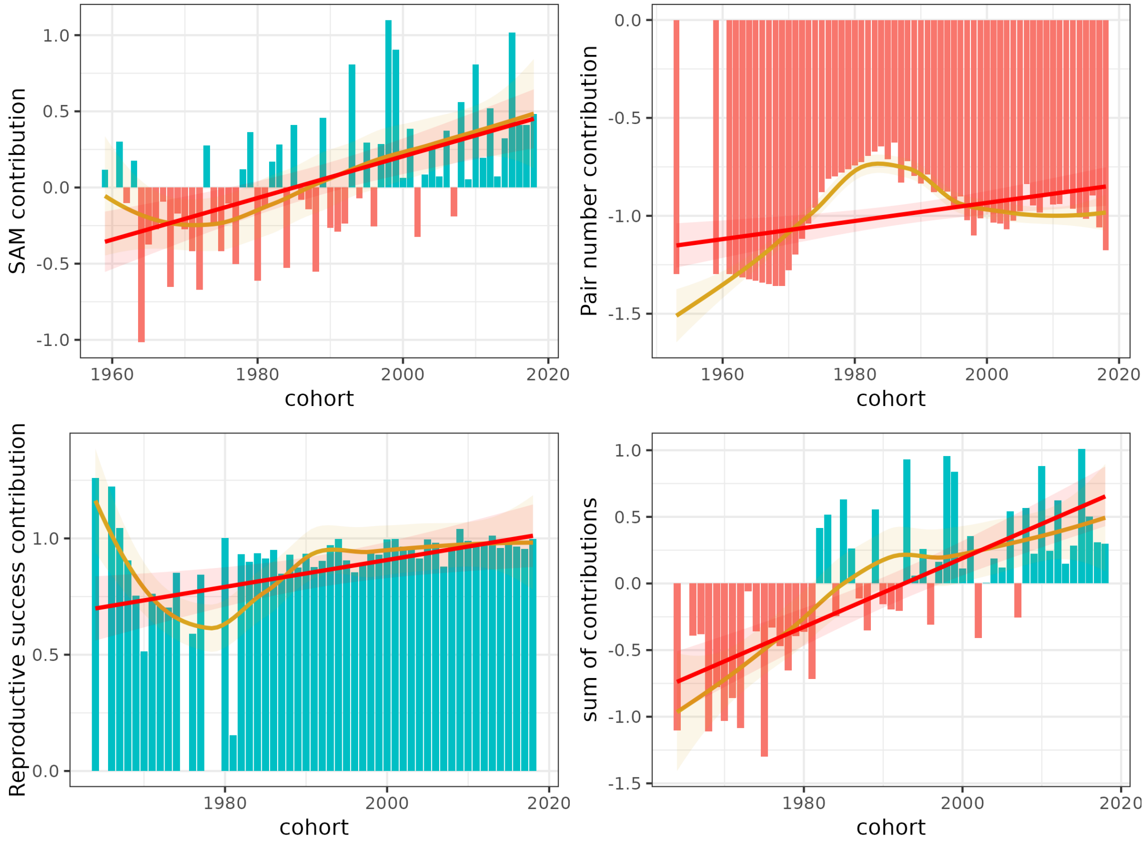

Figure 1: Estimated contributions of environmental variables to changes in bill length across cohorts. Red bars represent negative contributions, blue ones positive contributions. A red line represent a linear regression of contributions on cohorts, a golden line represents a local polynomial regression fit. We did not represent uncertainty in the estimation of contributions and did not propagate the uncertainty to the fit of the regressions as fitted here; however we did integrate the uncertainty in numbers presented in the text.

positively with relative juvenile survival (raw selection differential +0.20 mm). When accounting for sex, date of measurement, and cohort, bill length did not have a clear effect on juvenile survival probability ($\beta = 0.016$, 95%CI [-0.056;0.081]), and the predicted selection differential was +0.13 mm. Given the change in age structure in our sample, selective disappearance is therefore predicted to have contributed +0.37 mm over the study period, or about 60% of the contribution ascribed to mean age.

Discussion

Over the 60 years of monitoring, the mean bill length in the Possession Island population increased by around 4 mm when considering adults, or 2.7 mm when considering juveniles. The change is modest relative to the trait mean (2 to 3 %), but represents between 47% and 77% of the standard deviation of the trait in the population. This represents between 0.14 and 0.23 Haldanes per generation, which falls in the upper range of rates of phenotypic changes reviewed in Hendry (2016). Such a rate of change would likely be too high to be sustained by the population for more than a few generations if it was driven by natural selection and adaptive evolution (Kopp and Matuszewski, 2014).

