

Evidence for an age-dependent influence of environmental variations on a long-lived seabird's life-history traits

DEBORAH PARDO,¹ CHRISTOPHE BARBRAUD, MATTHIEU AUTHIER, AND HENRI WEIMERSKIRCH

CEBC-CNRS UPR, 1934, F 79360 Villiers-en-Bois, France

Abstract. Theoretical and empirical studies have highlighted the effects of age on several life-history traits in wild populations. There is also increasing evidence for environmental effects on their demographic traits. However, quantifying how individuals differentially respond to environmental variations according to their age remains a challenge in ecology. In a population of Black-browed Albatrosses monitored during 43 years, we analyzed how life-history traits varied according to age, and whether individuals of different ages responded in different ways to environmental conditions. To do so, we: (1) examined how age affected seven life-history traits, (2) investigated differences in temporal variance of demographic traits between age classes, and (3) tested for age-dependent effects of climate and fisheries covariates on demographic traits. Overall, there was a tendency for traits to improve during the first years of life (5–10 years), to peak and remain stable at middle age (10–30 years), and decline at old ages. At young ages, survival and reproductive parameters increased, except offspring body condition at fledging, suggesting that younger parents had already acquired good foraging capacities. However, they suffered from inexperience in breeding as suggested by their higher breeding failures during incubation. There was evidence for reproductive and actuarial senescence. In particular, breeding success and offspring body condition declined abruptly, suggesting altered foraging capacities of old individuals. Middle-aged individuals had the lowest temporal variance of demographic traits. Although this is predicted by the theory of environmental canalization, it could also result from a higher susceptibility of young and old birds due to their respective inexperience and senescence. The highest temporal variances were found in old individuals. Survival was significantly influenced by sea surface temperatures in the foraging zone of this albatross population during breeding. During warm events survival of young and old individuals improved, whereas a decrease was observed for middle-aged individuals. Presumably, during cold years with poor environmental conditions, young and old breeding birds may suffer more from intraspecific competition for resources than middle-aged individuals. This study showed that age, known as a major factor structuring demography in long-lived species, can also potentially influence the response of populations to global change.

Key words: *Black-browed Albatross; breeding probability; breeding success; capture–mark–recapture; chick body condition; fisheries bycatch; Kerguelen Islands; sea surface temperature; senescence; southern oscillation index; survival; Thalassarche melanophris.*

INTRODUCTION

Age is an essential factor to consider when studying population dynamics and evolution in wild populations (Charlesworth 1980) as it can have strong effects on a broad array of physiological, behavioral, phenotypical, and demographic traits (Reid et al. 2003, Lecomte et al. 2010). An increase in survival and breeding performance is expected at early ages due to selection (Curio 1983), constraint (Nur 1984), and restrained reproduction (Williams 1966). Subsequently, fitness is predicted to decline either immediately after the age of primiparity (Hamilton 1966) or after a period of stability of both

traits for middle age classes (Jones et al. 2008). Survival at old ages is expected to decrease, either due to senescence, an inevitable decrease in physiological functioning with age (Monaghan et al. 2008), and/or life-history trade-offs between investment in current reproduction vs. future reproduction and survival (Stearns 1989). Breeding performance could either decline or increase at later ages due to senescence effects or terminal investment, respectively (McNamara et al. 2009).

In addition to age effects, environmental variations can affect demographic parameters and ultimately shape population dynamics. In the current context of global changes and the increase of the rate of species extinction, the link between demographic traits and environmental covariates is extensively studied in a variety of organisms all around the globe (Parmesan 2006). However, there is evidence that all individuals of a given

Manuscript received 6 February 2012; revised 30 May 2012; accepted 5 July; final version received 27 July 2012.
Corresponding Editor: P. T. Raimondi.

¹ E-mail: deborah.pardo@gmail.com

population may not be impacted similarly by the same environmental variations (Barbraud and Weimerskirch 2005, Borrego et al. 2008, Lewis et al. 2009). Few studies have investigated how environmental variations can potentially differently affect individuals according to their age (Coulson et al. 2001, Gaillard and Yoccoz 2003). From a theoretical point of view, both sources of variability should be accounted for simultaneously in order to get proper estimates of age-related change in life-history traits as a function of environmental conditions. This is particularly relevant for long-lived organisms, where both information on age and environmental change are fundamental for understanding the evolution of their life-history. From an applied point of view, given the unprecedented global biodiversity crisis (Western 1992), understanding how individuals respond to climate change according to their age is crucial to properly model population trajectories and conduct conservation actions.

Two sorts of age-dependent differential responses to environmental variations are expected: firstly, differences in the intensity of the responses. In an age-structured population, the sensitivities of the population growth rate differ between demographic parameters (Saether and Bakke 2000). Previous studies have shown that variability is selectively disadvantageous for long-lived iteroparous species, and that fitness components with high sensitivities are canalized against temporal variability (Gaillard and Yoccoz 2003, Doherty et al. 2004, Nevoux et al. 2010b). Such canalization can also be observed between age classes. Since in iteroparous species, sensitivities of the population growth rate are generally higher for demographic parameters of middle-aged individuals (Caswell 2001), one can predict that young and old individuals should be more influenced by temporal environmental variations than middle-aged individuals. Secondly, differences in the direction of the responses are expected. Due to complex mechanisms such as differential spatiotemporal distribution, competition, inexperience, or senescence on foraging capacities, some age classes might be negatively influenced by changes in climate, while others are not, or even manage to take advantage of it.

Here, we address two questions: (1) How is demography influenced by age? (2) Are young and old individuals more sensitive to environmental variations? We used a 43-year data set on a long-lived seabird, the Black-browed Albatross (*Thalassarche melanophris*) and focused on seven major life-history traits: adult survival probability, breeding probability, breeding success, stage at reproductive failure, and offspring body condition and body size at independence according to parents' age. Although not considered as a classic life-history trait, we also examined the age-related pattern in detectability since, in animals that skip reproduction such as seabirds, this parameter may be considered as a proxy of the probability to reproduce (Viallefont et al. 1995). Previous studies on Black-browed Albatrosses

suggested an increase in survival and breeding performance with experience (Nevoux et al. 2007), the existence of a senescence in breeding success in relation to past experience and hormonal levels (Angelier et al. 2007b), and a sensitivity of demographic parameters to environmental variation (Nevoux et al. 2007, 2010a, Rolland et al. 2008, 2009).

Concerning age effects, we were particularly interested in examining if (and when) trait values improve during young ages to stabilize at middle-ages and if (and when) senescence can be detected in the seven traits studied. According to the relationship found by Jones et al. (2008) and the generation time of the Black-browed Albatross (~14 years estimated by the weighted mean age of the breeding population), an onset of senescence in survival and breeding success is predicted at ~10 years old, with a slow but significant rate (Jones et al. 2008).

Concerning age-dependent responses to the environment, previous studies found that differences in breeding performance (e.g., Laaksonen et al. 2002, Bunce et al. 2005) and survival probability (Gaillard et al. 1998, Coulson et al. 2001, Barbraud and Weimerskirch 2005) between juveniles or first-time breeders and more experienced breeders were particularly marked during poor environmental conditions with low resource availability. This was also found in Black-browed Albatrosses (Nevoux et al. 2007). In addition to environmental variability, albatrosses are affected by fisheries by being accidentally caught in fishing gear (Weimerskirch et al. 2000). It is known that juveniles represent the major part of birds killed by long-liners (Gales et al. 1998), including in Black-browed Albatrosses, but the demographic impact of fisheries-associated mortality has, to our knowledge, never been tested as a function of age in these species. We therefore predicted that young individuals would be more affected by environmental conditions and fisheries compared to older individuals. Finally, we tested the hypothesis that the oldest albatrosses would be more sensitive to environmental variations than middle-aged individuals (Coulson et al. 2001).

