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► **To cite this version:**

Laura Martinez Anton, Karine Delord, Christophe Barbraud, Cécile Ribout, Timothée Bonnet. Causes of recent changes in bill length in Crozet wandering albatross, a long-lived seabird. *Ecology and Evolutionary Biology*, 2024, 10.32942/X2NP72 . hal-04911050

HAL Id: hal-04911050

<https://hal.science/hal-04911050v1>

Submitted on 24 Jan 2025

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

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Keywords: Contemporary evolution, Micro-evolution, Phenotypic change, Climate change, Phenotypic plasticity, Demographic structure

1 Abstract

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

23 Introduction

24 Over the last decades, researchers have documented numerous shifts in the mean phenotypes of
25 wild populations (Gardner et al., 2011; Hendry and Kinnison, 1999; Parmesan, 2006). For in-
26 stance, many studies report recent changes in phenology (e.g., Barbraud and Weimerskirch, 2006;
27 Charmantier and Gienapp, 2014; Dobson et al., 2017), or changes in body size (e.g., Boutin and
28 Lane, 2014; Gardner et al., 2011). Recent phenotypic changes are often linked to environmental
29 changes due to human activities, in particular to anthropogenic climate change (Merilä and Hendry,
30 2014; Parmesan, 2006; Pelletier and Coltman, 2018). Phenotypic change can mediate demographic
31 responses to environmental change, but the relationship is heavily dependent on the mechanism
32 causing phenotypic change (Chevin et al., 2010; Coulson and Tuljapurkar, 2008). In a majority
33 of cases the mechanisms of phenotypic change are unknown (Merilä and Hendry, 2014), curtailing
34 our ability to understand the consequences of phenotypic change and to predict the demographic
35 responses to on-going environmental change. Broad categories of mechanisms are (i) changes in
36 demographic structure, such as shifting sex-ratio or age-class frequencies; (ii) phenotypic plastic-
37 ity; and (iii) genetic change, which include adaptive evolution in response to natural selection as
38 well as genetic drift, inbreeding depression, and gene flow. In addition, one may consider selective
39 disappearance within a generation as a separate mechanism, as it cause phenotypic change even in
40 the absence of an evolutionary response to selection or even of a genetic basis for variation in the
41 trait.

42 Phenotypic change due to phenotypic plasticity can be fast, especially when it occurs within
43 individuals, and therefore allow a population to respond quickly to changes in its environment.
44 However, phenotypic plasticity is often maladaptive if its expression is not itself shaped by selection
45 (Ghalambor et al., 2007), and may be bounded. Demographic change does not have particular
46 reasons to be adaptive or maladaptive, and in any case will always be transient, so it cannot offer a
47 long-term response to on-going directional environmental change. Similarly, non-adaptive genetic
48 change due to drift will usually not help a population sustain environmental change, or only in an
49 idiosyncratic way, whereas gene flow may favour or hinder adaptation depending on the pattern of

50 differences in local adaptation vs. direction of environmental change and the effect of admixture.
51 Selective disappearance as a result of viability selection within generations provides only a short-
52 term adaptive response, and carries a demographic costs as a direct function of the strength of
53 selection, so it is a double-edged sword for population and does not allow a long-term response
54 to on-going directional environmental change. In the end, only adaptive evolution in response to
55 selection provides a response that tends to systematically help the population sustain directional
56 environmental change on the long-term, although the change must not be too fast for too many
57 generations (Kopp and Matuszewski, 2014). If we are to predict the persistence of wild populations
58 to current environmental changes, it is crucial to disentangle the respective contributions of those
59 various mechanisms. In this regard, it is particularly interesting to estimate simultaneously the
60 respective contributions of different mechanisms that may drive phenotypic change (Bonnet et al.,
61 2019; Strickland et al., 2024).

62 Here we aim to decompose the mechanisms underlying an increase in bill length observed over
63 60 years as part of the monitoring of a wild population of wandering albatrosses. Bill length is an
64 important trait in the biology of Procellariiformes, as it is linked to vocalization, olfaction, sexual
65 selection, protection, feeding and territorial behaviour (Gémard et al., 2019; Pickering and Berrow,
66 2001; Tyler et al., 2023; Warham, 1996). In wandering albatross, bill size may play a specific role
67 in courtship, and given the need to process carrion prey that are larger than the albatross (Tickell,
68 1968) bill length may influence the range of prey that can be consumed. Besides, the increase in
69 bill length may be a reflection of the increase in the general size of individuals. Thus, bill length
70 could be indirectly related to the benefits of a larger size, such as efficient use of winds, which
71 is essential for reproductive success and foraging (Weimerskirch et al., 2012), or defence against
72 predator (Dilley et al., 2013; Tickell, 1968).