Demography

Sex is the most important variable structuring variation in bill length, with males bill being about 6 mm longer that females bill. Due to changes in sex ratio, sex had a negative contribution to the trend in bill length, effectively adding an extra -0.92 mm to be explained. The changes in sex ratio are understood to be a consequence of shifting by-catch mortality in the different oceanic regions favoured by males vs. females (Weimerskirch, 2018; Weimerskirch and Jouventin, 1987).

Beyond sex-structure, age structure is another important demographic property that can underlie phenotypic changes (Coulson and Tuljapurkar, 2008). Changes in the age structure of a trait can occur due to within-individual growth and ageing, but also due to change in the relative frequency of different age classes in the presence of among-individual stable differences. We found that bill length was highly repeatable ($R = 0.84$), and did not significantly changed as individuals aged beyond the end of their growth period (early to late October, or around 6 months after hatching). Nevertheless, excluding the growth period, the trend was towards slightly longer bills as birds aged ($beta = 0.05$ mm / year), and our model predicted a non-significant contribution of within-individual ageing of +0.30 mm. This positive effect may be real since birds bills are in part dynamic appendices, in which keratine layers can wear and regrow. There is however little room for post-growth within-individual changes to impact past or future dynamics of bill length. The raw correlation between age and bill length occurs largely among individuals, not within individuals. The among individual age effect is in part as a consequence of selective disappearance (see below) and possibly due to correlations between age and unmeasured environmental variables that cause plastic changes. The combined contributions of sex and age mostly cancel out, bringing the total contribution of demographic structure to around 0.10 mm.

Plasticity

We found that higher values of SAM during the birth year corresponded to longer bills. The increase in SAM during the monitoring corresponds to an increase in wind speeds in some regions used by wandering albatross for foraging. Wandering albatross rely on wind to limit the cost of travelling between breeding and feeding sites (Weimerskirch et al., 2012; Weimerskirch and Wilson, 2000), although excessive winds or associated bad weather reduce foraging efficiency (Darby et al., 2024). Changes in SAM over time have been related to shorter foraging trips, improved breeding success and mass gain in adults in the study population (Fay et al., 2015; Weimerskirch et al., 2012). It is therefore likely that changes in SAM also affected positively the feeding and growth conditions for chicks, which would explain the 0.85 mm increase in bill length ascribed to SAM in our study.

Although the two other environmental variables we tested did not have a clear effect, their trends matched our predictions. Thus, the number of breeding pairs on the birth year tended to correspond to shorter bills, and the annual reproductive success at the colony on the birth year tended to correspond to longer bills. The potential effect of breeding pairs corresponds to negative density dependence, and could be related to increased foraging competition, stress, disturbance or disease transmission. The potential effect of annual reproductive success would be only indirect and reflect the positive influence that some unmeasured environmental properties would have on the early life environment of chicks, in particular parental. We assume that some types of early life environments would at the same time be conducive of a good growth and a good rate of chick fledging.

In total, the plastic responses to those three environmental variables explained 1.34 mm of increase in bill length, which represents between 31 and 50% of the phenotypic change. Thus, between-cohorts plasticity dominated the contribution of phenotypic changes. This results implies that the trend of increasing bill length could be reversed quickly in future cohorts by further changes in the environment. The dominance of plasticity in the phenotypic change is in line with the literature, where a plastic effects are the main drivers identified in most cases of phenotypic change (Merilä and Hendry, 2014). There is, however, a deficit of studies that are able to test for genetic changes (Merilä and Hendry, 2014), as well as studies that explicitly quantify demographic contributions. It remains unclear to what extend the prevalence of plastic responses over genetic and demographic responses to current environmental changes is real. Our study adds to a small body of studies that quantified the contribution of genetic change along plastic and demographic contributions (Arnold et al., 2024; Bonnet et al., 2019).