MATERIALS AND METHODS

Study species and area

Black-browed Albatrosses are large seabirds breeding on subantarctic islands during the austral summer. They become mature at an average age of nine (Nevoux et al. 2010a), and lay a single egg per year without replacement clutch. The long-term demographic study was carried out at Canyon des Sourcils Noirs (49.4° S, 70.1° E), Kerguelen Islands, Southern Indian Ocean. In the colony of >1000 pairs, a study plot of ~200 nests delimited by natural borders was monitored each breeding season with a constant monitoring effort since 1978/1979 (hereafter named 1979), with banding starting in 1968. Each nest was checked three times: during early incubation in October to identify all pair members, at hatching in late

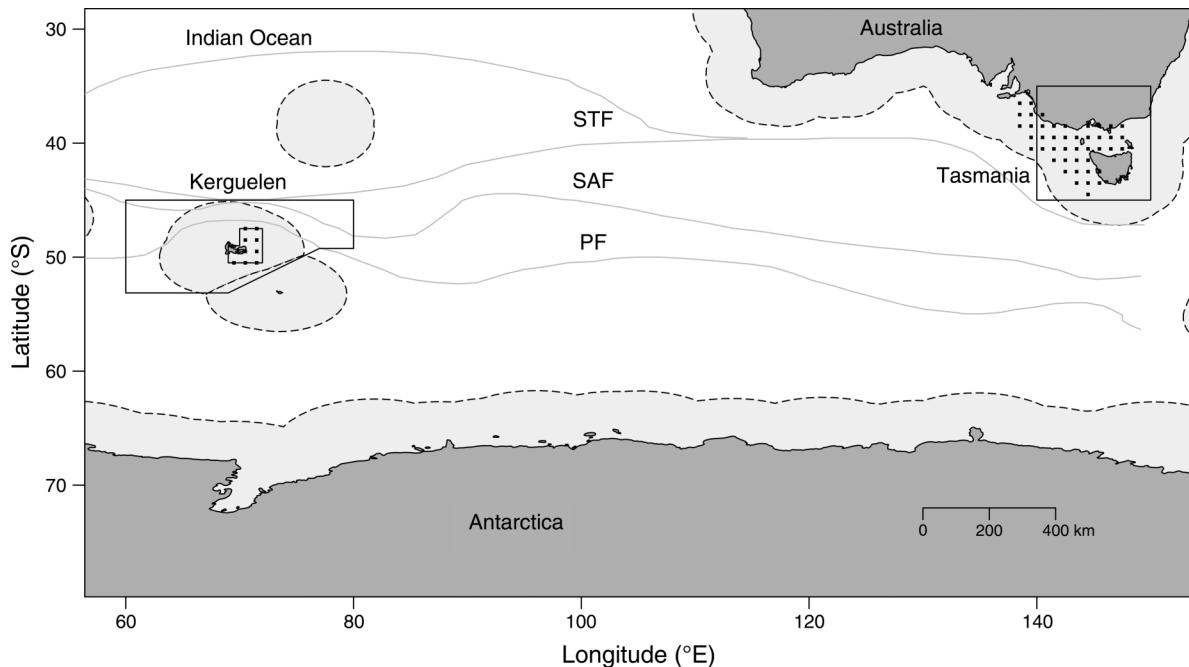


FIG. 1. Distribution area of Black-browed Albatrosses (*Thalassarche melanophris*) breeding at Canyon des Sources Noirs, Kerguelen Islands, Southern Indian Ocean. Black dots represent the foraging areas based on 50% kernels of the birds in summer around Kerguelen and in winter off southern east Australia. Areas delimited by a solid black line represent the zones from which the local covariates data were extracted, except for the illegal longline fishery effort for which data from the Commission for the Conservation of Antarctic Marine Living Resources (CCMLAR) zone 58.5.1 were used. Dotted lines represent the Exclusive Economical Zones (ZEE). Abbreviations are: STF, southern and northern subtropical fronts; SAF, subantarctic front; and PF, polar front.

December to note hatching success, and before fledging in late March for fledging success. Each year, all unmarked breeding individuals found in the study area were banded and all chicks were measured (culmen and wing length, ± 1 mm), weighed (± 5 g), and marked with a stainless-steel band between 21 and 30 March. Tracking studies in this colony have been carried out since 1994 (Argos loggers, $n = 26$; global positioning system (GPS) loggers, $n = 65$; global location sensing (GLS) loggers, $n = 28$), allowing the identification of foraging zones during breeding in summer and wintering (Fig. 1). In summer, Black-browed Albatrosses foraged in northeast and southeast regions of the peri-insular Kerguelen shelf (Pinaud and Weimerskirch 2002, Rolland et al. 2008). Their diet is composed mainly of fish (73%), penguins (14%), and squids (10%; Cherel et al. 2000). They are known to interact commonly with longline and trawl fisheries targeting patagonian toothfish (*Dissostichus eleginoides*) and mackerel icefish (*Champsocephalus gunnari*) feeding on discards and baits (Weimerskirch et al. 2000). In winter, breeding adults migrate in less than a week toward southeast Australia and north of Tasmania, where they remain until the next breeding season (Fig. 1; K. Delord, C. Barbraud, and H. Weimerskirch, unpublished data). It was shown that they attend long-liners fishing for southern bluefin tuna (*Thunnus thynnus*) and

other tuna species in their wintering zone (Gales et al. 1998).

Modeling age-dependent variations in multiple traits

We considered individuals banded as chicks ($n = 4235$) and recaptured during the period 1968–2010, allowing us to know the age at recaptures with precision. Individuals that were not seen again after their immature period because they never came back to the study colony were taken into account in order to avoid an overestimation of survival. Regular observations outside the study colony suggested that very few individuals (< 10) born in the study colony were breeding either in the neighboring main colony or in an adjacent colony (2 km distant), or distant colonies (100–450 km). As Black-browed Albatrosses are monomorphic, we do not have information on their sex. All parameters were estimated starting from age five, the minimum age of first reproduction (Nevoux et al. 2010a).

Adult survival and detection probabilities were estimated with capture–mark–recapture (CMR) models using program Mark version 5.1 (White and Burnham 1999). We started from the general full age-dependent model $\phi(\text{age})p(\text{age})$, where survival, ϕ , and detection probability, p , are age dependent. Goodness-of-fit was computed using parametric bootstrap (1000 iterations)

directly in program Mark from the general full-age model. The overdispersion coefficient was calculated by dividing the deviance from the original data by the mean of the simulated deviances and the quasi-AIC_c (QAIC_c) was used for model selection. The detection probability p was modeled first while keeping a full-age structure on ϕ . Then, ϕ was modeled using the best model structure selected on p .

All analyses on traits associated to fecundity were computed in program R, using package *lme4* and function *lmer* (Bates and Maechler 2010, R Development Core Team 2012). Pseudo-replication was present in the data for two reasons: Firstly, individuals were seen many times during their lifetime, and secondly, both individuals from the same pair were considered. Generalized linear mixed models (GLMM) were used to model reproductive traits along with age, while adding individual random effects to each model to correct for pseudo-replication. Individual random effects could not be used while estimating survival and detection probabilities because such effects are not yet available in program Mark and it would have probably resulted in too many parameters given the amount of data available.

Breeding and success probabilities and stage at failure were coded as binomial characters with, respectively: a one if an individual was seen breeding at a given year/age or a zero if it was seen as a nonbreeder; a one if an individual managed to bring its chick to fledging, a zero if it failed; a zero when an individual failed at the egg stage or a one if it failed at the chick stage. A body condition index of chicks about to fledge was calculated using the ratio of the mass (g) and the wing chord length (mm) to bring information on the possible causes of reproductive failure, linked in particular to the amount of food received by the chick (Weimerskirch and Lys 2000). Finally, culmen length of chicks about to fledge was considered as a proxy of the structural size of chicks. Our definition and calculation of breeding probability, breeding success, and stage at reproductive failure implies that these parameters were estimated from individuals whose detection probability was one. As it is known that the age of first breeding can influence the age at onset of senescence, its effect was tested on each trait (except detection) before analyzing the data (see Appendix A).

For both the analyses on age-related survival and reproduction, the fit of different types of models was assessed using a threshold methodology (Berman et al. 2009, Weladji et al. 2010; see developments of this methodology in Appendix B). A similar model selection procedure based on multi-model inference was used on each trait (Burnham and Anderson 2002; see the approach used in Appendix B).

Estimating parameter- and age-specific temporal variance

The temporal variance of the two traits most influential for the population growth rate (survival and

success probability) was calculated for each age class. Temporal variance includes both the sampling variance (that depends on the estimation process linked to sample size and on the fact that detectability is less than one) and the biological process variance. This last component represents the true temporal variation in the parameters of interest, which was used to validate our hypotheses of canalization of demographic parameters according to age. The estimated total temporal variance (S^2) was calculated following Gould and Nichols (1998; see Appendix C).

