Environmental variation and experience-related differences in the demography of the long-lived black-browed albatross

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Summary

1. It has been largely demonstrated that demographic performances of animals increase with age or experience as a result of an improvement of foraging skills, an increasing reproductive effort or a selection process. However, little is known about the age or experience-related response of populations to environmental variations. Theoretical studies consider that age-related variations of the performances are greater under more restricting conditions, but this has rarely been tested.

2. We tested this hypothesis on a long-lived species, black browed albatross *Thalassarche melanophrys* Temminck, using a long-term capture–mark–recapture data set. We investigated the responses of a population to climate, by studying the effects of climatic factors and breeding experience on survival and breeding success.

3. First-time breeders appear to be poorer performers compared with experienced adults, with lower reproductive success and lower survival. In addition, interannual variations of demographic traits were partly explained by climatic indices, reflecting environmental variations. The survival probability of black-browed albatrosses varied with experience and climate, and differences being greater under harsh conditions. By contrast, the reproductive success of inexperienced individuals was affected by climatic fluctuations in the same way as the experienced ones.

4. First breeding event acts as a strong selective process on the highly heterogeneous class of inexperienced individuals, suggesting the increase in survival and breeding success with experience may mainly reflect a reduction in the heterogeneity among individual qualities.

Key-words: adult survival, black-browed albatross *Thalassarche melanophrys*, breeding success, breeding experience, environmental variations.

Introduction

Life-history theory predicts that individuals could only acquire a limited amount of energy that should be allocated between many competitive components of an individual's fitness (Roff 1992; Stearns 1992). This prediction leads to a main trade-off between reproduction and survival. As reproductive performance is known to be strongly influenced by age, the reproductive costs should be the highest in younger individuals. In mammalian and avian populations, several studies have found evidence that first time breeders are often poor performers, with a lower probability to breed successfully (Forslund & Pärt 1995; Newton 1998; Reid *et al.* 2003), a higher probability to skip breeding the following year (Weimerskirch 1990; Viallefont, Cooke & Lebreton 1995) and a lower probability to survive after first breeding (Clutton-Brock *et al.* 1996; Reid *et al.* 2003) compared with older and more experienced individuals.

Such a difference can be explained by three non-exclusive hypotheses (Curio 1983; Sæther 1990; Weimerskirch 1992; Forslund & Pärt 1995). It can be due to an age-related improvement of foraging skills (Greig, Coulson & Monaghan 1983), an increase of the reproductive effort with age (Williams 1966) or to a

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decrease of the heterogeneity in individual quality among cohorts with time, based on selection pressure (Curio 1983; Forslund & Pärt 1995; Cam & Monnat 2000; Barbraud & Weimerskirch 2005).

There is increasing evidence that environmental variations and recent climatic changes (IPCC 2001) can have extensive impacts on population dynamics (Hughes 2000; Walther *et al*. 2002; Root *et al*. 2003; Walther, Berger & Sykes 2005), mainly through a control of the resources available for organisms, affecting energy acquisition and allocation. How environmental fluctuations might affect the demographic parameters of both inexperienced and experienced breeders is a critical issue, as inexperienced birds are likely to be more susceptible to perturbation, and any increase in mortality at this stage would affect population structure. But, the long-term demographic response of individuals to a variable environment, depending on the breeding experience, is poorly documented. It appears that the response of individuals is highly dependent on environment variability. The difference in the breeding performance (Ratcliffe, Furness & Hamer 1998; Laaksonen, Korpimäki & Hakkarainen 2002; Bunce, Ward & Norman 2005; Tavecchia *et al*. 2005) and in the survival probability (Gaillard, Festa-Bianchet & Yoccoz. 1998; Coulson *et al*. 2001; Barbraud & Weimerskirch 2005) of younger and prime-age breeders is particularly marked during poor environmental conditions with low resource availability (Bunce *et al*. 2005). Thus, this distinction between younger and less experienced birds and older and more experienced birds is fundamental to better explain population dynamics in variable ecosystems.