Here we considered only juvenile survival, as it is a period of high mortality for wandering albatrosses, with about 50% of fledgings never seen again. The mortality is especially high during the first two months after fledging, when juveniles forage inefficiently (Riotte-Lambert and Weimerskirch, 2013). The mortality rate of adults is as low at 2% per year, and offers comparatively less opportunity for selection and less statistical power to estimate it. A previous study found that in the study population, juvenile survival is not associated with the size of individuals but rather with sex, population density or environmental conditions (Fay et al., 2015). We also did not find a significant effect of bill length on juvenile survival. It is possible that bill length contributes somewhat to foraging efficiency, but our results do not support such a causal effect, and the selective disappearance may be entirely stochastic, or driven indirectly by selection on correlated traits. Nevertheless, it is important to realise that non-significant effects can still correspond to realised change, as quantified in covariance analysis of selection or extended Price equation (Coulson and Tuljapurkar, 2008). The small, non-significant, covariation between bill length and survival thus produces a selective disappearance, which contributed to a small increase in bill length of +0.37 mm, or about 10% of the phenotypic trend. Selective disappearance also helps explain half of the between-individuals effect of age.

We did not detect evidence of genetic change in bill length. The point estimate of genetic change represented only 3.6% of the additive genetic standard deviation. This is a much lower proportion than the phenotypic change representing 47 to 77% of the phenotypic standard deviation. Genetic change was thus much smaller than phenotypic change with respect to the amount of variation available in the population. The change was well within the range of changes likely under genetic drift alone, so no response to selection is required to explain it. The population has, however, substantial heritability and thus had the potential to respond quickly, at least on a per-generation basis, to selection for that trait, within the limited range afforded by the standing genetic variation. Selective disappearance of shorter bills before recruitment was modest (selection differential, S=0.13 mm), and corresponds to a predicted response to selection across generations of only 0.08 mm per generation (Sh^2, by the breeder's equation), or 0.27 mm over the study period, which is still more than the point estimate of genetic change (0.14 mm). Stronger selection could produce a rapid change of a few millimeters. However, if we express evolutionary "potential" as evolvability, that is, the genetic variance in relation to the trait mean, (Hansen et al., 2011) we see that at the scale of a few generations, genetic change can only be modest (0.6% of the squared mean). Whether such a change can be ecologically important remains to be seen.

Unexplained change

From our animal model we were able to explain 1.67 mm of increase in bill length, but 2.32 mm remained unexplained. Given that change in sex-ration opposed the increase in bill length, the total positive change to explain was about 5 mm, and we explained about 2.5 mm, or half the positive components of change. Unexplained change is likely related to several processes that we could not include in our model. First, there was probably plastic response to unmeasured environmental variables, not captured by SAM, breeding density and reproductive success. For instance, reproductive success is only an imperfect proxy of growth conditions, and it is likely that growth is influenced more directly by the availability of prey, itself a combination of oceanic productivity and of prey mortality, since wandering albatross forage in part on carrion. Breeding wandering albatrosses forage over thousands of kilometres and it is difficult to identify the areas that are relevant to their foraging and which variables would capture local prey availability.

Second, although we estimated the effect of change in breeding values, other genetic effects that might explain some of the phenotypic change (e.g., Bonnet et al., 2019) could not be modelled given our limited data. The average inbreeding in the population likely changed over the study period due to changes in population size. If inbreeding depression influences bill length, changes in average inbreeding would have contributed to bill length dynamics. Unfortunately, only 37 individuals have non-null pedigree inbreeding coefficients, not because the population is not inbred, but because the pedigree is not deep and dense enough to identify mating between relatives (Keller and Waller, 2002). As we do not have individual molecular data either, we cannot study inbreeding depression in the population at present. Moreover, gene-flow following successful immigration could also have contributed to changes in bill length if phenotypic differentiation exists between colonies. We know of immigrants recruiting into the colony each year. There is no trend in the proportion of immigrant among recruits and most immigrants probably come from other colonies in Crozet archipelago (Barbraud and Delord, 2020), and we are not aware of differentiation between La Possession and source populations that have been identified (i.e., Marion Island, Kerguelen Islands, and South Georgia). Therefore immigration is unlikely to have had a major effect on phenotypic change.

Author contributions

TB designed the study with input from CB and KD. KD curated and extracted data. CR run lab work. LM and TB run analyses and wrote the manuscript.

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Data and Code Availability Statement

Open data/code are not available yet but will be made available for reviewing when submitting to a journal, and to the public after acceptance in a journal.

Conflict of interest statement

The authors declare that there are no conflicts of interest regarding the publication of this paper.

Data accessibility

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