Testing for a differential impact of environmental variations with age

Age-specific environmental effects were analyzed on three of the seven life-history traits studied: adult survival, success probability, and chick body condition at fledging, as they are the traits most tightly linked to fitness. The same data sets were used as for the age effects, but 2010 was excluded since information on environmental covariates were lacking at the time analyses were performed. Seven environmental covariates were selected in order to encompass the potential climatic and fisheries effects in both the breeding and wintering areas of Black-browed Albatrosses: Southern Oscillation Index (SOI_w); sea surface temperature anomalies (SSTA_s and SSTA_w); longline fishing effort in number of hooks deployed (LL_s and LL_w); illegal, unreported, and unregulated longline fishing effort (IUU_s); trawling effort in number of hours (Trawl_s). Subscripts “_s” and “_w” mean summer and winter, respectively (see Appendix D for a full description of each covariate). For each trait we used the selected model structure describing best age-dependent variations to which the covariate effect was added. The effects of environmental covariates were tested following Grosbois et al. (2008) using likelihood ratio tests (LRT), analysis of deviance (ANODEV), and the proportion of variation explained by covariates (R^2).

RESULTS

Recruitment age had no effect on age-dependent survival or on traits linked to breeding performance (Appendix A).

Effects of age on survival and detection probabilities

The general age dependent model $\phi(\text{age})p(\text{age})$ was supported by parametric bootstrap, and the variance inflation factor ($\hat{c} = 1.03$) was taken into account in the CMR analysis. Detection probability was best modeled with two thresholds separating a sharp increase from age 5 to age 9, from a slow quadratic increase up to age 23, when detection reached 0.587 ± 0.024 , until the oldest age of 35 years (Fig. 2b, Table 1; Appendix E). For survival, multi-model inference suggested two thresholds (Table 2). A first threshold was selected at 8 years old until which survival increased, then a plateau in middle-aged individuals at 0.934 ± 0.040 , until age 30 and a

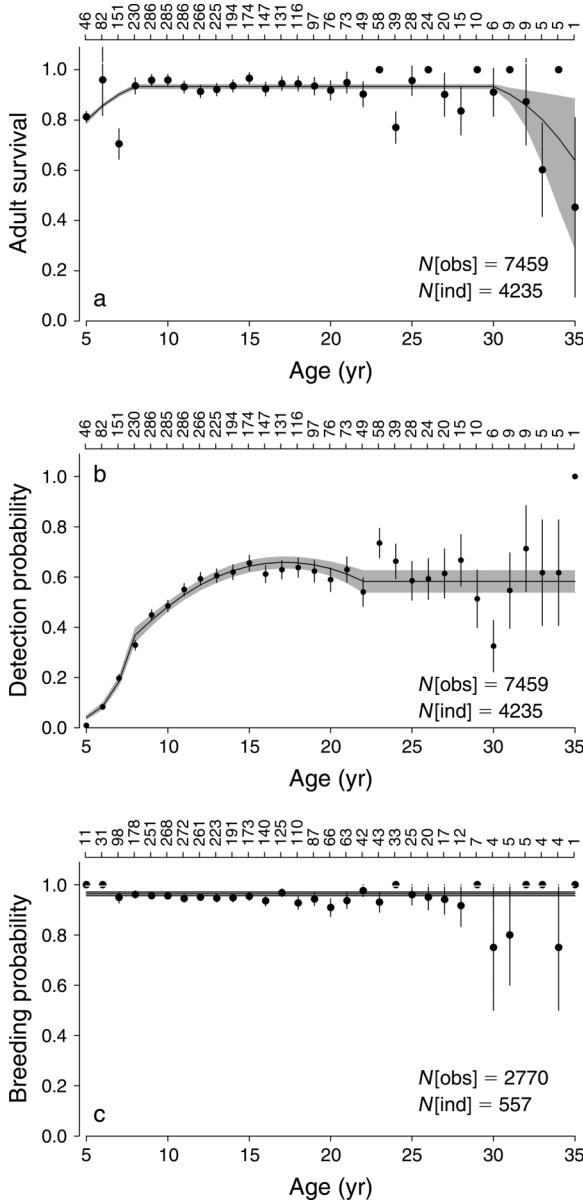


FIG. 2. Relationship between age and the (a) survival probability, (b) detection probability, and (c) breeding probability of Black-browed Albatrosses at Kerguelen (1968–2010). Solid circles correspond to the parameter estimates from model $\phi(\text{age})p(\text{age})$ for survival and detection probability, and from a generalized linear mixed model with full age dependence for reproduction probability. Error bars indicate \pm SE. The solid lines correspond to the best models selected using threshold models by multi-model inference, and the shaded areas represent 95% confidence intervals. $N[\text{obs}]$ and $N[\text{ind}]$ indicate the total number of observations and individuals, respectively, used for each trait. The numbers across the top of each panel represent the number of observations at each age.

strong decrease in the oldest birds. Evidence ratios between the Gompertz, Weibull, and linear functions were very close. However, they all corresponded to a significant decrease in survival in late ages (Fig. 2a,

Table 2), suggesting senescence. We chose to keep the linear function that had the best evidence ratio.

Effects of age on breeding performances

The breeding probability was constant at 5–35 years of age at a rate of 0.964 ± 0.004 (Table 1, Fig. 2c). Multi-model inference suggested a single threshold at 8 (Appendix F); however, the 95% confidence interval on this threshold encompassed all ages, and the slope of the linear phase before 8 was not significant so the constant model was selected.

Two thresholds were more likely to describe age variation in breeding success (Fig. 3a; Appendix G). It strongly increased until age 10, slightly increased until age 26, and then strongly decreased at older ages, suggesting reproductive senescence. The probability of fledging a chick decreased from 0.763 ± 0.027 before 26 years old to only 0.479 ± 0.120 when aged 34 (Table 1).

Two thresholds fit the data better on the stage at failure (Appendix H). Young breeders tended to fail more during incubation, but an increase was noted until 10 years old. For middle-aged individuals, it stabilized at 0.481 ± 0.021 (Fig. 3b), suggesting that individuals were nearly equally likely to fail at the egg or chick stage. At the oldest ages, after 27 years old, there was a significant increase suggesting that old birds failed more during the chick rearing stage (Table 1). A quadratic function was firstly selected on the last phase, but it was heavily influenced by the estimates of ages 30 and 31 that were at boundary. The more parsimonious linear function was thus chosen instead.

For chick body condition, a model with two thresholds best fit the data (Appendix I). However, the 95% confidence intervals of the threshold values of the two-threshold model were very large and overlapped, suggesting over-parameterization. A single threshold model was thus retained. Most models at that point identified a threshold at 23, which followed no biological hypothesis, forcing the last phase to be quadratic. All thresholds at 23 were thus removed, and multi-model inference suggested that chick body condition varied slightly with age until 27, and decreased strongly with age for older birds. Thus, older birds fledged chicks of almost 20% lower condition than chicks from young and middle-aged birds (Fig. 3c, Table 1).

Finally, the culmen length of chicks at fledging was best described by a two-threshold model with three linear phases (Fig. 3d; Appendix J): an increase between ages 6 and 8, an increase between 8 and 27, and a decrease for older individuals. All slopes were significant (Table 1).

Confidence intervals on the threshold values

Confidence intervals for threshold values are summarized in Table 1. They were relatively narrow for the thresholds detected during the first part of the reproductive life. On the contrary, 95% confidence intervals became large for the thresholds detected at later ages.

TABLE 1. Characteristics of the best threshold models selected by multi model inference on seven life-history traits of Black-browed Albatrosses (*Thalassarche melanophris*) at the Kerguelen Islands, Southern Indian Ocean (1968–2010).

