

Bet-hedging response to environmental variability, an intraspecific comparison

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Abstract. A major challenge in ecology is to understand the impact of increased environmental variability on populations and ecosystems. To maximize their fitness in a variable environment, life history theory states that individuals should favor a bet-hedging strategy, involving a reduction of annual breeding performance and an increase in adult survival so that reproduction can be attempted over more years. As a result, evolution toward longer life span is expected to reduce the deleterious effects of extra variability on population growth, and consequently on the trait contributing the most to it (e.g., adult survival in long-lived species). To investigate this, we compared the life histories of two Black-browed Albatross (*Thalassarche melanophrys*) populations breeding at South Georgia (Atlantic Ocean) and Kerguelen (Indian Ocean), the former in an environment nearly three times more variable climatically (e.g., in sea surface temperature) than the latter. As predicted, individuals from South Georgia (in the more variable environment) showed significantly higher annual adult survival (0.959, SE = 0.003) but lower annual reproductive success (0.285 chick per pair, SE = 0.039) than birds from Kerguelen (survival = 0.925, SE = 0.004; breeding success = 0.694, SE = 0.027). In both populations, climatic conditions affected the breeding success and the survival of inexperienced breeders, whereas the survival of experienced breeders was unaffected. The strength of the climatic impact on survival of inexperienced breeders was very similar between the two populations, but the effect on breeding success was positively related to environmental variability. These results provide rare and compelling evidence to support bet-hedging underlying changes in life history traits as an adaptive response to environmental variability.

Key words: bet-hedging strategy; Black-browed Albatross; environmental variability; evolutionary strategy; life history traits.

INTRODUCTION

In the context of global climate change, studies have shown that climatic conditions affect the dynamics of many populations (Hughes 2000, Stenseth et al. 2002, Walther et al. 2002, Root et al. 2003, Parmesan 2006, Sandvik and Erikstad 2008). In large vertebrates, the observed effects of climate changes have been mainly attributed to changes in the abundance, quality or predictability of food resources, rather than to direct impacts of temperature or precipitation (Harrington et al. 1999, Durant et al. 2007, Sandvik and Erikstad 2008). Climatic scenarios predict an increase of environmental variability as a result of more frequent extreme climatic events (IPCC 2007, Scientific Committee on Antarctic

Research 2009). A major challenge in ecology is thus to accurately predict the impact of such increased variability on populations (Drake 2005, Boyce et al. 2006). More variability would correspond to a higher probability of individuals encountering poor resource conditions in a given year, resulting in a lower probability of successful reproduction and survival. Life history theory holds that in the face of such annual resource variability, organisms should shift from semelparous to iteroparous reproductive patterns (Murphy 1968, Bulmer 1985, Orzack and Tuljapurkar 1989); and furthermore, under certain circumstances they should evolve a longer lifespan and reduced annual reproduction (bet-hedging; Stearns 1976, Gillespie 1977, Roff 2002). By this theory, bet-hedging evolves to reduce the probability of investing too much in reproduction during resource-poor years, which may ultimately result in null fitness. However, for logistical reasons, the theoretical prediction that environmental variability will lead to the evolution of longer life span (Murphy 1968, Roff 2002) has rarely been tested or detected in wild populations (Roff 2002). Such analysis requires comparing populations with similar ecological requirements living in

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environments of consistently different variability, over a period long enough to quantify the impact of the environment on relevant life history traits. As a consequence ecologists have limited understanding of the relevance of bet-hedging under natural conditions and of the ways in which it operates.

We investigated this bet-hedging theory using unique information from two populations of Black-browed Albatross (*Thalassarche melanophrys*, Temminck), a seabird widely distributed in the Southern Ocean, breeding respectively at South Georgia (Atlantic Ocean) and Kerguelen (Indian Ocean). Both populations have been intensively monitored over the last 25 years, but the environments in which they forage while breeding are substantially and consistently different. South Georgia is characterized by highly variable oceanographic conditions partly due to large-scale climatic processes such as the El Niño oscillation (Trathan and Murphy 2003, Murphy et al. 2007) and the Southern Annular Mode (Forcada and Trathan 2009). Consumers in the marine ecosystem around South Georgia depend extensively upon Antarctic krill (*Euphausia superba*), which varies greatly in abundance from year to year (Croxall 2006, Murphy et al. 2007, Quetin et al. 2007); low krill abundance is known to cause high reproductive failure in top predators (Reid and Croxall 2001, Forcada et al. 2008). At Kerguelen, Black-browed Albatrosses do not rely on krill, but on a fish community which is temporally less variable (Cherel et al. 2000b). The aims of this study were to use these long-term albatross data to test whether populations living in environments with contrasted variability showed differences in their life histories and in their ability to face climatic constraints, and to investigate the potential role of bet-hedging in the adaptive responses involved. To address this we (1) analyzed the long-term data sets from South Georgia and Kerguelen within a single capture–mark–recapture framework to compare inter-population adult survival and breeding success; (2) added climatic indices in models to characterize some of the observed variance in life history traits to investigate the potential role of bet-hedging in the response to the environment. In long-lived species, adult survival is assumed to be the trait that is most strongly related to population growth rate (Stearns and Kawecki 1994, Pfister 1998, Gaillard and Yoccoz 2003, Grether 2005). As a result, the impact of climatic fluctuations on adult survival is expected to be comparable in the two populations, while the impact on breeding success is thought to be related to the variability of the local environment. And (3), we examined whether some components of the population (e.g., inexperienced vs. experienced breeders) were more sensitive than others to environment variation, according to their contribution to population growth. We predict that if differences in life history traits truly result from an evolutionary response to variable environments: (1) adult survival should be higher at South Georgia than at Kerguelen, in response to a more variable