73 A priori, plastic, demographic, and genetic mechanisms are all plausible explanations for phe-
74 notypic change in this population. Bird bills consist of bones covered in an outer layer of keratin,
75 in the case of albatrosses made of several pieces (Hieronymus and Witmer, 2010; Piro, 2022). The
76 bones develop during the chick growth until around fledging, and their length could be influenced
77 by the quantity and quality of parent provisioning, as well as by aspects of the environment around

78 the nest. The study population experienced important changes in its environment over the study
79 period: climate change, fisheries, invasive species, and changes in population density (Weimerskirch,
80 2018). These changing conditions during the growth period, which is almost synchronous for all
81 chicks born on a given year, may have caused among-individuals phenotypic plasticity structured by
82 cohorts. The keratin pieces grow and erode continuously, which may produce age-structure in bill
83 length (hence a potential for phenotypic change due to change in demographic structure), and may
84 allow bill length to respond to various environmental variables by within individuals phenotypic
85 plasticity. Further, the study population went through a sharp decline driven by adult, particularly
86 female, mortality at the beginning of the monitoring, followed by a slow recovery. This change in
87 population size probably coincided also with change in sex-ratio and age-structure, which could
88 have driven changes in bill length. Given the importance of bills in avian ecology, even small differ-
89 ences in bill length with the population could be subject to natural selection. Selection could result
90 directly in selective disappearance, which would change the average bill length within cohorts. In
91 addition, selection could cause genetic change in response to selection across generations (hence,
92 across cohorts). Although wandering albatrosses have a slow life-cycle, with a generation time of
93 about 18 years, the monitoring spans 60 years, thus giving enough span for some genetic change to
94 take place.

95 **Methods**

96 **Species and population monitoring**

97 The wandering albatross (*Diomedea exulans*, Procellariiformes: Diomedidae) breeds in the Antarc-
98 tic zone on different islands such as South Georgia, Prince Edward Islands, Kerguelen, Macquarie
99 Island and on Crozet Archipelago (Brooke, 2004). This species has a slow life history, with repro-
100 duction beginning at around 10 years of age, high adult survival, and a lifespan sometimes exceeding
101 60 years (Bennett and Owens, 2002; Croxall et al., 1990). Their breeding season starts in November,
102 and lasts for a full year. Successful breeding is usually followed by a full sabbatical year at sea,

103 so they breed every two years only. They lay a single egg and care is bi-parental (Tickell, 1968).
104 During sabbatical years wandering albatross travel long distances in the southern hemisphere, regu-
105 larly circling around Antarctica (Weimerskirch, 1995; Weimerskirch et al., 2014; Weimerskirch and
106 Wilson, 2000). Foraging areas during the breeding season depend on sex although this segregation
107 is less marked during the sabbatical year (Ceia et al., 2012; Weimerskirch et al., 2014). However,
108 birds are highly philopatric and will usually breed close to their birth colony (Charmantier et al.,
109 2011; Inchausti and Weimerskirch, 2002).

110 The population of wandering albatross on Possession Island, Crozet Archipelago (46°S, 51°E)
111 has been monitored annually since 1958 as part of programs carried out by the French Polar
112 Institute (IPEV). Between 1961 and 1990, wandering albatross populations underwent a major
113 decline, likely as a consequence of by-catch due to the development of longline fishing (Croxall,
114 1979; Croxall et al., 1990; Tomkins, 1985; Weimerskirch and Jouventin, 1987). On Possession
115 Island, the annual rate of decline was around 4.9% between 1969 and 1985 (Weimerskirch and
116 Jouventin, 1987). Most populations, including Possession Island, then gradually recovered possible
117 due to changes in exposure to by-catch (Inchausti and Weimerskirch, 2002; Weimerskirch et al.,
118 2018).