Age-dependent trait	Phase 1	Threshold 1	Phase 2	Threshold 2	Phase 3	Age at onset of senescence (yr)	Rate of senescence
Survival probability	linear	8 [7.8, 10.2]	constant	30 [11.9, 34.0]	linear	30	−0.414*
Detection probability	quadratic	9 [8.2, 9.8]	quadratic	23 [11.0, 30.5]	constant	no senescence	...
Breeding probability	constant	no senescence	...
Success probability	linear	10 [9.8, 11.1]	linear	26 [18.4, 33.0]	linear	26	−0.210*
Stage at reproductive failure	linear	10 [8.9, 13.6]	constant	27 [23.2, 30.2]	linear	27	0.355*
Chick body condition	linear	27 [24.8, 30.0]	linear	27	−0.215*
Culmen length of chicks	linear	8 [7.0, 8.7]	linear	27 [23.7, 29.5]	linear	27	−0.638*

Notes: Phases 1, 2, and 3 represent the age categories delimited by the selected thresholds in young, middle-aged, and old individuals, respectively. For each trait, age at threshold is indicated, with its 95% CI in square brackets. The age at onset of senescence stands for the age at which a trait value starts to decrease. The rate of senescence is given by the slope of the relationship between the demographic parameter and age for the last phase. Ellipses (...) indicate that there is no information given the selected threshold model.

* The slope is significant at the 0.05 level.

Parameter- and age-specific temporal variance

As expected, temporal variances were higher in young and old individuals than in middle-aged individuals (Fig. 4). The lowest temporal variance was observed for middle-aged individuals’ survival. The highest temporal variance was observed for old individuals’ survival. For young individuals, the lowest temporal variance was for success probability. For survival and success probabilities, the largest temporal variance was observed for old individuals, and temporal variance was the smallest for survival in middle-aged individuals, whereas it was the opposite for young and old individuals.

Age dependent sensitivity to environmental conditions

For survival, the best age-dependent model selected was used to test the effects of environmental covariates on three age classes (Table 1): young individuals from 5 to 8 years old with a linear age effect (number of observations, $N[\text{obs}] = 509$, number of individuals, $N[\text{ind}] = 355$), middle-aged individuals from 9 to 29 ($N[\text{obs}] = 2599$, $N[\text{ind}] = 571$) with no age effect, and old individuals from 30 to 35 with a linear age effect ($N[\text{obs}] = 35$, $N[\text{ind}] = 16$). Whatever the covariate considered, residual unexplained variation in survival was detected by $LRT_{\text{cov}/t}$ tests (Table 3). Among the seven covariates, only sea surface temperature anomalies in the breeding zone in summer had a significant effect (SSTA_s, ANODEV $F_{3,90} = 4.649$, $P_{\text{Bonf}} = 0.035$). This climatic covariate explained only 12% of the variability in survival over time once age was accounted for. When sea surface temperatures were warmer, young and old individuals survived better, whereas middle-aged individuals survived less (Fig. 5, Table 3). Two particularly warm events that occurred in 1997 and 2002 are visible on Fig. 5.

No environmental covariate had a significant effect on breeding success (Appendix K) or offspring body condition at fledging (Appendix L) of young, middle-aged, or old individuals.

TABLE 2. Results of multi-model inference procedure used to select the best model structure on the survival probability of Black-browed Albatrosses at Kerguelen (1968–2010).

Survival trait model structure	ΣQAIC_c weights	n	Evidence ratio
No. thresholds			
0	0.193	5	2.47
1	0.332	15	1.43
2	0.475	45	1.00
First threshold (age)			
7 years	0.00	8	2.50×10^5
8 years	0.71	36	1.00
9 years	0.10	12	7.07
Second threshold (age)			
23 years	0.00	6	2.43×10^5
24 years	0.00	2	3.58×10^5
28 years	0.02	2	20.27
29 years	0.02	1	20.47
30 years	0.41	29	1.00
Model first phase			
Constant	0.00	21	3.11×10^5
Linear	0.12	21	7.28
Quadratic	0.88	21	1.00
Model second phase			
Constant	0.30	18	1.00
Linear	0.26	18	1.17
Quadratic	0.12	18	2.08
Model third phase			
Constant	0.07	9	1.99
Linear	0.13	9	1.00
Quadratic	0.05	9	2.52
Gompertz	0.11	9	1.20
Weibull	0.12	9	1.08

Notes: The number of models used to obtain the sum of quasi-AIC_c (QAIC_c) weights for a given type of model is indicated by n . Evidence ratios were calculated following Burnham and Anderson (2002) and give an idea of the closeness between two types of models. A negative quadratic model was initially selected on this phase, yet this function was excessively influenced by the first three points and did not possess any biological meaning. First, the number of thresholds was selected, and then the ages at which those thresholds are the most likely to occur, and finally, the best fitting type of function for each phase (Appendix B). Tables corresponding to the other traits are given in Appendices E–J. Models in boldface type indicate mod3el structure selected.

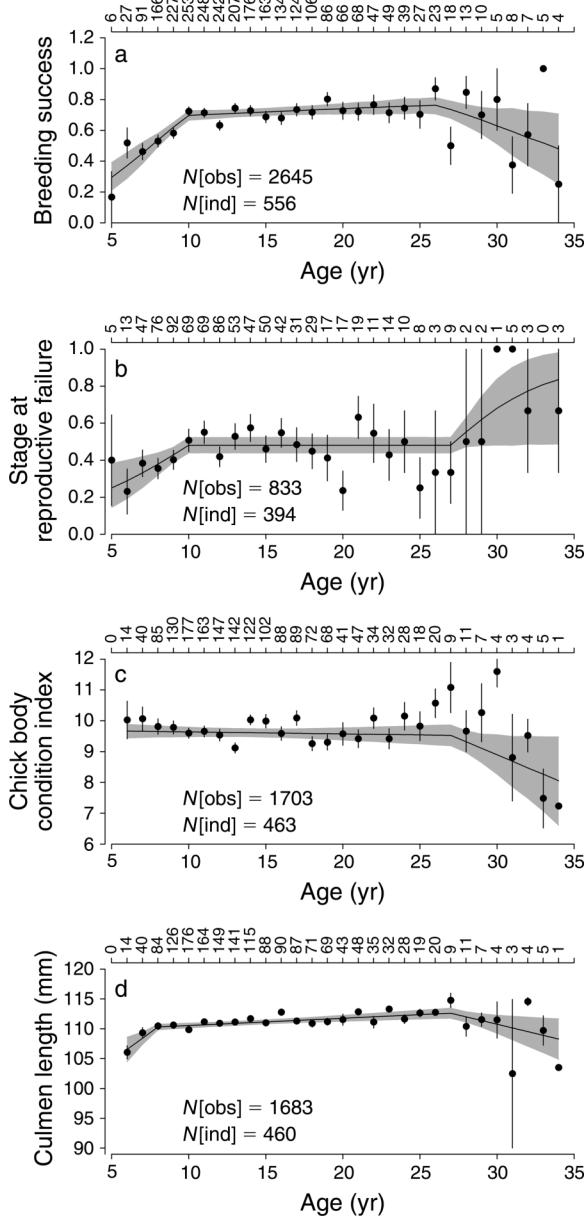


FIG. 3. Relationship between age and the (a) breeding success probability, (b) stage at reproductive failure (0 corresponds to a failure at the egg stage, and 1 corresponds to a failure at the chick stage), (c) chick body condition according to parents' age, and (d) chick culmen length according to parents' age of Black-browed Albatrosses at Kerguelen (1968–2010). Solid circles correspond to the parameter estimates from generalized linear mixed models with full age dependence. Error bars indicate \pm SE. The solid lines correspond to the best models selected using threshold models by multi-model inference, and the shaded areas represent 95% confidence intervals. $N[\text{obs}]$ and $N[\text{ind}]$ indicate, respectively, the total number of observations and individuals used for each trait. The numbers across the top of each panel represent the number of observations at each age.

DISCUSSION

We found evidence for age-related changes in five reproductive traits and in survival in a population of Black-browed Albatrosses. In addition to expected increases with age in most traits at younger ages, there was evidence for reproductive and actuarial senescence. Importantly, environmental variability differentially affected age classes. There was a lower temporal variance of demographic traits in middle-aged individuals, while young and old birds presented higher temporal variance, particularly in survival for old individuals. Furthermore, the survival of birds was differently affected by local climatic conditions during breeding according to their age; the effect being larger for senescent individuals.