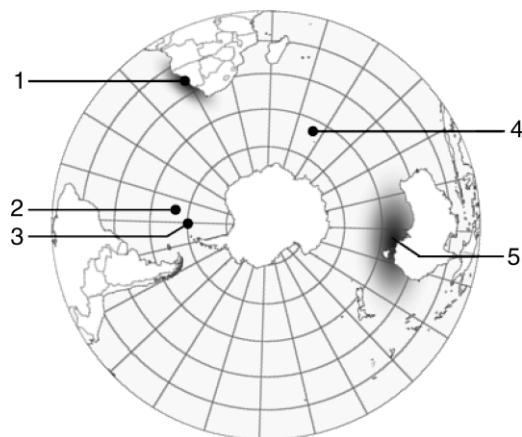


FIG. 1. The Southern Ocean, situation of the main foraging grounds of the Black-browed Albatross populations from South Georgia and Kerguelen during the breeding season (2, 3, 4) and the non-breeding season (1, 5), respectively: 1, Benguela, Angola; 2, South Georgia; 3, South Orkneys; 4, Kerguelen; and 5, Australia.

environment; (2) the demographic impact of climatic fluctuations, i.e., the strength of the relationship between adult survival and climate variables, should not differ between the two populations; and (3) impacts of climate on breeding success should differ between the two populations, in response to the level of variability in their respective local environments.

METHODS

Study species, site, and data collection

The Black-browed Albatross is a large procellariiform seabird inhabiting the Southern Ocean (see Plate 1). During the austral summer, it breeds in dense colonies on some sub-Antarctic Islands, laying one egg each year (Marchant and Higgins 1990). In this study, we compared two populations breeding respectively at Bird Island, South Georgia and at Cañon des Sourcils Noirs, Kerguelen archipelago (see Fig. 1). During the breeding season the population from Bird Island is highly dependent on Antarctic krill (Prince 1980, Veit and Prince 1997, Xavier et al. 2003). Foraging zones are generally concentrated around South Georgia and the South Orkney Islands, but the areas used appear highly variable from one year to another in relation to krill availability (Veit and Prince 1997). During the non-breeding season, most (80%) individuals migrate to the Benguela Current, off the west coast of southern Africa (Phillips et al. 2005). When breeding, birds from the Kerguelen population consistently forage over the northeast and southeast parts of the Kerguelen shelf (Weimerskirch et al. 1997, Pinaud and Weimerskirch 2002), feeding mainly on fish and squid (Cherel et al. 2000b). During winter, band recoveries (Weimerskirch et al. 1985), stable-isotope analyses (Cherel et al. 2000a), and geolocation studies (H. Weimerskirch, unpublished data) reveal that this population migrates mainly to

TABLE 1. Variables used in this study to model survival, transition, and breeding success probabilities in the Black-browed Albatross.

Variable name	Type	Variable level	Description
POP	two groups	POP _{ker} POP _{sg}	individuals breeding at Cañon des Sourcils Noirs, Kerguelen population individuals breeding at Bird Island, South Georgia population
ST	two groups	ST _{ka} ST _{ua}	known-aged individuals, ringed as chicks unknown-aged individuals, ringed as adults
REPRO	three states	REPRO _{nb} REPRO _{fb} REPRO _{sb}	non-breeding individuals, who have bred previously at least once but deferred breeding at the present occasion breeding individuals who failed to produce a fledgling breeding individuals who produced a fledgling
EXP	two age classes	EXP _{in} EXP _{exp}	inexperienced individuals, breeding for the first time experienced individuals, breeding at least for the second time
<i>T</i>	continuous	<i>T_i</i>	temporal variability

waters off southern Australia. The data analyzed in this study came from the long-term monitoring of the two Black-browed Albatross colonies at Bird Island and Cañon des Sourcils Noirs. Similar field protocols resulted in highly comparable data sets. Each summer, all chicks as well as all new adults found in the study colonies were banded with uniquely numbered stainless steel rings, all breeding pairs were recaptured on nests during the breeding season and their breeding success recorded (Prince et al. 1994, Weimerskirch and Jouventin 1997).

Estimation of demographic parameters

The estimation of the demographic parameters was based on the combined capture histories of breeding individuals from the two populations for the seasons 1979–1980 to 2004–2005 (thereafter named 1980 to 2005). This involves 2615 individuals over 25 time intervals (1461 individuals from Bird Island and 1154 from Cañon des Sourcils Noirs). Adult survival and transition probabilities of birds in different reproductive states were estimated under a multistate capture–mark–recapture (CMR) framework (Lebreton and Pradel 2002) using the M-Surge software (Choquet et al. 2004). These parameters were modeled according to the following: the population (POP), to allow interpopulation comparisons between South Georgia and Kerguelen; the age status (ST), where known-aged birds (banded as chicks) were distinguished from unknown-aged individuals (banded as adults); the individual reproductive state at each encounter occasion (REPRO), to differentiate adult nonbreeders, failed breeders, and successful breeders; the breeding experience (EXP), to distinguish inexperienced breeders (the first capture occasion of a known-aged individual was considered as the first breeding attempt of that individual) from experienced breeders (reproducing at least for the second time); and the temporal variability (*T*). The variables listed above are detailed in Table 1. By combining the reproductive states with the experience category, we obtained a life cycle with five breeding stages, as described in Fig. 2. The first capture occasion was excluded from the unknown-aged group in order to

focus only on experienced birds that bred for at least the second time. These unknown-aged individuals of the data set were included into the model to improve the robustness of estimates involving experienced breeders. We considered as an umbrella model the general Arnason-Schwarz (AS) model: $p(\text{POP} \times \text{ST} \times \text{REPRO} \times T)$, $\Phi(\text{POP} \times \text{ST} \times \text{REPRO} \times T)$, $\Psi^{i,j}(\text{POP} \times \text{ST} \times \text{REPRO} \times T)$, where probabilities of recapture (p), survival (Φ) and transition from reproductive states i to j ($\Psi^{i,j}$) varied according to population, age status, reproductive state, time, and the interaction between these variables. The goodness-of-fit (GOF) of this initial model was tested using the methods of Pradel et al. (2003), as implemented in the U-Care software (Choquet et al. 2003). The breeding success (BS), defined as the probability to produce a fledgling, was modeled as a generalized linear model with a binomial distribution of errors, using the statistical software R (R Development Core Team 2004). Our umbrella model: BS (POP \times EXP \times T), expressed the probability to breed successfully as a function of the population, the breeding experience, the time, and their interactions.