The aim of this study is to investigate the demographic response of experienced and inexperienced individuals of a long-lived migrating seabird to climatic variation in breeding and wintering grounds, by analysing simultaneously adult survival and reproductive success. We study the black-browed albatross *Thalassarche melanophrys* population of Kerguelen. A previous study demonstrated an impact of climatic variations on its reproductive success (Pinaud & Weimerskirch 2002). First, we estimate the breeding success and the adult survival probability of inexperienced and experienced individuals using long-term capture–mark–recapture data sets. Then, we test for correlations between environmental fluctuations in summer and wintering grounds and demographic parameters to study a potential experience-based response of breeders to climatic fluctuations, which has rarely be done at the same time on both reproductive success and survival probability (Gaillard *et al*. 2000). Based on previous findings on birds (Laaksonen *et al*. 2002; Barbraud & Weimerskirch 2005; Bunce *et al*. 2005) and mammals (Gaillard *et al*. 1993, 1998, 2000; Coulson *et al*. 2001), we make the prediction that younger and less experienced breeders should reproduce and survive less well than older and more experienced breeders. This difference should increase under increasing climate severity,

based on their respective ability to face environmental fluctuations.

Materials and methods

SPECIES AND STUDY SITE

The black-browed albatross is a medium-sized albatross (3–4 kg), inhabiting the Southern Ocean and breeding on sub-Antarctic islands during the austral summer (Marchant & Higgins 1990). This annual breeder arrives on colonies in September, laying occurs in late October, hatching in late December and fledging in April (Weimerskirch, Zotier & Jouventin 1989; Marchant & Higgins 1990). At the Kerguelen Islands – southern Indian Ocean (48·4° S, 68·4° E) the study colony of Cañon des Sourcils Noirs with 100–200 nests was monitored annually since the breeding season 1979–80 (thereafter 1980). During the breeding season, each nest was checked three times (during early incubation, at hatching and before fledging), pair members were identified and their breeding performance was determined. Each year, new individuals found in the study colony and all chicks were ringed with a stainless steel band. In summer, satellite tracking indicated that birds from this colony foraged on the northeast and southeast regions of the peri-insular Kerguelen shelf (Weimerskirch, Mougey & Hindermeyer 1997; Pinaud & Weimerskirch 2002), feeding on fish, squids (Cherel, Hobson & Weimerskirch 2000) and on offal from fisheries (Weimerskirch *et al*. 1988). In winter, birds migrate off southern Australia, as indicated by band recoveries (Weimerskirch *et al*. 1985) and stable isotopes analyses (Cherel *et al*. 2000).

ESTIMATION OF DEMOGRAPHIC PARAMETERS

As the black-browed albatross is long-lived and start breeding late (average age at first breeding is 9·8 years, Weimerskirch, Clobert & Jouventin 1987), in order to obtain a sufficient number of sightings of birds whose age and breeding history were known, we selected the capture histories of breeders seen between 1992 and 2003 that were ringed as chicks from 1979. This represented 82 black-browed albatrosses. We did not consider any differences between sexes because the very small sexual dimorphism did not allow us to obtain enough sexed individuals.

The breeding success (BS) was estimated at the end of each reproductive season as the proportion of eggs that produced a fledgling. We did not choose to work with the age of individuals because in these long-lived species with delayed maturity the variance on the age of recruitment is very high. So, a given age-class gathers individuals with very different breeding histories. Thus, we considered experience, defined as the number of breeding events. Preliminary analyses on the definition of breeding experience (Table 1) highlighted that differentiating first-time breeders (thereafter called

Table 1. Modelling experience on survival probability using different experience-classes for black-browed albatrosses at Kerguelen Islands

No.	Model	*np*	Dev	AICc	ΔAICc
	Modelling experience for black-browed albatrosses				
1	Exp (1+)	2	357·240	670·243	12·761
2	**Exp (1, 2+)**	**3**	**342·444**	**657·481**	**0·000**
3	Exp (1, 2, 3+)	4	341·799	658·881	1·400
4	Exp (1, 2, 3, 4+)	5	341·240	660·340	2·858
5	Exp (1, 2, 3, 4, 5+)	6	340·303	661·511	4·029
6	Exp (1, 2, 3, 4, 5, 6+)	7	339·027	662·314	4·833