Life-history traits at early ages

As predicted by the hypotheses of selection, constraint, and reproductive restraint, and as suggested by previous findings in this species (Angelier et al. 2007b, Nevoux et al. 2007), an increase in several demographic traits was observed at early ages. The multi-trait analysis suggested that the increase in breeding success observed early in life was mainly due to a decrease in failure probability at the egg stage. This and the high body condition of chicks raised by younger parents suggest that young breeding individuals had already acquired good foraging capabilities. These capacities might still be under the ones of older adults given the observed increase in culmen length of chicks. However, young individuals are poor performers for incubating successfully. In most albatrosses, incubation is the stage when most failures occur (Weimerskirch 1992, Catry et al.

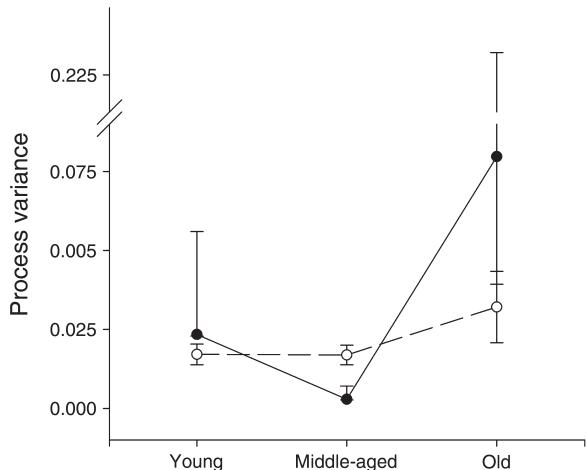


FIG. 4. Temporal variance and 95% confidence intervals of two demographic parameters for young, middle-aged, and old Black-browed Albatrosses at Kerguelen (1968–2010). Adult survival probability (solid dots, solid line) for young (5–8 years), middle-aged (9–29 years), and old (30–35 years) individuals, and breeding success (open dots, dashed lines) for young (5–10 years), middle-aged (11–25 years), and old (26–34 years) individuals.

TABLE 3. Testing for the effects of climatic and fisheries covariates on adult survival probability of Black-browed Albatrosses at Kerguelen (1968–2009).

Model	np	Deviance	p_{Bonf} LRT cov/t	p_{Bonf} LRT cst/cov	p_{Bonf} ANODEV	R^2	Slope youngs (\pm SE)	Slope mid (\pm SE)	Slope old (\pm SE)
General models									
TIME	99	5935.17							
CST	10	6119.21							
CST_SSTA_S	30	6098.38							
CST_SSTA_W	32	6095.27							
CST_Trawl_s	26	6105.63							
Covariate models									
SOI_W	13	6100.57	*	...	0.183	...	-0.282 (0.013)	-0.411 (0.017)	-2.433 (no est.)
SSTA_S	33	6075.61	*	...	0.032	0.124	+0.146 (0.003)	-0.353 (0.009)	+0.873 (0.161)
SSTA_W	35	6085.84	*	...	1.000	...	-0.194 (0.015)	-0.151 (0.032)	-0.020 (1.135)
LL_s	13	6112.12	*	...	1.000	...	-0.046 (0.005)	+0.041 (0.008)	+6.522 (no est.)
IUU_s	13	6106.49	*	...	0.715	...	+0.110 (0.007)	-0.166 (0.007)	+0.416 (0.145)
Trawl_s	29	6088.77	*	...	0.202	...	-0.226 (0.033)	+0.219 (0.078)	+0.844 (0.118)
LL_w	13	6104.60	*	...	0.404	...	+0.196 (0.033)	-0.206 (0.021)	+3.900 (0.207)

Notes: The seven climatic and fisheries covariates used are: SOI_w, Southern Oscillation Index in winter; SSTA_s and SSTA_w, sea surface temperature anomalies in summer and in winter, respectively; LL_s and LL_w, longline fishing effort (in number of hooks deployed) in summer and in winter, respectively; IUU_s, illegal, unreported, and unregulated longline fishing effort (in number of hooks deployed) in summer; and Trawl_s, trawling effort (in number of hours) in summer. TIME and CST correspond to models where survival is time dependent and constant, respectively. Age classes were obtained from the modeling of the effect of age on survival (young, 5–8 years old; middle-aged [mid], 9–29 years old; and old, 30–35 years old). All models had a linear age effect, except in the middle-age class. Likelihood ratio tests (LRT) and analysis of deviance (ANODEV) were computed to test the effects of environmental covariates following Grosbois et al. (2008). Ellipses (...) indicate that the test was not or could not be calculated. R^2 indicates the proportion of variance explained by the covariate. Slopes are given on the logit scale. “No est.” indicates that the SE of slopes could not be calculated due to a lack of data (essentially in old individuals).

* Significant p_{Bonf} (<0.05).

2006). Successful incubation requires synchronization between partners since eggs left alone even for short periods are taken by predators, whereas large chicks can be left unfed for days. Thus, young and inexperienced partners may be less well synchronized during incubation (Weimerskirch 1992).

Interestingly, the observation that survival reaches its maximum value at an earlier age than breeding success suggests that part of the improvement of breeding success was due to ontogenetic development, an average change in performance of the selected survivors, as recently found in the Common Tern *Sterna hirundo* (Rebke et al. 2010). Such a conclusion was also reached by Nevoux et al. (2010a) when studying recruitment in Black-browed Albatrosses. Other studies suggested a combined action of selection of the best performing individuals and a progressive homogenization of seabirds's skills through learning in Black-legged Kittiwakes (*Rissa tridactyla*; Cam and Monnat 2000), Shags (*Phalacrocorax aristotelis*; Daunt et al. 1999), and Herring Gulls (*Larus argentatus*; Greig et al. 1983).

The initial increase in detection probability with age was probably essentially due to the progressive return of the birds to the colony for their first breeding attempt, and not to a lack of detection at early ages. Indeed, in this highly philopatric species, individuals recruit between 5 and 15 years old, and the probability of first breeding increases to 0.53 from age 5 to age 10 (Nevoux et al. 2010a). The constant slope of breeding probability showed that, once they have recruited, birds breed at a very high and constant rate independently of their age.

Multi-trait interpretation of the patterns of senescence

Contrary to our prediction, survival and breeding success did not start to decrease following primiparity. Rather, all traits remained relatively constant for middle-aged individuals and eventually started to decline only at an average age of 27 for breeding traits, and 30 for adult survival. Similarly, the predicted age at onset of senescence for the southern fulmar (*Fulmarus glacialisoides*), was underestimated compared to the one observed (Jones et al. 2008, Berman et al. 2009). Individual heterogeneity can affect the detection of senescence in wild populations (Cam et al. 2002, Péron et al. 2010). In this study we detected actuarial senescence without accounting for this heterogeneity. In a study on the same data set where heterogeneity in survival was explicitly modeled (G. Péron et al., *unpublished manuscript*), results also indicated a decline in survival at older ages and revealed a nonsignificant amount of heterogeneity in age-dependent survival.

Breeding parameters started to decrease, on average, three years before survival. McNamara et al. (2009) formalized the order at which survival and breeding performance should start to decrease by discriminating internal (damage accumulation) and external causes of mortalities in the optimal energy allocation framework. Therefore, contrary to highly polygynous and dimorphic mammal species such as male bighorn sheep (*Ovis canadensis*), for which the damage accumulated with reproduction is very high due to costly mating tactics (Gaillard et al. 2003), old seabirds such as Black-browed Albatrosses might benefit from allocating more to