The selection procedure used in this analysis was based on the information theoretic approach and consisted in the progressive simplification of the umbrella model to select the most appropriate model to describe the data, using the Akaike's information criterion (AIC_c; Burnham and Anderson 1998). The lower the AIC_c, the better the fit of the model, with two models assumed to be not different from each other to explain the processes that generated the data when the difference in their AIC_c (ΔAIC_c) is less than 2. The effect of EXP was not included in the umbrella CMR model and was tested later for each parameter on a simplified version of the model. Note that by definition nonbreeders (REPRO_{nb}) are experienced individuals (Fig. 2) and the combination REPRO_{nb} \times EXP_{1r} was fixed to zero in all models. Once the best time-dependent model has been identified, we wanted to examine the effects of environmental variability on survival and breeding success probabilities for each population. The data set was split in two to perform analyses separately on the two colonies to reduce computing time. For each colony,

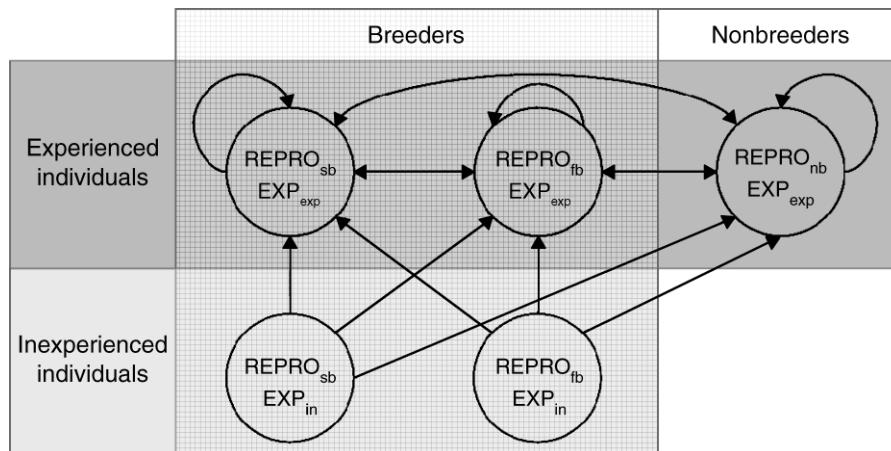


FIG. 2. Representation of the adult life cycle of the Black-browed Albatross used to build mark–recapture models. Reproductive states are: $REPRO_{nb}$, nonbreeders; $REPRO_{fb}$, failed breeders; $REPRO_{sb}$, successful breeders. Experience classes are: EXP_{in} , inexperienced breeders; EXP_{exp} , experienced breeders (>1 reproductive event).

we built a model exactly derived from the best time-dependent model in which we included one climatic variable at a time, following Grosbois et al. (2008). In these wild populations where survival is most likely influenced by multiple factors, the statistical support for the effect of climatic variables on demographic traits was measured using the null hypothesis testing approach derived from fixed effect models, as recommended by Grosbois et al. (2008). The slopes of the relationships between climate and life history traits are presented with their 95% confidence interval to provide an indication of effect size.

Climatic covariates

We fitted models with covariates to assess the part of the interannual variability in adult survival and breeding success explained by climatic indices as proxies of the environmental variability. We used standardized indices to allow comparisons between different indices and populations. The climatic indices were selected according to the annual distribution of both populations, as illustrated in Fig. 3. The global Southern Oscillation Index (SOI), associated with El Niño/La Niña effects (National Oceanic and Atmospheric Administration; *available online*),⁵ has been shown to interact with adult survival at the Kerguelen population (Nevoux et al. 2007), and is correlated with variability in the South Georgia ecosystem (Forcada et al. 2005). We used sea surface temperature (SST) to characterize the oceanographic environment of the main foraging grounds at a smaller spatial scale (Reynolds and Smith 1994, Integrated Global Ocean Services System, *available online*).⁶ In accordance with the summer distribution of breeding Black-browed Albatrosses from South

Georgia, we selected two areas: one corresponding to offshore waters of South Georgia (SST_{sg}); the other being waters around the South Orkney Islands (SST_{so}) (Phillips et al. 2004). For the winter period, we selected the region of the Benguela Current upwelling along the coast of Namibia (SST_{beng}), where most South Georgia birds are known to overwinter (Phillips et al. 2005). For the Kerguelen population, we chose a sector over the Kerguelen shelf (SST_{ker}), which is a main foraging area during summer (Weimerskirch et al. 1997, Pinaud and Weimerskirch 2002), as well as a larger region south of Australia that represents the winter distribution of this population (SST_{aus}) (Weimerskirch et al. 1985; H. Weimerskirch, *unpublished data*). We averaged and standardized monthly values of each variable over three periods, in relation to the annual life cycle of Albatrosses: October to January for incubation, February to May for chick rearing and fledging period, and June to September for the non-breeding period. Lagged effects of up to one year were also considered, as climatic conditions may potentially affect the environmental conditions (food resources; Forcada et al. 2005) experienced by the birds several months later.