Experience-classes: 'Exp (1, 2, 3+)' stands for a model with individuals pooled into three categories depending on their breeding experience: (1) birds that breed for the first time; (2) birds that breed for the second time; and (3) birds that breed for at least the third time. *np*, number of parameters estimated for the model; Dev, relative deviance; AICc, second-order Akaike's information criterion; ΔAICc, difference between the current and the lowest AICc model. Bold characters = models selected.

inexperienced birds) from individuals with at least one breeding attempt (called experienced birds) allows us to differentiate between young and prime-age adults. We considered that the first reproductive event was correctly detected, based on the high recapture probability of breeders (see Results). In addition, modelling survival for different experience-classes (Table 1, see Results) allowed us to state that the survival of first-time breeders differed from the survival of individuals breeding for at least a second time.

Adult survival probabilities were estimated with capture–mark–recapture (CMR) models, using the M-Surge software (Choquet *et al.* 2004). By taking into account the probability to detect birds (the probability that a ringed bird that is alive and in the study area at time *t* was seen at time *t*), this method allows us to obtain unbiased estimates of annual survival probabilities (Lebreton *et al.* 1992). First, a goodness-of-fit test (GOF) was performed using the U-Care software (Choquet *et al.* 2003) to test whether the data fitted the assumptions the models are based on. Two major violations of the assumptions are transience and trap dependence (respectively survival and recapture probability not independent of the first occasion of capture). If detected, these effects could be integrated in models by considering that survival as well as capture probability just after capture are different from all other occasions. In our case, the GOF was performed on the more complex model Φ (Exp * *t*) p (Exp * *t*), where both survival (Φ) and capture (p) probabilities are experience (Exp) and time (*t*) dependent. Experience was modelled using two classes where 'Exp1' stands for individuals that breed for the first time (i.e. inexperienced birds) and 'Exp2' stands for individuals that breed for the second time and more (i.e. experienced birds). Indeed, this model was an equivalent of the Cormack–Jolly–Seber model (CJS, written Φ (*t*) P (*t*)) on which we would have modelled a transient and a

trap dependence effect (Lebreton *et al.* 1992). Thus, the GOF of the model Φ (Exp * *t*) P (Exp * *t*) was the sum of tests 3.Sm and 2.Cl (Choquet *et al.* 2003).

The selection among time-dependent models was done using a second-order Akaike's Information Criterion (AICc; Burnham & Anderson 1998), following the parsimony principle between the deviance and the number of parameters. The model with the smallest AICc value was considered as the best model. The ability of two models to describe the data is assumed to be not different if the difference in their AICc is below than 2 (Lebreton *et al.* 1992). The selection among models with climatic covariates was done using the analysis of deviance test with a Fisher–Snedecor distribution (*Anodev*; Skalski, Hoffmann & Smith 1993) that evaluates the impact of a covariate by comparing the amount of deviance explained by the covariate against the amount of deviance not explained by this covariate (White & Burnham 1999). It is calculated as

$$Anodev = \frac{(Dev\,M. - Dev\,M_{cov})/(np\,M_{cov} - np\,M.)}{(Dev\,M_{cov} - Dev\,M_{+})/(np\,M_{+} - np\,M_{cov})}$$

where *Dev* and *np* are, respectively, the deviance and the number of parameters estimated for the constant model ($M.$), the model with climatic covariate (M_{cov}) and the time-dependent model (M_t).

Once the survival and the breeding success were estimated, we compared the variances between groups using a *F*-test. To compare the variance of the survival probability estimates, we had to break away from the intrinsic variance of the sampling. The temporal variation in survival probability $\hat{\sigma}^2_{proc}$ was thus assessed using variance decomposition, which allows the separation of the sampling variance from the process variance (respectively the proportion of total variance due to the sampling error or to underlying processes, (Burnham & Anderson 2002). Process variance was computed using the Mark software (White & Burnham 1999).

In order to analyse the influence of environmental fluctuations on adult survival, we selected some ecologically pertinent indices to be incorporated in models. These variables were used in log-linear models to test for correlations with demographic traits. For survival, the percentage of variation that was explained by a covariate (r^2) was estimated as: $r^2 = 1 - (\hat{\sigma}^2_{proc(cov)}/\hat{\sigma}^2_{proc(t)})$, where $\hat{\sigma}^2_{proc}$ is the process variance of the model with covariate (cov) or the time-dependent model (*t*).