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

128 Wandering albatrosses are socially monogamous, so we constructed a social pedigree by matching
129 each ringed chick to the adults identified at the nest. Extra pair mating have been reported and
130 may concern 10% of the chicks based on a small sample (Jouventin et al., 2007). This introduces

131 errors in the pedigree which probably lowers slightly the precision of quantitative genetic parameter
132 estimation (Charmantier and Réale, 2005). pedigree. We computed pedigree properties using the
133 R-package pedantics (Morrissey and Wilson, 2010). The pedigree contains 11232 individuals. Both
134 parents are missing for 2673 of them. The pedigree has a maximal depth of five generations, reached
135 for 31 individuals, and an average depth of 1.37 generations.

136 We measured several biometric variables for most ringed chicks, as well as for adults according
137 to opportunities. Firstly, we measured the length of the bill as well as the maximum height of the
138 hook using a caliper with 0.1 millimetre accuracy. The measurements are likely very accurate given
139 the long bill of wandering albatrosses. In museum conditions, the measurement error variance
140 for bill around 160 mm long, and measured with similar equipment, is approximately 0.1 mm^2 ,
141 corresponding to an error standard deviation of around 0.3 mm and a within sample measurement
142 repeatability of over 99% (Subasinghe et al., 2021). We measured tarsus length with callipers as for
143 bill length and wing length using a millimetre precision ruler. In addition, we measured body mass,
144 with a precision of 5 grams. Individuals, both chicks and adults, were sometimes caught several
145 times during the same year and across years in the case of individuals that survived to recruitment.
146 Before any filtering process the biometric dataset of individuals ringed as chicks consisted of 2
147 849 observations of 1 861 individuals and the biometric dataset of individuals ringed adults was
148 composed of 396 observations of 275 individuals (Table 1).

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

156 Some morphological measurements were done during growth. Since we do not know the exact
157 age of chicks (i.e. hatching date) we could not easily model growth to correct for it. Because
158 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.

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

168 **Environmental predictors**

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

180 in other dimensions of environmental quality, we included annual reproductive success (number of
181 fledged birds divided by the number of eggs laid) as an environmental variable in models.

182 **Statistical analyses**

183 All statistical analyses were carried out using the R statistical program, version 4.4.12 (2024-06-14
184).

185 **Phenotypic change**

186 To estimate the change in bill length over years, we fitted linear regressions with year as a predictor
187 and individual identity as a random intercept. For year, we used both year of measurement, and
188 cohort (i.e., birth year). In one set of regressions we filtered data to keep only measurements taken
189 on birds that are 5 years old or older. Birds are never seen at the colony between fledging and
190 at least 5 years old. This filters out completely juvenile measurements, which may be influenced
191 by growth, to focus on birds that are back to the colony as sub-adults or adults. In another set
192 of regression, we retained juveniles measurements that were done after some threshold dates, to
193 reduce the influence of growth on the estimation. We determined the thresholds with a sensitivity
194 analysis, computing the rate of phenotypic change for every threshold date to identify above which
195 date the trends stabilized. We obtained thresholds of the 330th Julian day for the cohort trend and
196 275th Julian day for the measurement year trend.

197 **Model of source of variation in bill length among cohorts**

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

$$z_{ij} = \mu + \mathbf{X}^T \mathbf{b} + a_i + p_i + m_i + c_i + y_j + r_{ij} \quad (1)$$

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

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

227 We filtered out data with missing values in predictors, and with measurements taken before the
 228 330th day of the year in juveniles (to avoid biases due to growth, see above). We run the model in
 229 the R-package MCMCglmm (Hadfield, 2010). We assumed a Gaussian family. We run the model

230 for 250000 iterations, with a burnin of 50000, and thinning of 200 (computation time of secondary
 231 calculations). We checked convergence by visual inspection of the trace for all parameters, and by
 232 running the model three times. We used default normal broad priors for fixed effects, and parameter-
 233 expanded priors for random effects (with parameter V=1, nu=1, alpha.mu=0, alpha.V=1000). We
 234 recorded Best Linear Predictors (BLUPs) to run derived calculations of predicted breeding values
 235 (using the option "pr=TRUE"). All derived calculations were integrated over the full posterior
 236 distribution to propagate uncertainty.

237 **Repeatability and heritability**

238 We computed repeatability in two ways. First,

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

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

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

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

247 We computed heritability as

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

248 In contrast to the calculation of repeatability, here we also included V_C and V_b , as heritability may

249 be thought of as the proportion of additive genetic variance across environments experienced by all
250 individuals.