RESULTS

Goodness of fit test

The GOF test indicated a poor fit of the umbrella AS model ($\chi^2 = 2449.95$, $df = 1280$, $P < 0.001$) mostly for the population of South Georgia (South Georgia: $\chi^2 = 1842.71$, $df = 652$, $P < 0.001$; Kerguelen: $\chi^2 = 607.24$, $df = 628$, $P = 0.967$). Transience was nonsignificant (test 3G), but we observed a strong trap-dependent effect (test M) as well as nonrandom transitions between states (test WBWA) in all groups. The most common breeding states were failed breeders for South Georgia, and successful breeders for Kerguelen. The test statistic values produced a variance inflation factor of 1.914

⁵ <http://www.cpc.noaa.gov/data/indices/soi>

⁶ http://iridl.ldeo.columbia.edu/SOURCES/.IGOSS/.nmc/.Reyn_SmithOIv1/

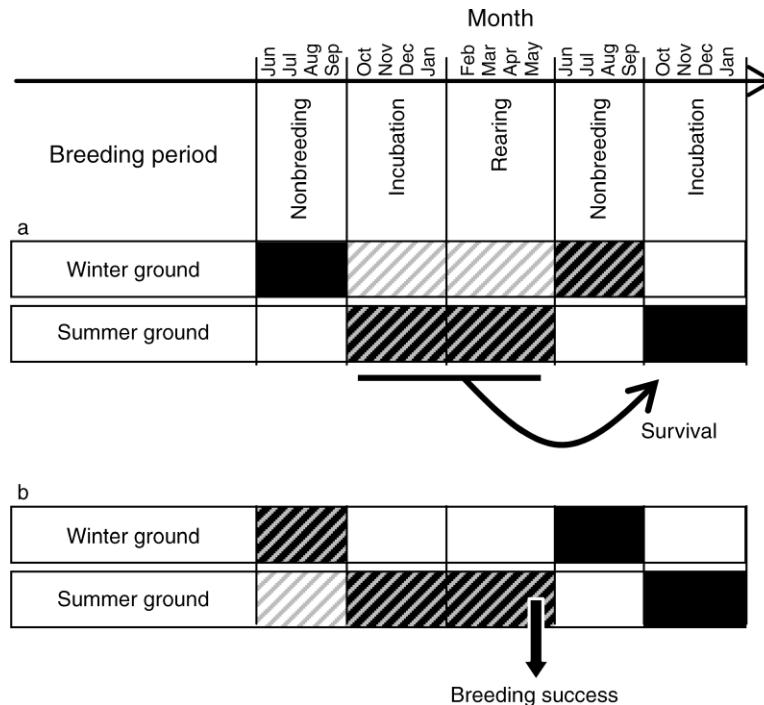


FIG. 3. Selection of the climatic variables used to explain the variability in (a) survival and (b) breeding success in relation to the seasonal distribution of the Black-browed Albatross. Black squares indicate the presence of the albatrosses in a given ground for a given period of the year. Hatched squares represent the geographical area and the period of the year covered by the climatic indices used to explain the variability of the demographic traits. Note that hatching on a white background corresponds to variables testing for a potential lagged effect of the climatic condition on the environment several months later.

(Lebreton et al. 1992); thus we used the AIC corrected for lack of fit and adjusted for small sample size (QAIC_c, Burnham and Anderson 1998), for the model selection.

Time-dependent models

Survival and transition probabilities.—Model selection procedure aimed at simplifying the general umbrella AS model (Table 2, model 1). No effect of ST was detected on recapture, survival, and transition probabilities at South Georgia (models 2, 7, and 16) or at Kerguelen (models 5, 13, and 17), suggesting that the sampling effort was comparable for known- and unknown-aged adults, which share similar life-history parameters. At South Georgia, recapture did not vary over time in breeders (model 3), and was independent of the breeding success (model 4). Survival did not vary over time in breeders (model 8), was affected by the breeding experience (model 9), but not by the breeding success (models 10 and 11), whereas survival of nonbreeders was time dependent (model 12). Transitions differed according to the reproductive states and the time (model 16). At Kerguelen, time variations on recapture were parallel between the reproductive states (model 6), survival was constant through time (model 14) but it was affected by the reproductive state and the experience of birds (model 15). Transitions differed according to the breeding success and time in breeders (model 17) but were constant in nonbreeders. These results were all included

in the best time-dependent model (model 18, QAIC_c weight = 0.996), which can be written as follows: p [$\text{POP}_{\text{sg}} \times (\text{REPRO}_{\text{nb}} \times T + \text{REPRO}_{\text{fb, sb}}) + \text{POP}_{\text{ker}} \times (\text{REPRO}_{\text{nb, fb, sb}} + T)$], Φ [$\text{POP}_{\text{sg}} \times (\text{REPRO}_{\text{nb}} \times T + \text{REPRO}_{\text{fb=sb}} \times \text{EXP}_{\text{in, exp}}) + \text{POP}_{\text{ker}} \times (\text{REPRO}_{\text{nb}} + \text{REPRO}_{\text{fb, sb}} \times \text{EXP}_{\text{in, exp}})$], $\Psi^{i,j}$ [$\text{POP}_{\text{sg}} \times \text{REPRO}_{\text{nb, fb, sb}} \times T + \text{POP}_{\text{ker}} \times (\text{REPRO}_{\text{nb}} + \text{REPRO}_{\text{fb, sb}} \times T)$]. Models 19–23 were derived from this best time-dependent model to compare the apparent survival probabilities of the two Black-browed Albatross populations for different reproductive states and experiences. Models highlighted that all the survival parameters differed between the two populations, being on average higher at South Georgia (Table 3). This result was confirmed by Z -tests (Lebreton et al. 1992), all comparisons between South Georgia and Kerguelen breeders survival being significantly different at $P < 0.0001$ (except in nonbreeders, $Z = 2.91$, $P = 0.002$). However, a common pattern emerged: first-time breeders had a lower survival probability than more experienced ones. Nonbreeders had the lowest survival at South Georgia, and among those surviving, the inter-annual propensity to stay a nonbreeder (Ψ [$\text{REPRO}_{\text{nb}} \rightarrow \text{REPRO}_{\text{nb}}$]; Table 3) was high. By contrast, survival of nonbreeders was intermediate between inexperienced and experienced breeders at Kerguelen, and the probability to become and then stay a nonbreeder was low. At Kerguelen, successful breeders had a high probability to become successful again the

TABLE 2. Model selection for recapture, survival, and transition probabilities in the Black-browed Albatross.