ENVIRONMENTAL VARIABLES

In most cases, climatic fluctuations are suspected to affect populations through an indirect mechanism, where climate should first affect the primary production, then integrated along the trophic web up to top predators. In marine ecosystems, meteorological and oceanographic data could be used as proxies of the biotic production because they are strongly involved in the vertical mixing of the water masses, controlling the

quality of the physico-chemical environment available for the primary production (Wilson & Adamec 2002). To limit the number of covariates to test in models, monthly values of indices were averaged over a season of 4 months, consistent with the presence of birds on different sites: birds are at sea off Australia in austral winter (May–August), and present at the colony in spring (September–December) and in summer (January–April). Global indices were used to characterize environmental conditions over wintering areas as their distribution is not precisely known. All indices were standardized over the study period in order to allow comparisons.

The Southern Oscillation Index (SOI), reflecting the El Niño/La Niña oscillations through changes in sea-level pressure over the tropical Pacific sector, has been selected in relation to albatross migrations. As this index reflects oceanographic conditions between Chile and Australia, we consider a direct spatio-temporal effect, with no lag, which coincides with the presence of birds during winter off southern Australia. Seasonal SOI was obtained from the Australian Bureau of Meteorology (ABM – http://www.bom.gov.au/climate/current/soihtm1.shtml). As distribution and foraging grounds are more precisely known during the summer period, local indices can be used. Pinaud *et al.* (2002) showed that Sea Surface Temperature Anomalies (SSTA) that occurred on foraging areas had an influence on black-browed albatrosses breeding success at Kerguelen Islands. Indeed, SSTA have been used in several studies as a proxy of the oceanographic conditions that may determine the development of the whole trophic web. Based on telemetry analyses (see 'Species and study site'), we selected SSTA values over the eastern Kerguelen shelf defined as the main foraging ground for black-browed albatrosses (46·5–50·5° S, 69·0–72·0° E). Data were available from the Integrated Global Ocean Services System (Reynolds & Smith 1994; IGOSS – http://ingrid.ldeo.columbia.edu/(plotaxislength)540+def/SOURCES/.IGOSS/.nmc/.Reyn_SmithOIv1/.monthly/.ssta/).

Results

EFFECT OF EXPERIENCE AND CLIMATE ON SURVIVAL PROBABILITIES

Based on the definition of breeding experience, we selected the model with only two experience-classes (Table 1, model 2), which has the lowest AICc. It distinguished first-time breeders (hereafter inexperienced birds) from individuals with at least one breeding attempt (experienced birds). This model allows us to differentiate in the survival probability between inexperienced and experienced adults. This definition was also applied for analyses dealing with the breeding success.

The GOF test on the black-browed albatross data set ($\chi^2 = 10\cdot817$, d.f. = 16, p = 0·821) indicated that the general model derived from model CJS with two

experience classes on capture and survival correctly fitted the data. Starting with this model (Table 2, model 1), we first examined whether capture probability varied with time and/or experience. The selection indicated that models with time dependence on capture (models 1–5) were not preferred to models with constant capture probability over the period (model 6), at least for more experienced birds (model 4). However, the AICc indicated that taking into account the experience did not improve the estimates computed by the constant model (model 7 vs. model 6). Thus, the capture rate for both experienced and inexperienced albatrosses was p = 0·749, SE = 0·023. Second, we modelled survival probability where both experience and time interacted (model 7) or not (models 8, 10 and 12), and compared time (model 9), experience (model 13) and constant models (model 14). The lowest AICc was obtained for a model where survival of inexperienced birds was time-dependent, whereas survival of experienced birds was constant throughout the study period (model 10). That model gave a mean survival probability of $\Phi = 0\cdot765$, SE = 0·049 with a temporal process variance $\hat{\sigma}^2_{proc} = 0\cdot023$ for inexperienced individuals (Fig. 1a). For experienced individuals, we obtained a higher survival probability of $\Phi = 0\cdot943$, SE = 0·014 (with a null process variance due to a constant model). The comparison of process variance between experience-class (based on the model Φ (Exp ∗ t) p (·)) showed that the survival probability was significantly more variable for inexperienced birds ($\hat{\sigma}^2_{proc} = 0\cdot023$) than for more experienced ones ($\hat{\sigma}^2_{proc} = 0\cdot001$; $F_{8,7} = 45\cdot000$, $P < 0\cdot001$). When testing for a trend on survival of inexperienced breeders, we obtained a nonsignificant decreasing trend that did not improve the time-dependent model (model 11). We then tested whether we were able to detect a climatic parameter that may influence the survival of inexperienced breeders (models 15–18). The variables were not correlated and did not show any significant trends. In model 15, we noted a significant impact of the covariate (*Anodev* = 19·853; d.f. = 1,5; $P = 0\cdot007$), the SOI during the winter explaining more than 60% of the variability observed on survival probability ($r^2 = 0\cdot626$). Indeed, interannual fluctuations of that index during the study period were strongly in opposition with the variations in survival (Fig. 1a,b). We observed that during positive phases of SOI, the survival probability of inexperienced individuals decreased, with a slope $\beta = -1\cdot021$, SE = 0·343 (Fig. 1c).