251 **Estimated contributions of environmental and demographic variables**

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

259 **Genetic change**

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

269 **Selection**

270 To estimate selection on bill length between fledging and the return to the colony, from around
271 5 years old (Tickell, 1968; Weimerskirch et al., 2014), we retained only measurements taken on
272 juveniles. We retained only measurements taken after the 275th Julian day, because there is no
273 correlation between measurement day and survival after that point, and because the growth of bill

274 length is almost complete at this time (mean bill size between 275th and 285th day: 166.6mm, vs.
275 mean bill size among birds above 5 years old: 166.9mm). We discarded individuals born after 2012,
276 as those cohorts had just started, or not started at all, to come back to the colony and we do not
277 know which individuals survived yet. We retained a single measurement per individual, the last
278 one before fledging.

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

286 **Results**

287 **Phenotypic change**

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

295 **Sources of variation in bill length**

296 Males had longer bills than females (difference = 6.11 mm, $p_{MCMC} < 0.001$). Bill length was
297 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 mm² (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.

310 Demographic structure

311 Early in the monitoring the sex ratio tended to be male biased, but it became about balanced from
312 1975, and then rather female-biased after 2000. Thus, the proportion of males decreased during the
313 study period. Since males have longer bills than female, the change in sex ratio was predicted to
314 have changed mean bill length by -0.92 mm (95%CI [-1.01; -0.83]). The effect of within-individual
315 age variation was not clear, but tended to be positive. Over years, we tended to measure older birds
316 on average, which predicts a contribution of +0.30 mm over the study period (95%CI [-0.18;0.76]).
317 The effect of mean age was clearly positive. Since most of our sample consisted of birds first
318 measured as juveniles, the average mean age tended to increased in our sample (although this may
319 not reflect the true dynamic of age structure in the population). Therefore, our model predicts a
320 positive contribution of mean age of + 0.60 mm over the study period (95%CI [0.27;1.28]). The
321 sum of sex contribution and age contributions largely cancel out to a net demographic contribution
322 of +0.10 mm over the study period (95%CI [-0.88;1.03]).

323 Plastic responses

324 Only the effect of the Southern annular mode (SAM) was clear in the model (Table 4), but all
325 three environmental variables were predicted to have more positive contributions across cohorts,
326 and the sum of their contributions was positive and large (Fig. 1). SAM had a positive estimated
327 effect on bill length, and SAM tended to become more positive through time, giving an estimated
328 change in its contribution of 0.85 mm over the study period (95%CI [0.16;1.43]). The number of

329 breeding pairs had a non-significant negative effect on bill length, and since the number of breeding
330 pairs decreased overall despite a recent recovery, its contribution tended to be positive with +0.22
331 mm (95%CI [-0.19;0.73]) over the study period. Annual reproductive success had a non significant
332 positive effect on bill length, and since it increased over the study period, it tended to contribute
333 to an increase in bill length of +0.21 mm (95%CI [-0.045;0.73]). Summing the three environmental
334 variables, the total contributions of plasticity in response to the environment across cohorts was
335 estimated to +1.34 mm (95%CI [0.33;2.33]).

336 **Genetic change**

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

343 **Explained and unexplained changes**

344 The estimated effect of cohort, as fixed effect, in our animal model is meant to capture the change
345 in bill length left unexplained by other predictors. Since cohort is correlated to other predictors,
346 there should be large uncertainty in the estimation of this effect. Indeed, the unexplained change
347 over the study period was estimated to +2.32 mm, with 95%CI [-1.96;7.51]. The change explained
348 by contributions of sex, age, environment and genetic change added up to +1.67 mm (95%CI
349 [0.10;2.88]).