Model	Model description		NP†	Deviance	QAIC _c	ΔQAIC _c
	Reference	Difference from this reference model				
Model 1	—	umbrella AS model : effects of population, age status, breeding state, and time on recapture, survival, and transition probabilities	897	45 844	25 852	1214
Model 2	Model 1	no effect of the age status on recapture at SG	857	45 777	25 727	1090
Model 3	Model 2	no effect of time on recapture of failed and successful breeders at SG	807	45 118	25 272	634
Model 4	Model 3	equal recapture of failed and successful breeders at SG	803	45 132	25 270	633
Model 5	Model 4	no effect of the age status on recapture at K	755	45 173	25 186	549
Model 6	Model 5	additive effect of time on recapture at K	724	45 250	25 157	519
Model 7	Model 6	no effect of the age status on survival at SG	692	45 289	25 108	470
Model 8	Model 7	no effect of time on survival at SG	633	45 515	25 098	460
Model 9	Model 8	effect of breeding experience on survival of failed and successful breeders at SG	634	45 503	25 094	456
Model 10	Model 9	equal survival of inexperienced failed and inexperienced successful breeders at SG	631	45 505	25 089	451
Model 11	Model 10	equal survival of experienced failed and experienced successful breeders at SG	630	45 506	25 086	449
Model 12	Model 11	effect of time on survival of non breeders at SG	641	45 449	25 081	443
Model 13	Model 12	no effect of the age status on survival at K	613	45 415	25 003	365
Model 14	Model 13	no effect of time on survival at K	556	45 499	24 924	286
Model 15	Model 14	effect of breeding experience on survival of failed and successful breeders at K	560	45 473	24 918	281
Model 16	Model 15	no effect of the age status on transitions at SG	474	45 661	24 833	195
Model 17	Model 16	no effect of the age status on transitions at K	395	45 792	24 735	97
Model 18	Model 17	no effect of time on transitions of non breeders at K	316	45 923	24 638	0
Model 19	Model 18	equal survival of inexperienced failed breeders at SG and K	316	45 943	24 649	11
Model 20	Model 18	equal survival of inexperienced successful breeders at SG and K	315	45 957	24 654	16
Model 21	Model 18	equal survival of non breeders at SG and K	293	46 098	24 682	44
Model 22	Model 18	equal survival of experienced failed breeders at SG and K	294	46 107	24 688	50
Model 23	Model 18	equal survival of experienced successful breeders at SG and K	294	46 129	24 700	62

Notes: A reduced sequence of model adjustments is presented from top to bottom, starting with the umbrella AS model (model 1). Every model has the properties of the preceding model ("Reference"), except one parameter ("Difference from this reference model"). For example, model 4 has the structure of the general AS model except that the recapture at South Georgia has no age status effect and no time effect on failed and successful breeders, which are equal. "SG and "K" refer to South Georgia and Kerguelen populations, respectively.

† Number of parameters.

following season, and both nonbreeders and failed breeders had also a good chance to become successful breeders.

Breeding success.—The most general model for describing breeding success (Table 4, model 1) was simplified by a progressive deletion of the interactions between explanatory variables. The interaction between experience and time was not retained (model 2 vs. model 3), suggesting that interannual variability in breeding success was independent of experience. However, interannual variability in breeding success differed between the two populations (model 3 vs. model 4). The best model (model 5) excluded the interaction between experience and population (model 4 vs. model 5), suggesting that the difference in the breeding performance of inexperienced and experienced birds was comparable in the two populations. Breeding success increased with experience (model 5 vs. model 6), and was lower but more variable at South Georgia (inexperienced breeders: 0.227 [95% CI: 0.104, 0.394], $\sigma = 0.058$ and experienced breeders: 0.285 [0.208, 0.362], $\sigma = 0.039$) than at Kerguelen (inexperienced breeders = 0.488 [0.399, 0.577], $\sigma = 0.033$, $Z = -3.91$, $P < 0.001$;

and experienced breeders = 0.694 [0.640, 0.747], $\sigma = 0.017$, $Z = -9.61$, $P < 0.001$; Fig. 4).

Covariates models

We derived from the best time-dependent model (Table 2, model 18) the following models: $p(\text{REPRO}_{\text{nb}} \times T + \text{REPRO}_{\text{fb, sb}})$, $\Phi(\text{REPRO}_{\text{nb}} \times T + \text{REPRO}_{\text{fb=sb}} \times \text{EXP}_{\text{in, exp}})$, $\Psi^{i,j}(\text{REPRO}_{\text{nb, fb, sb}} \times T)$ for South Georgia, and: $p(\text{REPRO}_{\text{nb, fb, sb}} + T)$, $\Phi(\text{REPRO}_{\text{nb}} + \text{REPRO}_{\text{fb, sb}} \times \text{EXP}_{\text{in, exp}})$, $\Psi^{i,j}(\text{REPRO}_{\text{nb}} + \text{REPRO}_{\text{fb, sb}} \times T)$ for Kerguelen, to test in each population separately for an impact of climatic variables on survival. For the breeding success, the simplified population specific model was: BS ($\text{EXP}_{\text{in, exp}} + T$), for both South Georgia and Kerguelen data sets.