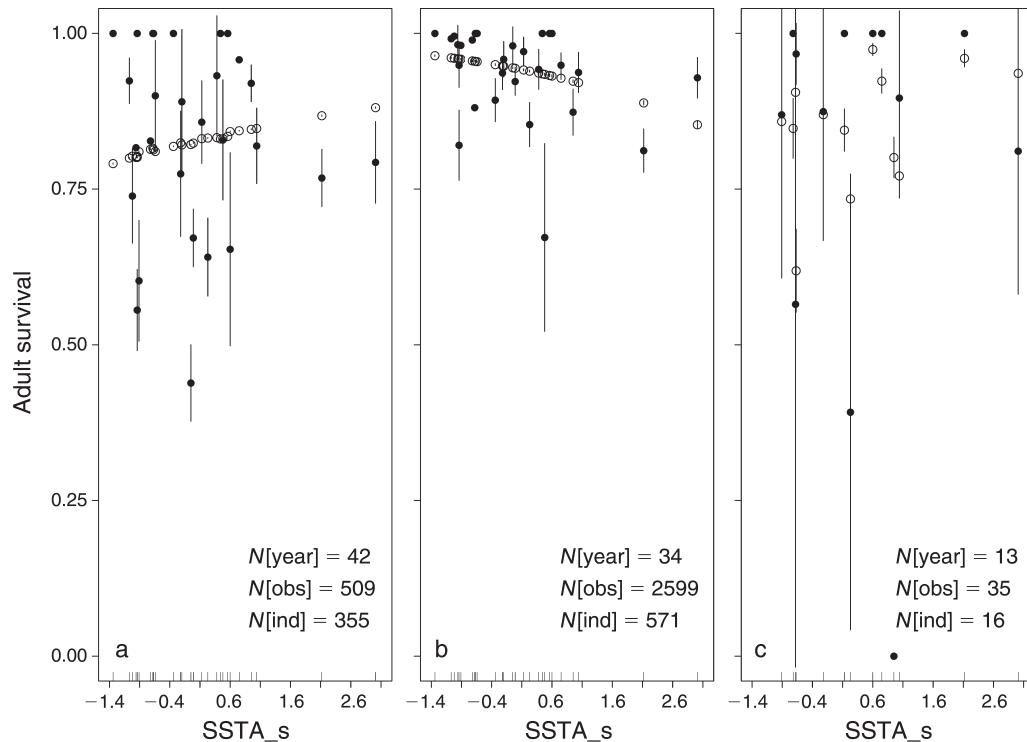


FIG. 5. Relationship between sea surface temperature anomaly in summer ($SSTA_s$) and adult survival of Black-browed Albatrosses at Kerguelen (1982–2009) for (a) young (5–8 years old), (b) middle-aged (9–29 years old), and (c) old (30–35 years old) breeding individuals. Solid circles correspond to parameter estimates from models with survival as a function of time with a linear age effect in young and old age classes. Open circles correspond to parameter estimates from models with survival as a function of sea surface temperature anomaly in summer ($SSTA_s$) with a linear age effect in young and old age classes. The slopes of the relationship between survival and $SSTA_s$ were significant in each age class (see Table 3). Age classes and linear trends were determined following multi-model inference (see *Results*). Error bars indicate $\pm SE$. $N[\text{year}]$, $N[\text{obs}]$, and $N[\text{ind}]$ give the number of years, observations, and individuals, respectively, considered in each age class.

maintenance than reproduction, as demonstrated by the smaller size and body condition of fledglings produced by older birds. However, given the large confidence intervals around the threshold values at old ages, the onsets of senescence should be interpreted cautiously.

Evidence of senescence in breeding success was found in several other species: mammals (Gaillard et al. 2003); fishes (Reznick et al. 2002); and birds (Reid et al. 2003), including several seabird taxa (Velando et al. 2006, Reed et al. 2008, Nisbet and Dann 2009, Lecomte et al. 2010, Rebke et al. 2010). Our multi-trait analysis gave some insights into the underlying demographic and behavioral mechanisms. The poor breeding success of older individuals was primarily due to increased failures after hatching. Since the brooding period is very energy demanding in pelagic birds raising a single chick (Ricklefs 1983), it is highly probable that old birds suffered the most at that time of the breeding period, particularly if their foraging performances were affected. The decreases in chick's body condition and culmen size at fledging raised by old parents suggested lower growth rates for these chicks, and thus, poorer foraging and provisioning performances of older parents (Weimerskirch and Lys 2000). This decline was so important that

it cannot be explained only by potential phenological changes (such as a later laying by older birds as demonstrated in Mute Swans *Cygnus olor* by McCleery et al. [2008]). Indeed, according to specific growth curves (Tickell and Pinder 1975), this decline would represent a difference at laying of approximately three weeks, which is not consistent with the short duration of egg laying in this species. Similar decreases were found in mammals: in grey seals (*Halichoerus grypus*), the weaning mass depended largely on daily milk consumption and duration of suckling (Bowen et al. 2006). Furthermore, since fledging body condition may affect juvenile survival, the fitness of older parents may be further decreased (Naef-Daenzer et al. 2001). Consistently, old Black-browed Albatrosses showed an increase in corticosterone levels during brooding (Angelier et al. 2007b), which is supposed to reflect a degradation of the foraging skills of the oldest individuals (Angelier et al. 2007a). Deficiencies in the foraging capacities of very old individuals have already been detected in closely related species: Wandering Albatrosses *Diomedea exulans* (Lecomte et al. 2010) and Grey-headed Albatrosses *Thalassarche chrysostoma* (Cтры et al. 2006).

Both the probability of being detected if present at the colony and the probability of breeding when detected at the colony did not decline with age. This suggests that it is unlikely that reproductive skipping increased with age in Black-browed Albatrosses.

Age-dependent temporal variance in life-history traits

As expected, the lowest temporal variability was observed in middle-aged individuals, who had the highest survival and breeding success, thus appearing as the least influenced part of the population by environmental factors. Similarly to the findings of Gaillard and Yoccoz (2003) for juvenile ungulates, we found that the variance in survival in young breeding birds was consistently higher than the variance in adult survival. This result suggests that adult survival is canalized against environmental variations or alternatively that juveniles and/or young breeders might just be more sensitive to environmental “insults” (Goodman 1979), given their potentially immature immune system, poorer foraging skills, lack of experience, and energy allocation pattern giving priority to growth over maintenance.

For survival and breeding success, the highest temporal variance was observed for old individuals. These results are coherent with theoretical and empirical findings of declining sensitivities of the population growth rate to survival and fertility with age for stable or increasing populations of long lived species (Caswell 2001:211–213) and may be linked to senescence or accumulated damage over time. Indeed, our results suggest that old individuals suffer from actuarial and reproductive senescence possibly linked to declining foraging capacities. This might enhance their susceptibility to poor environmental conditions, and/or competitiveness during inter- or intraspecific competition events for resources. Also coherent with the findings of Caswell (2001) and the canalization hypothesis, in old individuals the temporal variance in survival was much higher than the temporal variance in breeding success. This is also in accordance with what McNamara et al. (2009) pointed out in the case of senescent long-lived individuals, for which favoring reproduction over survival in late life becomes more valuable for the remaining fitness. Nevertheless, given the small sample sizes of old age classes, a positive bias is expected on temporal variance estimates (results not shown), and variance estimates are imprecise as shown by the large confidence intervals in particular for survival (Fig. 4). Thus, these results for old-aged individuals should be interpreted with caution.

Age-related differential impact of environmental covariates

As previously found in this species, sea surface temperature anomalies in the summer foraging zones affected some demographic parameters (Pinaud and Weimerskirch 2002, Nevoux et al. 2007, Rolland et al.

2008). During warm events, both young and old individuals survived better, whereas middle-aged individuals survived less, although their survival remained higher than for young or old individuals. Additionally, the magnitude of the response of old birds was, respectively, 6 and 2.5 times greater than that of young and middle-aged ones, as indicated by the slopes between survival and SSTA_s. A potential explanation could be that the foraging zones of young and old birds differ from those of middle-aged birds. An alternative explanation could be that, in years of low SSTA_s, the amount of food in the usual foraging zones is reduced, as suggested by the positive relationship between SSTA_s and breeding success (Pinaud and Weimerskirch 2002, Nevoux et al. 2007, Rolland et al. 2008), and that during these years, middle-aged individuals outcompete young and old ones via interference and/or exploitation competition. This was demonstrated in the Soay sheep (*Ovis aries*) by Coulson et al. (2001), who highlighted the particular sensitivity of old individuals to poor weather condition at high densities compared to other more competitive age classes.

Contrarily to previous studies on this population (Pinaud and Weimerskirch 2002, Nevoux et al. 2007, Rolland et al. 2008), we did not find a significant relationship between SSTA_s and breeding success, although the slopes of the relationships between breeding success and SSTA_s followed exactly the same trends as for survival, supporting our previous explanation. Coherent with our findings on temporal variance, older individuals were more intensively affected by variations in SSTA_s than younger ones. Diverse reasons could explain this lack of significance. First, by considering the age effects, we built more complex models with an inevitable associated loss of statistical power. Second, we used a data set with a much longer time period than previous studies. Third, the geographical zone selected around Kerguelen in summer was different as well, due to a better knowledge of the foraging zones used by albatrosses and to a displacement of foraging zones toward more southern waters observed in the past five years (H. Weimerskirch, *unpublished data*). Finally, we used the Bonferroni correction, which is very conservative; therefore, only very strong relationships remained significant.