350 **Selective disappearance**

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

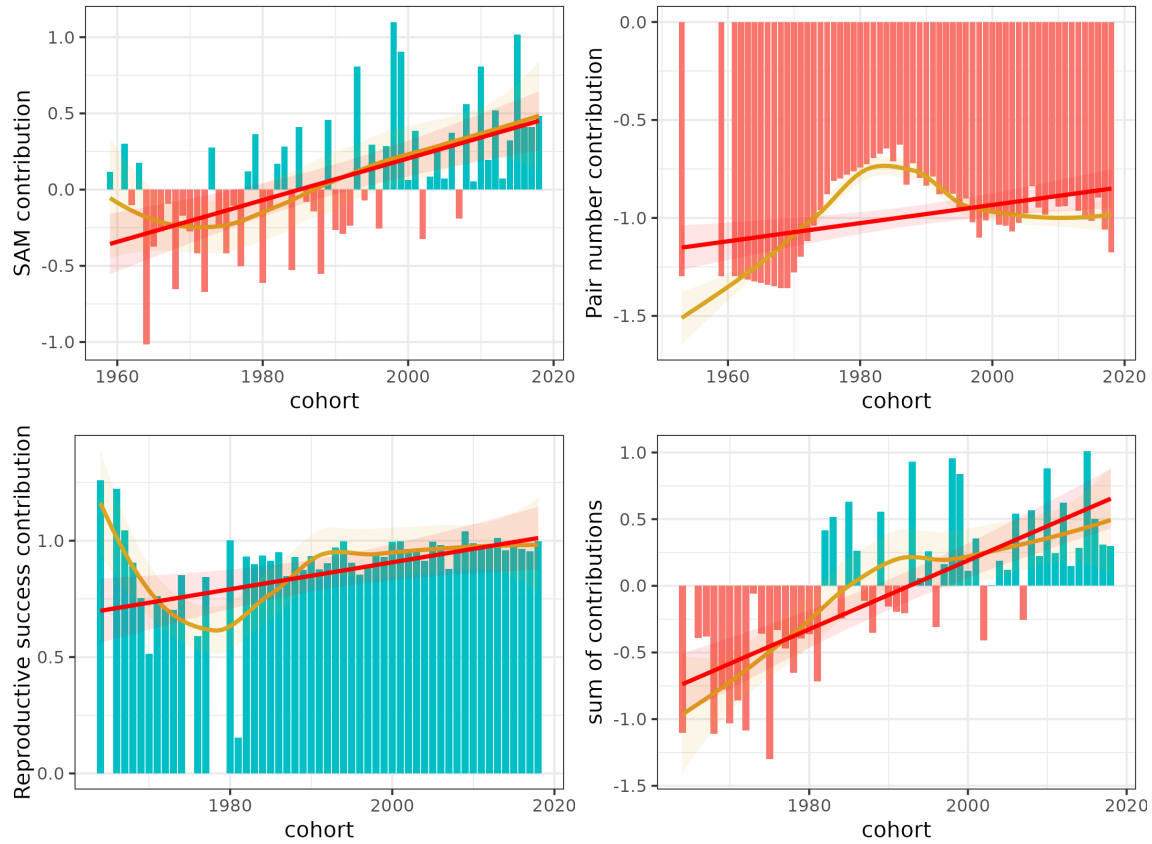


Figure 1: Estimated contributions of environmental variables to changes in bill length across cohorts. Red bars represent negative contributions, blue ones positive contributions. A red line represent a linear regression of contributions on cohorts, a golden line represents a local polynomial regression 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.

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

359 Discussion

360 Over the 60 years of monitoring, the mean bill length in the Possession Island population increased
361 by around 4 mm when considering adults, or 2.7 mm when considering juveniles. The change
362 is modest relative to the trait mean (2 to 3 %), but represents between 47% and 77% of the
363 standard deviation of the trait in the population. This represents between 0.14 and 0.23 Haldanes
364 per generation, which falls in the upper range of rates of phenotypic changes reviewed in Hendry
365 (2016). Such a rate of change would likely be too high to be sustained by the population for more
366 than a few generations if it was driven by natural selection and adaptive evolution (Kopp and
367 Matuszewski, 2014).

368 Demography

369 Sex is the most important variable structuring variation in bill length, with males bill being about
370 6 mm longer than females bill. Due to changes in sex ratio, sex had a negative contribution to the
371 trend in bill length, effectively adding an extra -0.92 mm to be explained. The changes in sex ratio
372 are understood to be a consequence of shifting by-catch mortality in the different oceanic regions
373 favoured by males vs. females (Weimerskirch, 2018; Weimerskirch and Jouventin, 1987).

374 Beyond sex-structure, age structure is another important demographic property that can un-
375 derlie phenotypic changes (Coulson and Tuljapurkar, 2008). Changes in the age structure of a
376 trait can occur due to within-individual growth and ageing, but also due to change in the relative
377 frequency of different age classes in the presence of among-individual stable differences. We found

378 that bill length was highly repeatable ($R = 0.84$), and did not significantly changed as individu-
379 als aged beyond the end of their growth period (early to late October, or around 6 months after
380 hatching). Nevertheless, excluding the growth period, the trend was towards slightly longer bills
381 as birds aged ($\beta = 0.05$ mm / year), and our model predicted a non-significant contribution of
382 within-individual ageing of +0.30 mm. This positive effect may be real since birds bills are in part
383 dynamic appendices, in which keratine layers can wear and regrow. There is however little room for
384 post-growth within-individual changes to impact past or future dynamics of bill length. The raw
385 correlation between age and bill length occurs largely among individuals, not within individuals.
386 The among individual age effect is in part as a consequence of selective disappearance (see below)
387 and possibly due to correlations between age and unmeasured environmental variables that cause
388 plastic changes. The combined contributions of sex and age mostly cancel out, bringing the total
389 contribution of demographic structure to around 0.10 mm.