South Georgia population.—The apparent survival of inexperienced breeders was negatively associated with SST in the Benguela Current region during the nonbreeding season ($P = 0.032$, slope = -0.866 [$-1.470, -0.261$], Appendix A), explaining up to 32% of the interannual variability in this trait. There was a strong negative effect of SST around the South Orkney Islands on survival of nonbreeders during summer ($P =$

TABLE 3. Estimates of survival (Φ) and transition (Ψ) probabilities in the Black-browed Albatross populations at South Georgia and Kerguelen between 1980 and 2005.

Parameter	South Georgia	Kerguelen
Adult survival probability		
Φ (REPRO _{fb} × EXP _{in})	0.925 (0.016)	0.781 (0.034)
Φ (REPRO _{sb} × EXP _{in})	0.925 (0.016)	0.758 (0.033)
Φ (REPRO _{nb} × EXP _{exp})	0.898 (0.005)	0.838 (0.020)
Φ (REPRO _{fb} × EXP _{exp})	0.959 (0.003)	0.894 (0.009)
Φ (REPRO _{sb} × EXP _{exp})	0.959 (0.003)	0.925 (0.004)
Transition probability		
Ψ (REPRO _{nb} → REPRO _{nb})	0.681 (0.008)	0.083 (0.015)
Ψ (REPRO _{nb} → REPRO _{fb})	0.221 (0.007)	0.235 (0.023)
Ψ (REPRO _{nb} → REPRO _{sb})	0.098 (0.005)	0.682 (0.025)
Ψ (REPRO _{fb} → REPRO _{nb})	0.243 (0.006)	0.045 (0.005)
Ψ (REPRO _{fb} → REPRO _{fb})	0.546 (0.007)	0.282 (0.011)
Ψ (REPRO _{fb} → REPRO _{sb})	0.211 (0.006)	0.673 (0.012)
Ψ (REPRO _{fs} → REPRO _{nb})	0.127 (0.007)	0.049 (0.003)
Ψ (REPRO _{fs} → REPRO _{fb})	0.600 (0.010)	0.210 (0.006)
Ψ (REPRO _{fs} → REPRO _{sb})	0.272 (0.009)	0.741 (0.006)

Notes: Estimates are presented according to the reproductive states (REPRO: nb, nonbreeder; fb, failed breeder; sb, successful breeder) and the breeding experience (EXP: in, inexperienced breeder; exp, experienced breeder). Mean annual estimates (SE) came from a time-independent version of the best model (model 18, Table 2): p [$\text{POP}_{\text{sg}} \times \text{REPRO}_{\text{nb,fb,sb}} + \text{POP}_{\text{ker}} \times \text{REPRO}_{\text{nb,fb,sb}}$], Φ [$\text{POP}_{\text{sg}} \times (\text{REPRO}_{\text{nb}} + \text{REPRO}_{\text{fb=sb}} \times \text{EXP}_{\text{in,exp}}) + \text{POP}_{\text{ker}} \times (\text{REPRO}_{\text{nb}} + \text{REPRO}_{\text{fb,sb}} \times \text{EXP}_{\text{in,exp}})$], $\Psi^{i,j}$ [$\text{POP}_{\text{sg,ker}} \times \text{REPRO}_{\text{nb,fb,sb}}$]. See Table 1 for key to variable names.

0.037, slope = -1.593 [$-1.928, -1.258$], Appendix A), explaining 23% of its variability. No significant relationship was detected between survival of experienced birds and climatic covariates. Several climatic indices could explain a significant part of the interannual variability of the breeding success, when used as single covariates: SOI and SST_{sg} during the non breeding period, SST_{so} during incubation, and SST_{sg} and SST_{so} during the rearing period (Appendix B), with absolute values of slopes ranging from 0.442 [0.387, 0.497] to 0.535 [0.481, 0.589]. To avoid potential confounding effects, we added, stepwise, all the significant variables into the model, controlling for the significance of each addition. The best model explained 56% of the variability on the breeding success and it highlighted a cumulative effect of SST_{so} and SST_{sg} during the rearing period ($P = 0.003$, slope = 0.391 [0.333, 0.449] and $P = 0.010$, slope = 0.344 [0.282, 0.405], respectively) and SST_{sg} during the nonbreeding period ($P = 0.029$, slope = -0.318 [$-0.379, -0.258$]). This latest relationship between SST_{sg} during the nonbreeding period and breeding success suggested a four-month lag in the impact of winter conditions over the summer foraging grounds on reproduction.

Kerguelen population.—The survival of inexperienced failed breeders was negatively affected by SST off the South of Australia during the incubation period ($P = 0.013$, slope = -0.572 [$-1.033, -0.110$], Appendix C). This accounted for 36% of the variability on survival. Some 43% of the variability in breeding success was explained by the negative effect of SST off South Australia the winter preceding the breeding season ($P = 0.001$, slope = -0.342 [$-0.403, -0.283$], Appendix D).

Comparisons.—The intensity of the climatic impacts on vital rates was described by the absolute value of the slope of the relationships between survival or breeding success and the standardized covariates. Climate impact on survival of breeding birds tended to be higher at South Georgia than at Kerguelen, although the 95% confidence intervals overlapped indicating little difference and potentially a lack of statistical power to detect differences. By contrast, the impact of summer SST_{so} on nonbreeders survival from South Georgia was higher than any of the effects detected at Kerguelen. The intensity of the climatic impacts on breeding success was stronger at South Georgia than at Kerguelen.