Again, these results and conclusions for old individuals must be taken carefully given the small sample size of old individuals from which the regressions were done, although this is inherent to all studies on senescence in wild populations.

CONCLUSION

A multi-trait approach covering an array of seven life-history traits that presented age-dependent variations allowed a better understanding of complex age–environment linkages. Inferences could be drawn on both the phase of improving performances of young breeders and the decreases in capacities associated to old age.

Middle-aged birds' traits appeared canalized against environmental variations, and environmental variations had a lower impact on middle-aged than on young and old individuals that appeared less robust when facing poor environmental conditions probably due to their respective inexperience and senescence. This suggests that age, known as a major factor structuring the demography in long-lived species, can also potentially influence the response of populations to global changes. The next step will be to quantify, using matrix population models, the contribution of each age class to the population growth rate on a gradient of environmental quality.

ACKNOWLEDGMENTS

We are very grateful to all the field workers involved in the monitoring program over the past 40 years on the Black-browed Albatross at Canyon des Sourcils Noirs. We thank Dominique Besson and Karine Delord for data management, and Guy Duhamel and Patrice Pruvost for providing fishing effort data in the French EEZ. We thank Christophe Bonenfant, Virginie Rolland, Vincent Lecomte, Nigel Yoccoz, and the "Comparative Evolutionary Demography" French working group for fruitful statistical and bibliographical help. We thank Dan Nussey and three anonymous reviewers for useful comments to improve the manuscript. The work carried out at Kerguelen was supported by the Institut Paul Emile Victor (IPEV program number 109), Terres Australes et Antarctiques Françaises, Zone Atelier de Recherches sur l'Environnement Antarctique et Subantarctique (CNRS-INEE) and has been approved by the ethics committee of IPEV and by the Comité de l'Environnement Polaire. Deborah Pardo was supported by a grant from CNRS-INEE.

LITERATURE CITED

- Angelier, F., S. A. Shaffer, H. Weimerskirch, C. Trouvé, and O. Chastel. 2007a. Corticosterone and foraging behavior in a pelagic seabird. *Physiological and Biochemical Zoology* 80:283–292.
- Angelier, F., H. Weimerskirch, S. Dano, and O. Chastel. 2007b. Age, experience and reproductive performance in a long-lived bird: a hormonal perspective. *Behavioral Ecology and Sociobiology* 61:611–621.
- Barbraud, C., and H. Weimerskirch. 2005. Environmental conditions and breeding experience affect costs of reproduction in blue petrels. *Ecology* 86:682–692.
- Bates, D., and M. Maechler. 2010. Package lme4: Linear mixed effects models using S4 classes. R Foundation for Statistical Computing, Vienna, Austria.
- Berman, M., J. M. Gaillard, and H. Weimerskirch. 2009. Contrasted patterns of age-specific reproduction in long-lived seabirds. *Proceedings of the Royal Society B* 276:375–382.
- Borrego, N., A. Ozgul, K. B. Armitage, D. T. Blumstein, and M. K. Oli. 2008. Spatiotemporal variation in survival of male yellow-bellied marmots. *Journal of Mammalogy* 89:365–373.
- Bowen, W. D., S. J. Iverson, J. I. McMillan, and D. J. Boness. 2006. Reproductive performance in grey seals: age-related improvement and senescence in a capital breeder. *Journal of Animal Ecology* 75:1340–1351.
- Bunce, A., S. J. Ward, and F. I. Norman. 2005. Are age related variations in breeding performance greatest when food availability is limited? *Journal of Zoology* 266:163–169.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and Multi-Model Inference, a practical information-theoretic approach. Springer, New York, New York, USA.
- Cam, E., W. A. Link, E. G. Cooch, J. Y. Monnat, and E. Danchin. 2002. Individual covariation in life-history traits: Seeing the trees despite the forest. *American Naturalist* 159:96–105.
- Cam, E., and J. Y. Monnat. 2000. Apparent inferiority of first-time breeders in the kittiwake: the role of heterogeneity among age classes. *Journal of Animal Ecology* 69:380–394.
- Caswell, H. 2001. Matrix population models: construction, analysis and interpretation. Second edition. Sinauer Associates, Sunderland, Massachusetts, USA.
- Catry, P., R. A. Phillips, B. Phalan, and J. P. Croxall. 2006. Senescence effects in an extremely long-lived bird: the grey-headed albatross *Thalassarche chrysostoma*. *Proceedings of the Royal Society B* 273:1625–1630.
- Charlesworth, B. 1980. The evolution in age-structured populations. Cambridge University Press, Cambridge, UK.
- Cherel, Y., H. Weimerskirch, and C. Trouve. 2000. Food and feeding ecology of the neritic-slope forager black-browed albatross and its relationships with commercial fisheries in Kerguelen waters. *Marine Ecology-Progress Series* 207:183–199.
- Coulson, T., E. A. Catchpole, S. D. Albon, B. J. T. Morgan, J. M. Pemberton, T. H. Clutton-Brock, M. J. Crawley, and B. T. Grenfell. 2001. Age, sex, density, winter weather, and population crashes in Soay sheep. *Science* 292:1528.
- Curio, E. 1983. Why do young birds reproduce less well? *Ibis* 125:400–404.
- Daunt, F., S. Wanless, M. P. Harris, and P. Monaghan. 1999. Experimental evidence that age-specific reproductive success is independent of environmental effects. *Proceedings of the Royal Society of London B* 266:1489–1493.
- Doherty, P. F., Jr., E. A. Schreiber, J. D. Nichols, J. E. Hines, W. A. Link, G. A. Schenk, and R. W. Schreiber. 2004. Testing life-history predictions in a long lived seabird: a population matrix approach with improved parameter estimation. *Oikos* 105:606–618.
- Gaillard, J. M., M. Festa-Bianchet, and N. G. Yoccoz. 1998. Population dynamics of large herbivores: variable recruitment with constant adult survival. *Trends in Ecology and Evolution* 13:58–63.
- Gaillard, J. M., A. Loison, M. Festa-Bianchet, N. G. Yoccoz, and E. Solberg. 2003. Ecological correlates of life span in populations of large herbivorous mammals. *Population and Development Review* 29:39–56.
- Gaillard, J. M., and N. G. Yoccoz. 2003. Temporal variation in survival of mammals: A case of environmental canalization? *Ecology* 84:3294–3306.
- Gales, R., N. Brothers, and T. Reid. 1998. Seabird mortality in the Japanese tuna longline fishery around Australia, 1988–1995. *Biological Conservation* 86:37–56.
- Goodman, D. 1979. Regulating reproductive effort in a changing environment. *American Naturalist* 113:735–748.
- Gould, W. R., and J. D. Nichols. 1998. Estimation of temporal variability of survival in animal populations. *Ecology* 79:2531–2538.
- Greig, S. A., J. C. Coulson, and P. Monaghan. 1983. Age-related differences in foraging success in the Herring gull (*Larus argentatus*). *Animal Behavior* 31:1237–1243.
- Grosbois, V., O. Gimenez, J. M. Gaillard, R. Pradel, C. Barbraud, J. Clobert, A. P. Moller, and H. Weimerskirch. 2008. Assessing the impact of climate variation on survival in vertebrate populations. *Biological Reviews* 83:357–399.
- Hamilton, W. D. 1966. The moulding of senescence by natural selection. *Journal of Theoretical Biology* 12:12–45.
- Jones, O. R., et al. 2008. Senescence rates are determined by ranking on the fast-slow life-history continuum. *Ecology Letters* 11:664–673.
- Laaksonen, T., E. Korpimäki, and H. Hakkarainen. 2002. Interactive effects of parental age and environmental variation on the breeding performance of Tengmalm's owls. *Journal of Animal Ecology* 71:23–31.
- Lecomte, V. J., G. Sorci, S. Cornet, A. Jaeger, B. Faivre, E. Arnoux, M. Gaillard, C. B. D. Trouvé, O. Chastel, and H. Weimerskirch. 2010. Patterns of aging in the long-lived