390 **Plasticity**

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

400 Although the two other environmental variables we tested did not have a clear effect, their
401 trends matched our predictions. Thus, the number of breeding pairs on the birth year tended to
402 correspond to shorter bills, and the annual reproductive success at the colony on the birth year
403 tended to correspond to longer bills. The potential effect of breeding pairs corresponds to negative
404 density dependence, and could be related to increased foraging competition, stress, disturbance or

405 disease transmission. The potential effect of annual reproductive success would be only indirect
406 and reflect the positive influence that some unmeasured environmental properties would have on
407 the early life environment of chicks, in particular parental. We assume that some types of early
408 life environments would at the same time be conducive of a good growth and a good rate of chick
409 fledging.

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

422 Here we considered only juvenile survival, as it is a period of high mortality for wandering alba-
423 trosses, with about 50% of fledgings never seen again. The mortality is especially high during the
424 first two months after fledging, when juveniles forage inefficiently (Riotte-Lambert and Weimer-
425 skirch, 2013). The mortality rate of adults is as low as 2% per year, and offers comparatively less
426 opportunity for selection and less statistical power to estimate it. A previous study found that
427 in the study population, juvenile survival is not associated with the size of individuals but rather
428 with sex, population density or environmental conditions (Fay et al., 2015). We also did not find
429 a significant effect of bill length on juvenile survival. It is possible that bill length contributes
430 somewhat to foraging efficiency, but our results do not support such a causal effect, and the selec-
431 tive disappearance may be entirely stochastic, or driven indirectly by selection on correlated traits.
432 Nevertheless, it is important to realise that non-significant effects can still correspond to realised

433 change, as quantified in covariance analysis of selection or extended Price equation (Coulson and
434 Tuljapurkar, 2008). The small, non-significant, covariation between bill length and survival thus
435 produces a selective disappearance, which contributed to a small increase in bill length of +0.37
436 mm, or about 10% of the phenotypic trend. Selective disappearance also helps explain half of the
437 between-individuals effect of age.

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

454 **Unexplained change**

455 From our animal model we were able to explain 1.67 mm of increase in bill length, but 2.32 mm
456 remained unexplained. Given that change in sex-ratio opposed the increase in bill length, the
457 total positive change to explain was about 5 mm, and we explained about 2.5 mm, or half the
458 positive components of change. Unexplained change is likely related to several processes that
459 we could not include in our model. First, there was probably plastic response to unmeasured

460 environmental variables, not captured by SAM, breeding density and reproductive success. For
461 instance, reproductive success is only an imperfect proxy of growth conditions, and it is likely
462 that growth is influenced more directly by the availability of prey, itself a combination of oceanic
463 productivity and of prey mortality, since wandering albatross forage in part on carrion. Breeding
464 wandering albatrosses forage over thousands of kilometres and it is difficult to identify the areas
465 that are relevant to their foraging and which variables would capture local prey availability.

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

482 **Author contributions**

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

485 **Acknowledgements**

486 The authors thank all the fieldworkers who collected data over 60 years as part of the project IPEV
487 109 ORNITHO2E “Seabirds and marine mammals as sentinels of global changes in the Southern
488 Ocean: eco-evolutionary trends and processes”. The authors thank D. Joubert for data management
489 and the "Service d'Analyses Biologiques du CEBC" for their expertise and their technical help in
490 conducting laboratory analyses. Data were collected with the logistical and financial support from
491 Institut Polaire Francais, Paul-Emile Victor (IPEV), Terres Australes et Antarctiques Francaises
492 and Zone Atelier Antarctique et Terres Australes (LTSER France). This study is part of the long-
493 term Studies in Ecology and Evolution (SEE-Life) program of the CNRS.

494 **Data and Code Availability Statement**

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

497 **Conflict of interest statement**

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

499 **Data accessibility**

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