DISCUSSION

This study is a pioneer effort in the critical comparison of the long-term effects of environmental variability at the population level, as mediated through the performance of individuals of known status. We have identified important similarities between populations, such as the absence of climatic effect on the high survival rate of experienced adults, and the significant impact of climate on both the survival of inexperienced adults and on breeding success. We also highlight fundamental differences in life history traits and in the strength of the impact of climatic conditions on survival of inexperienced breeders that relate directly to the different levels of variation to which the two different populations are exposed. Examining these similarities and differences in the light of the specific environmental variability at each site provides an exceptional basis for testing predictions of bet-hedging theory.

TABLE 4. Model selection of the breeding success of the Black-browed Albatross populations at South Georgia and at Kerguelen between 1980 and 2005, in relation to population (POP), breeding experience (EXP), and time (T).

Model	Description of the models	NP	Deviance	AIC	Δ AIC
1	EXP + POP + T + EXP \times POP + POP \times T + EXP \times POP \times T	86	15 458	15 630	35
2	EXP + POP + T + EXP \times POP + POP \times T + EXP \times T	70	15 470	15 610	15
3	EXP + POP + T + EXP \times POP + POP \times T	49	15 499	15 597	2
4	EXP + POP + T + EXP \times POP	28	16 286	16 342	9389
5	EXP + POP + T + POP \times T	48	15 499	15 595	0
6	POP + T + POP \times T	47	15 565	15 659	64
7	EXP + POP + T	27	16 286	16 340	9397

Comparison of life history traits

Our two populations presented life history traits characteristic of organisms with high life expectancy: a low and variable fecundity but a high and constant adult survival (Stearns 1992). Adult survival probability was very high while the breeding success was low and more variable. We also detected an impact of breeding experience on individual performance in both populations, as previously reported at Kerguelen for a shorter study period (Nevoux et al. 2007). However, a detailed analysis of life history traits indicated some significant differences between populations. At Kerguelen, adult survival probability was lower than at South Georgia; furthermore, among experienced birds, successful breeders had a higher probability of survival than failed breeders. In contrast, the benefit of experience on survival appeared much smaller at South Georgia than at Kerguelen. This could be related to a longer period of immaturity enabling a greater acquisition of skills not related to reproductive activities in the population from South Georgia (Weimerskirch et al. 1987, Prince et al. 1994), as much relevant “experience” may be achieved before the first breeding attempt. The breeding success was higher at Kerguelen than at South Georgia and individuals showed a higher probability to remain or become a successful breeder in the former population. By extending previous findings (Prince et al. 1994, Weimerskirch and Jouventin 1997), this comparative study confirms that adult individuals from South Georgia were longer lived than those from Kerguelen.

Comparison of the response to climate

In both populations, the survival of experienced breeders was not significantly affected by any kind of temporal variability, whereas climatic conditions explained substantial and significant parts of the variability in the survival of inexperienced breeders and the breeding success. The survival of inexperienced breeders at South Georgia was sensitive to winter conditions over the Benguela Current region, where cold temperatures, characteristic of an enhanced primary production in the area due to the intense activity of the Benguela Current upwelling, presented favorable oceanographic conditions. Nonbreeders seemed to use foraging areas similar to those of active breeders in summer (Phillips et al. 2005), which may explain the positive influence on their

survival of cold temperatures at the South Orkney Islands during the breeding season. The breeding success at South Georgia was mainly related to the climatic conditions in the summer foraging grounds. Cold winter SST_{sg} is generally associated with high krill productivity (Quetin et al. 2007) and may be essential to support a high breeding success in birds from this area, in agreement with previous findings for this and other krill predators (Croxall 2006). Conversely, summer temperature over the foraging grounds was positively related with the breeding success. This could be related to the alternation of warm and cold cycles of ENSO, the signs of which are evident in the Scotia Sea and the South Georgia area (Trathan and Murphy 2003, Murphy et al. 2007). In this area, low krill biomass is associated with warm SST during the previous year, and the opposite is true for high krill productivity and low SST_{sg}. Because cold years tend to follow warm years and vice-versa, according to ENSO cycles (Murphy et al. 2007), a positive correlation of SST_{sg} and breeding success may occur with a different lag than a negative correlation between SST_{sg} and breeding success. At Kerguelen, the survival of inexperienced failed breeders was negatively related to the spring SST off southern Australia.

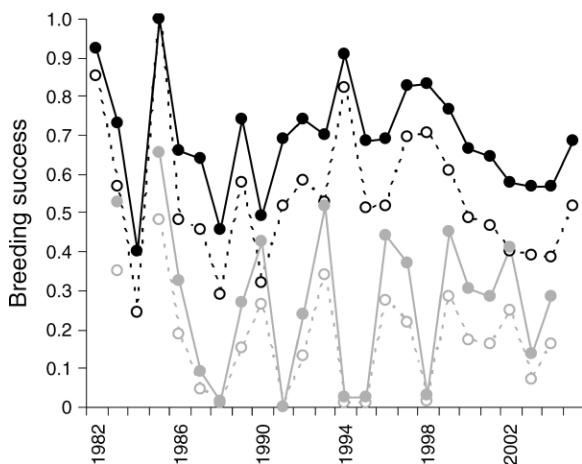


FIG. 4. Interannual variability in the breeding success of the Black-browed Albatross, in relation to the population and the breeding experience. Black and gray lines represent the populations at Kerguelen and South Georgia respectively; open and filled dots stand for inexperienced and experienced breeders respectively. Estimates came from model 5 (Table 4).



PLATE 1. Adult Black-browed Albatross and its chick on the nest. Photo credit: M. Nevoux.