EFFECT OF EXPERIENCE AND CLIMATE ON BREEDING SUCCESS

The breeding success of black-browed albatrosses at the Kerguelen Islands (Fig. 2a) was dependent on the experience of birds ($t = -4\cdot473$, d.f. = 11, $P = 0\cdot001$): inexperienced adults produced on average 0·548, SE = 0·142 fledgling, compared with experienced ones that reared 0·752, SE = 0·111 chick per year. The breeding success did not show a significant linear trend over the

Table 2. Modelling capture and survival probabilities according to time, experience and climatic covariates for black-browed albatrosses at Kerguelen Islands

No.	Model	np	Dev	AICc	ΔAICc	P-Anodev
Modelling capture probability						
1	Φ (Exp * t) p (Exp * t)	30	297·200	671·823	26·112	
2	Φ (Exp * t) p (Exp + t)	27	304·741	672·265	26·554	
3	Φ (Exp * t) p (t)	26	305·466	670·651	24·940	
4	Φ (Exp * t) p (Exp1(t) Exp2(·))	21	301·681	655·384	9·673	
5	Φ (Exp * t) p (Exp1(·) Exp2(t))	25	304·838	667·700	21·989	
6	Φ (Exp * t) p (Exp)	17	309·312	654·071	8·360	
7	**Φ (Exp * t) p (·)**	**16**	**309·808**	**652·364**	**6·653**	
Modelling survival probability						
8	Φ (Exp + t) p (·)	12	328·789	662·627	26·916	
9	Φ (t) p (·)	11	348·579	680·277	34·566	
10	**Φ (Exp1(t) Exp2(·)) p (·)**	**9**	**322·637**	**650·121**	**4·410**	
11	Φ (Exp1(trend) Exp2(·)) p (·)	4	334·439	650·996	5·285	
12	Φ (Exp1(·) Exp2(t)) p (·)	9	329·557	657·041	11·330	
13	Φ (Exp) p (·)	3	352·445	657·482	11·771	
14	Φ (·) p (·)	2	357·210	670·244	24·533	
Modelling climatic covariates						
15	**Φ (Exp1(SOI_w) Exp2(·)) p (·)**	**4**	**328·629**	**645·711**	**0·000**	**0·007**
16	Φ (Exp1(SOI_s) Exp2(·)) p (·)	4	339·520	656·077	10·366	0·108
17	Φ (Exp1($SSTA_w$) Exp2(·)) p (·)	4	340·964	657·521	11·810	0·137
18	Φ (Exp1($SSTA_s$) Exp2(·)) p (·)	4	343·287	659·844	14·133	0·197

With survival (Φ) and capture (p) probability modelled as a function of time (t), experience (Exp, including inexperienced breeders (Exp1) and experienced breeders (Exp2)), constant (·), southern oscillation index (SOI) and sea surface temperature anomaly close to Kerguelen (SSTA), in winter (w) or in summer (s). Interaction or additivity among variables are written (*) and (+), respectively. np: number of parameters estimated for the model; Dev: relative deviance; AICc: second-order Akaike's information criterion; ΔAICc: difference between the current and the lowest AICc model; P-Anodev: P-value of the Anodev test on climatic covariates. In bold characters: models selected.