- wandering albatross. *Proceedings of the National Academy of Sciences USA* 107:6370–6375.
- Lewis, S., D. A. Elston, F. Daunt, B. Cheney, and P. M. Thompson. 2009. Effects of extrinsic and intrinsic factors on breeding success in a long lived seabird. *Oikos* 118:521–528.
- McCleery, R. H., C. M. Perrins, B. C. Sheldon, and A. Charmantier. 2008. Age-specific reproduction in a long-lived species: the combined effects of senescence and individual quality. *Proceedings of the Royal Society B* 275:963–970.
- McNamara, J. M., A. I. Houston, Z. Barta, A. Scheuerlein, and L. Fromhage. 2009. Deterioration, death and the evolution of reproductive restraint in late life. *Proceedings of the Royal Society B* 276:4061–4066.
- Monaghan, P., A. Charmantier, D. H. Nussey, and R. E. Ricklefs. 2008. The evolutionary ecology of senescence. *Functional Ecology* 22:371–378.
- Naef-Daenzer, B., F. Widmer, and M. Nuber. 2001. Differential post-fledging survival of great and coal tits in relation to their condition and fledging date. *Journal of Animal Ecology* 70:730–738.
- Nevoux, M., J. Forcada, C. Barbraud, J. Croxall, and H. Weimerskirch. 2010a. Bet-hedging response to environmental variability, an intraspecific comparison. *Ecology* 91:2416–2427.
- Nevoux, M., H. Weimerskirch, and C. Barbraud. 2007. Environmental variation and experience-related differences in the demography of the long-lived black-browed albatross. *Journal of Animal Ecology* 76:159–167.
- Nevoux, M., H. Weimerskirch, and C. Barbraud. 2010b. Long and short-term influence of environment on recruitment in a species with highly delayed maturity. *Oecologia* 162:383–392.
- Nisbet, I. C. T., and P. Dann. 2009. Reproductive performance of little penguins *Eudyptula minor* in relation to year, age, pair bond duration, breeding date and individual quality. *Journal of Avian Biology* 40:296–308.
- Nur, N. 1984. The consequences of brood size for breeding blue tits I. Adult survival, weight change and the cost of reproduction. *Journal of Animal Ecology* 53:479–496.
- Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics* 37:637–669.
- Péron, G., P. A. Crochet, R. Choquet, R. Pradel, J. D. Lebreton, and O. Gimenez. 2010. Capture-recapture models with heterogeneity to study survival senescence in the wild. *Oikos* 119:524–532.
- Pinaud, D., and H. Weimerskirch. 2002. Ultimate and proximate factors affecting the breeding performance of a marine top-predator. *Oikos* 99:141–150.
- R Development Core Team. 2012. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Rebke, M., T. Coulson, P. H. Becker, and J. W. Vaupel. 2010. Reproductive improvement and senescence in a long-lived bird. *Proceedings of the National Academy of Sciences USA* 107:7841–7846.
- Reed, T. E., L. E. B. Kruuk, S. Wanless, M. Frederiksen, E. J. A. Cunningham, and M. P. Harris. 2008. Reproductive senescence in a long-lived seabird: rates of decline in late-life performance are associated with varying costs of early reproduction. *American Naturalist* 171:89–101.
- Reid, J. M., E. M. Signal, S. Signal, D. I. McCracken, and P. Monaghan. 2003. Age-specific reproductive performance in red-billed choughs *Pyrhcorax pyrrhcorax*: patterns and processes in a natural population. *Journal of Animal Ecology* 72:765–776.
- Reznick, D., C. Ghalambor, and L. Nunney. 2002. The evolution of senescence in fish. *Mechanisms of Aging and Development* 123:773–789.
- Ricklefs, R. E. 1983. Some considerations on the reproductive energetics of pelagic seabirds. *Studies of Avian Biology* 8:84–94.
- Rolland, V., C. Barbraud, and H. Weimerskirch. 2008. Combined effects of fisheries and climate on a migratory long-lived marine predator. *Journal of Applied Ecology* 45:4–13.
- Rolland, V., M. Nevoux, C. Barbraud, and H. Weimerskirch. 2009. Respective impact of climate and fisheries on the growth of an albatross population. *Ecological Applications* 19:1336–1346.
- Sæther, B.-E., and O. Bakke. 2000. Avian life-history variation and contribution of demographic traits to the population growth rate. *Ecology* 81:642–653.
- Stearns, S. C. 1989. Trade-offs in life-history evolution. *Functional Ecology* 3:259–268.
- Tickell, W. L. N., and R. Pinder. 1975. Breeding biology of the black-browed albatross *Diomedea melanophris* and grey-headed albatross *D. chrysostoma* at Bird Island, South Georgia. *Ibis* 117:433–452.
- Velando, A., H. Drummond, and R. Torres. 2006. Senescent birds redouble reproductive effort when ill: confirmation of the terminal investment hypothesis. *Proceedings of the Royal Society B* 273:1443.
- Viallefont, A., E. G. Cooch, and F. Cooke. 1995. Estimation of trade-offs with capture-recapture models: A case study on the lesser snow goose. *Journal of Applied Statistics* 22:847–861.
- Weimerskirch, H. 1992. Reproductive effort in long-lived birds: age-specific patterns of condition, reproduction and survival in the wandering albatross. *Oikos* 64:464–473.
- Weimerskirch, H., D. Capdeville, and G. Duhamel. 2000. Factors affecting the number and mortality of seabirds attending trawlers and long-liners in the Kerguelen area. *Polar Biology* 23:236–249.
- Weimerskirch, H., and P. Lys. 2000. Seasonal changes in the provisioning behaviour and mass of male and female wandering albatrosses in relation to the growth of their chick. *Polar Biology* 23:733–744.
- Weladji, R. B., O. Holland, J. M. Gaillard, N. G. Yoccoz, A. Mysterud, M. Nieminen, and N. C. Stenseth. 2010. Age-specific changes in different components of reproductive output in female reindeer: terminal allocation or senescence? *Oecologia* 162:261–271.
- Western, D. 1992. The biodiversity crisis: a challenge for biology. *Oikos* 29–38.
- White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* 46:120–139.
- Williams, G. C. 1966. Natural selection, the costs of reproduction, and a refinement of Lack's principle. *American Naturalist* 100:687.

SUPPLEMENTAL MATERIAL

Appendix A

Modeling the effect of age at first breeding ([Ecological Archives E094-017-A1](#)).

Appendix B

Description of the threshold methodology used to identify ageing patterns in all life-history traits and of the model selection procedure ([Ecological Archives E094-017-A2](#)).

Appendix C

Estimating age-specific temporal variances (*Ecological Archives* E094-017-A3).

Appendix D

Description of the seven climatic and fisheries covariates used to test for a differential impact of environmental variations with age (*Ecological Archives* E094-017-A4).

Appendix E

Results of the multi-model inference procedure for detection probability of Black-browed Albatrosses at Kerguelen from 1968 to 2010 (*Ecological Archives* E094-017-A5).

Appendix F

Results of the multi-model inference procedure for breeding probability of Black-browed Albatrosses at Kerguelen from 1968 to 2010 (*Ecological Archives* E094-017-A6).

Appendix G

Results of the multi-model inference procedure used to select the best model structure on breeding success probability of Black-browed Albatrosses at Kerguelen from 1968 to 2010 (*Ecological Archives* E094-017-A7).

Appendix H

Results of the multi-model inference procedure used to select the best model structure on stage at reproductive failure of Black-browed Albatrosses at Kerguelen from 1968 to 2010 (*Ecological Archives* E094-017-A8).

Appendix I

Results of the multi-model inference procedure used to select the best model structure on chick body condition at fledging of Black-browed Albatrosses at Kerguelen from 1968 to 2010 (*Ecological Archives* E094-017-A9).

Appendix J

Results of the multi-model inference procedure used to select the best model structure on culmen length of chicks of Black-browed Albatrosses at Kerguelen from 1968 to 2010 (*Ecological Archives* E094-017-A10).

Appendix K

Testing for the effects of climatic and fisheries covariates on breeding success of Black-browed Albatrosses at Kerguelen from 1968 to 2009 (*Ecological Archives* E094-017-A11).

Appendix L

Testing for the effects of climatic and fisheries covariates on chick body condition at the fledging of Black-browed Albatrosses at Kerguelen from 1968 to 2009 (*Ecological Archives* E094-017-A12).