Although albatrosses are supposed to be restricted to the area around Kerguelen during the breeding season, this relationship might be explained by a lag of a few months between a climatic event and its integration throughout the food web, up to the higher-level predators (Stenseth et al. 2004). In addition, failed breeders may arrive at the nonbreeding grounds early in the season, because most failures in procellariiforms occur during the incubation period (Warham 1990, Chaurand and Weimerskirch 1994). In this population, reproduction may depend upon the climatic conditions experienced by the birds during the winter, suggesting that individuals should rely on winter resources to acquire sufficient body condition to breed successfully the next season (Chastel et al. 1995). Surprisingly, the relationship between breeding success and SST_{ker} , previously detected in this population for a recent period, did not seem to have occurred over the whole study period (Pinaud and Weimerskirch 2002, Nevoux et al. 2007).

When comparing the impact of climate, the response on the survival of inexperienced breeders was very similar between the two populations for a comparable amount of variability explained (South Georgia, $r^2 = 32\%$; Kerguelen, $r^2 = 36\%$). The main difference came

from the strength of the climatic impact on the breeding success. Although the multiple relationships detected on this trait with climate may be difficult to interpret, all responses were stronger at South Georgia than at Kerguelen. This suggests that the variable breeding success observed at South Georgia may be related to the high sensitivity of this trait to climatic fluctuations, which was exacerbated by the high variability of this environment. Another interesting difference between the two populations was the strong impact of climatic conditions on the survival of nonbreeders at South Georgia. Transitions between breeding states revealed that a large proportion of the nonbreeders would not reproduce again the following year and might skip several successive breeding seasons. Therefore their contribution to the population growth rate should be extremely low as they did not contribute to the reproduction. This skipping tactic has been reported in populations successfully responding to environmental variability (Forcada et al. 2008). It constitutes one of the mechanisms leading to the low fecundity observed in variable environments and it may allow individuals to use optimally changing environments by waiting for more favorable conditions to start breeding.

Bet-hedging as a response to environmental variability?

We compared two seabird populations inhabiting environments characterized by very different levels of variability. Climatic conditions over breeding grounds were more variable at South Georgia than at Kerguelen, being almost three times greater for, e.g., SST at South Georgia, where Black-browed Albatrosses are also known to rely on a more variable food resource (Cherel et al. 2000b, Croxall 2006, Murphy et al. 2007, Quetin et al. 2007). In this context, bet-hedging might be an optimal response to preserve population dynamics. The observed differences in life histories between the Black-browed Albatross populations of South Georgia and Kerguelen were in accordance with the bet-hedging hypothesis, with a lower and more variable breeding success but a higher adult survival supported by the more variable environment. However, any change in life history traits would reasonably be attributed to bet-hedging as an adaptive response only if the individuals benefit from it, i.e., only if this strategy reduces the impact of the extra variability on life history traits, and ultimately on the population growth. We investigated the impact of the environment on life history in our two populations particularly to check for this assumption. In order to maximize population growth rate, the theory of the canalization of life history traits (Stearns and Kawecki 1994, Gaillard and Yoccoz 2003) predicts that traits having the highest influence on fitness should be those most strongly canalized (i.e., preserved) against environmental variability. In such a long-lived species, the contribution to fitness of breeding success and survival of inexperienced breeders were expected to be much lower than the contribution made by survival of

experienced adults (Sæther and Bakke 2000, Rolland et al. 2009), which is expected to be the trait to be preserved. In both populations, climatic conditions affected the breeding success of all breeders and the survival of inexperienced breeders, whereas the survival of experienced breeders was not affected by any kind of temporal variability. The strength of the climatic impact on survival of inexperienced breeders was very similar between the two populations, but the effect on breeding success was weaker at Kerguelen than at South Georgia. These results are in accordance with our prediction of a comparable impact of the environment on survival traits between the two populations. In the more variable environment, this impact may have been minimized at the expense of the breeding success, which appeared consequently more strongly dependent on environmental variability (Murphy 1968, Cooch and Ricklefs 1994, Smith and Charnov 2001, Roff 2002). Environmental variability may be one of the major factors leading to the life history trait variability reported in different populations of the same species (Coulson 2002, Weimerskirch 2002), and bet-hedging may underpin population responses to such variability in these long-lived vertebrates.

By linking changes in life history traits to changes in environmental impacts, this study provides new insights on bet-hedging as an adaptive response of populations to environmental variability. This approach also reduced problems arising from the fact that changes in life histories may often result from processes unrelated to environmental variations (Cooch and Ricklefs 1994). As predicted, the observed differences in life histories were related to different variability in environmental conditions, with the population experiencing a higher environmental variability also showing a longer-lived strategy (Murphy 1968, Coulson 2002, Roff 2002, Weimerskirch 2002, Church et al. 2007). This study underlines the need to consider the magnitude of environmental variation associated with any change in mean value, when attempting to make realistic predictions about the impact of climatic changes on vertebrates. In the present context of climate change, adaptive processes are generally thought to be too slow to allow an accurate response by organisms (Parmesan 2006). Nevertheless it would be important to investigate the timing of the bet-hedging response to environmental variability, in relation to the amount of variability this strategy could enable populations to cope with.

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APPENDIX A

Testing for the effect of climatic indices on the survival probability of the Black-browed Albatross population at South Georgia between 1980 and 2005, using methods of Grosbois et al. (2008) (*Ecological Archives* E091-173-A1).

APPENDIX B

Testing for the effect of climatic indices on the breeding success of the Black-browed Albatross population at South Georgia between 1980 and 2005, using methods of Grosbois et al. (2008) (*Ecological Archives* E091-173-A2).

APPENDIX C

Testing for the effect of climatic indices on survival probability of the Black-browed Albatross population at Kerguelen Islands between 1980 and 2005, following Grosbois et al. (2008) (*Ecological Archives* E091-173-A3).

APPENDIX D

Testing for the effect of climatic indices on the breeding success of the Black-browed Albatross population at Kerguelen Islands between 1980 and 2005, following Grosbois et al. (2008) (*Ecological Archives* E091-173-A4).