study period ($F_{1,22} = 2·021$, $P = 0·169$) and variance of interannual fluctuations was not significantly different between the two groups over the study period ($F_{11,11} = 1·630$, $P = 0·215$). The breeding success showed a significant positive relationship with SSTA on the main foraging areas around the Kerguelen Islands during spring ($F_{1,21} = 4·455$, $P = 0·047$; Fig. 2b,c), which explained up to 50% of the variations in breeding success ($r^2 = 0·514$). A warming of the surface water improve the breeding success, with a slope coefficient equal to $\beta = 0·051$, SE = 0·024, independently of experience (linear model: BS = Exp + $SSTA_{spring}$).

Discussion

This study demonstrates that experience significantly influences survival and breeding success in the black-browed albatross, but differently according to the environmental conditions. First-time breeders had a lower and more variable probability of surviving (17·8% difference) and a lower but equally variable probability to produce fledglings (10·4% difference) than experienced breeders. These results are in accordance with theoretical (Forslund & Pärt 1995; Newton 1998) and empirical studies (Gaillard *et al*. 1998, 2000; Cam & Monnat 2000; Pinaud *et al*. 2002; Reid *et al*. 2003; Barbraud & Weimerskirch 2005; Crespin *et al*. 2006), but stress that environmental variations influence

differently year-to-year variations of adult survival and reproductive success.

ENVIRONMENTAL CONDITIONS

We found a significant influence of climatic indices, standing for environmental changes, on demographic traits. The climatic conditions on the wintering grounds off southern Australia (winter SOI) are the major factors affecting albatross survival probability. During negative SOI, characteristic of El Niño episodes, cooler waters in the western part of the tropical Pacific and southern Australia seemed to favour enhanced productivity in this oligotrophic area (Wilson & Adamec 2002). Therefore these oceanographic conditions may increase the food availability for albatrosses and reduce their mortality risks associated with starvation. Conversely, we find a positive relationship between the breeding success and the SSTA on the main foraging ground of the black-browed albatross around Kerguelen Islands, in accordance with the study of Pinaud & Weimerskirch (2002). The state of the local environment during the beginning of the breeding season appears to have a significant effect on the reproductive output, as previously showed for other species of seabirds (Guinet *et al*. 1998; Jenouvrier, Barbraud & Weimerskirch 2005). Cold sea surface temperatures anomalies lead to a decrease in primary productivity in this nutrient-rich
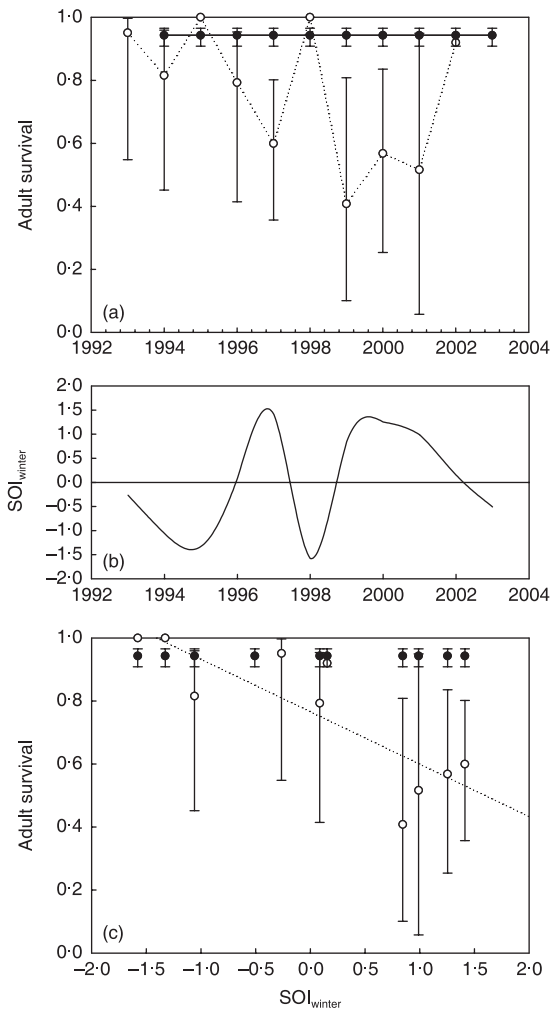
Fig. 1. Adult survival probability and climatic index for black-browed albatrosses at Kerguelen Islands. (a) Adult survival probability for inexperienced (○) and experienced (●) breeders; estimates are from model Φ (Exp1(*t*) Exp2(·)) p (·) (Table 1, model 10) are given ± 1 SE. (b) Annual variation of the standardized southern oscillation index (SOI) in winter. (c) Relationship between adult survival and SOI in winter for inexperienced (○) and experienced (●) breeders; estimations from model Φ (Exp1(*t*) Exp2(·)) p (·) (Table 1, model 10) are given ± 1 SE.

Fig. 2. Breeding success and climatic index for black-browed albatrosses at Kerguelen Islands. (a) Breeding success for inexperienced (○) and experienced (●) breeders. (b) Standardized annual variation of the sea surface temperature anomaly (SSTA) on the Kerguelen shelf in spring. (c) Relationship between breeding success and SSTA in spring for inexperienced (○) and experienced (●) breeders; linear model: breeding success = Experience + SSTA$_{spring}$, $F_{1,21} = 17.747$, $P < 0.001$; $F_{1,21} = 4.455$, $P = 0.047$ for each factor, respectively.

area (Blain *et al.* 2001), that in turn may lead to food shortages during incubation, perhaps forcing birds to desert eggs in order to restore their own body condition (Chaurand & Weimerskirch 1994; Chastel, Weimerskirch & Jouventin 1995).

INTERACTION BETWEEN EXPERIENCE AND CLIMATE

When focusing on the experience-related responses of populations to climate, we found in the black-browed albatross a common pattern with previous studies on birds (Ratcliffe *et al.* 1998; Laaksonen *et al.* 2002; Barbraud & Weimerskirch 2005; Bunce *et al.* 2005) and on mammals (Gaillard *et al.* 1993, 1998, 2000; Coulson *et al.* 2001) where environmental variations may mask age or experience-related differences in demographic
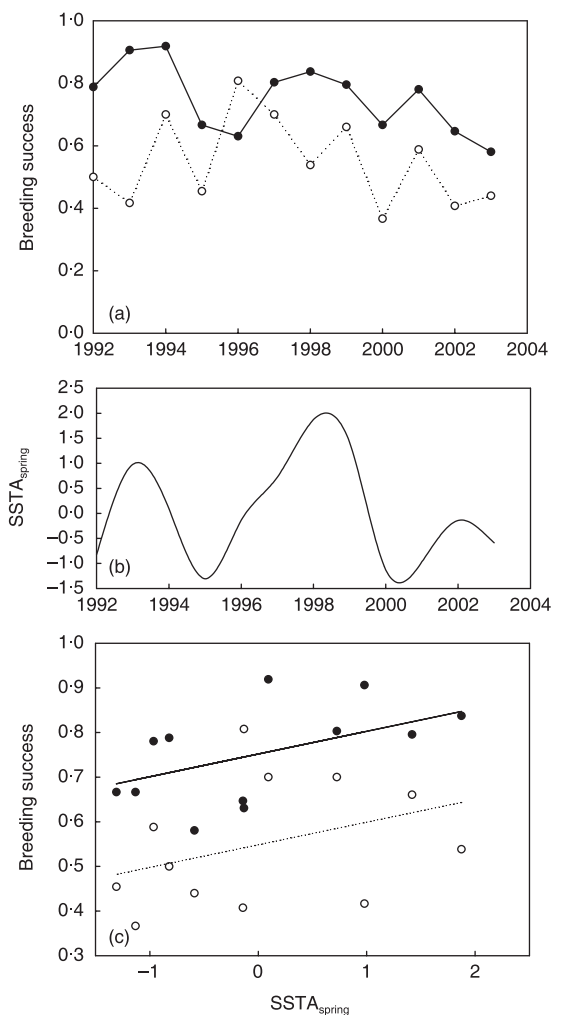
traits, as differences appeared to be greater when food availability was reduced.

According to our predictions, it appears that fluctuations in the survival rate of inexperienced adults are strongly influenced by climatic conditions, whereas experienced birds have a constant survival probability during the whole study period. Under unfavourable oceanographic conditions, inexperienced breeders seem to be highly affected while experienced birds could face warm winters without putting their survival in jeopardy. However, under more favourable circumstances, inexperienced birds are able to survive as well as more experienced ones.

By contrast, for the breeding success, the demographic response of populations does not match with our predictions. An additive model between experience and time or climate indices was selected to explain

interannual variations of the reproductive output. Although they have lower performances, inexperienced individuals are affected by climatic fluctuations in the same manner as the experienced ones. Survival and reproduction of inexperienced and experienced birds appear to be affected differently by climatic variations.

MECHANISMS

We have to keep in mind that in this analysis, we estimated the apparent adult survival that could not distinguish real mortality from permanent emigration. However, we only detected one ringed breeder over the 695 occupied nests of the adjacent colony in 2006, indicating that dispersal might be limited in that population.

From our results, it could be hypothesized that breeders appear to improve their average performances with growing reproductive experience, without improving their ability to face climatic fluctuations. Contrary to an hypothesis explaining age-related differences among breeders by an improvement of foraging skills (Williams 1966; Curio 1983; Greig *et al*. 1983; Sæther 1990; Forslund & Pärt 1995), younger breeders appeared to have the same foraging capabilities than experienced ones. This difference might be explained by the high longevity of albatrosses, compared with biological models used in previous studies, and specially the delayed maturity associated with this life history. During an immature stage lasting on average 9·8 years (Prince *et al*. 1994; Weimerskirch *et al*. 1997), young birds may have the opportunity to acquire foraging skills comparable with those of older birds, as birds may only start breeding when they have acquired good foraging skills and a sufficient body condition (Weimerskirch 1992). The residual difference between breeder's performances could be due to the first reproductive event that confronts birds to an activity needing the contribution of both members of a pair, which requires a fine synchronization of individual activities (Weimerskirch, Barbraud & Lys 2000). This particular training share is supposed to add an extra cost of reproduction to inexperienced breeders, independently of external conditions.

In addition, the selection hypothesis (Forslund & Pärt 1995) seems to have a large capability to explain the experience-related improvement in survival. The higher variance in survival for inexperienced breeders highlights that younger adults may constitute a highly heterogeneous portion of the population. Although inexperienced individuals of good quality should be able to perform as well as experienced breeders, poor quality individuals were susceptible to be highly affected by adverse conditions, contributing to the decrease in the average performance of that class. As reproduction demands an increased energetic investment for individuals, a selection process may act as a significant selective filter on the heterogeneous pool of inexperienced adults attempting at the first breeding event, leading to a

progressive decrease in the proportion of lower quality individuals among cohorts (Curio 1983; Forslund & Pärt 1995; Cam *et al*. 2000; Barbraud & Weimerskirch 2005). Consistently, our analysis demonstrates that the difference between inexperienced breeders and experienced ones could be made with only two experience-classes, supporting the singularity of the first reproductive event. This occasion could be considered as a key event after which the average performances increased in the population. Selection probably occurred during the nonbreeding period, as the winter following the first breeding season was a period of relatively high adult mortality. These elements lead to a scenario where inexperienced breeders, a class of the population showing important differences between individual qualities, produced on average a low reproductive output for their first reproduction. Winter may thus operate as a strong selective filter on poorer quality inexperienced adults weakened by first reproduction. Models show that the amplitude of this selection process was dependant of the climatic conditions severity affecting the wintering area. It remains that individuals presenting highest body conditions would be the only breeders entering the class of experienced adults, reducing at the same time the heterogeneity among individual quality through this selective process. Whereas climatic severity seemed to be a major parameter that controls the survival probability of inexperienced albatrosses and also the amplitude of the selection acting on the winter following first reproduction, environmental variations affected the breeding success of individuals, independently of the experience.

Now it should be interesting to carry on this study by testing in a more explicit way the relative part of experience, breeding effort or selection hypothesis proposed to explain this experience-related improvement of demographic performances. As proposed by Mauck, Huntington & Grubb (2004), the relation between early breeding success and longevity of individuals could permit to detect the dominant mechanism. In species with such a delayed maturity, the age at first breeding may also represents an important discriminative trait to compare the relative importance of these three hypotheses.

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