ENVIRONMENTAL CONDITIONS AND BREEDING EXPERIENCE AFFECT COSTS OF REPRODUCTION IN BLUE PETRELS

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Abstract. Using data from a 17-year study of individually marked Blue Petrels, we examined how survival and breeding probability varied with experience and breeding status, and looked for costs of first reproduction, taking into account environmental and individual variability. Using multistate capture–recapture models with four states (inexperienced nonbreeders, first-time breeders, experienced breeders, and experienced nonbreeders), we found that first-time breeders had a lower probability of surviving and breeding in the next year than experienced breeders. Survival of first-time breeders was lower than that of inexperienced nonbreeders, indicating a cost of first reproduction. Survival of inexperienced individuals (both breeders and nonbreeders), but not of experienced ones, was negatively affected by poor environmental oceanographic conditions. The costs of reproduction for first-time breeders were particularly marked during harsh weather conditions. Survival and the probability of breeding in the next year for experienced birds were higher for breeders than for nonbreeders. Similarly, the probability of breeding in the next year for first-time breeders was higher than for inexperienced nonbreeders. This suggests heterogeneity in quality among individuals. Experienced breeders had a higher body condition than first-time breeders and nonbreeders. Body condition did not affect the probability of surviving or breeding in the next year. These results can be interpreted in the light of a change in the proportion of individuals with different survival (selection hypothesis: low-quality individuals die sooner). The inferiority of first-time breeders may be linked to a higher proportion of lower-quality individuals in younger age classes. First reproduction may act as a filter, selecting individuals of higher quality. Sea surface height, reflecting food availability, is probably a key selective agent.

Key words: Blue Petrel; body condition; breeding probability; environmental stochasticity; experience; Halobaena caerulea; *multistate capture–recapture models; nonbreeding; reproductive cost; sea surface height; survival probability.*

INTRODUCTION

How do animals balance their investment in offspring against their own chances to survive and reproduce in the future? This life history trade-off, referred to as the cost of reproduction (Williams 1966), holds a central place in life history theory (Roff 1992, Stearns 1992, McNamara and Houston 1996). Because individuals can only acquire a limited amount of energy, reproduction and survival, as well as current and future reproduction, are considered as functions competing for the same resources. In this framework individuals may optimize life history decisions. If the reproductive effort in one year leads to a loss in future reproductive output through decreased adult survival or reduced fecundity, then the optimal effort in the current season is less than the effort that would maximize the number of offspring produced in that season (Charnov and Krebs 1974, Goodman 1974).

There are two major questions linked to the assessment of the costs of reproduction. (1) Does present

reproductive effort have an adverse effect on future life history (survival or future reproduction)? (2) Are the costs of reproduction the same for the different phenotypes of the population? Theoretically, because nonbreeders avoid potential costs of reproduction, they are expected to have a higher survival and higher future breeding probability at the next occasion than breeders (prudent parent hypothesis; Goodman [1974], Drent and Daan [1980]). Secondly, several studies have shown an increase in survival and reproductive output with age, particularly after first reproduction, with first-time breeders having a lower probability of breeding successfully (Newton 1986, Reid et al. 2003), a higher probability of nonbreeding in the following year (Coulson and Thomas 1985, Weimerskirch 1990, Wooller et al. 1990, Viallefont et al. 1995*a*, *b*), and a lower survival or return rate than experienced individuals (Wooller et al. 1989, Promislow 1991, Chastel et al. 1995*a*, Clutton-Brock et al. 1996, Reid et al. 2003).

However, at least two kinds of factors are likely to confound the measurement of the costs of reproduction in the wild. First, phenotypic heterogeneity can mask or exacerbate individual allocation patterns when trends are averaged across a population (heterogeneity

hypothesis; Vaupel and Yashin [1985], Nur [1988], Cam and Monnat [2000]). Evidence for individual heterogeneity in quality has led to the development of a state-dependent approach to life history theory to examine the costs of reproduction (Nur 1988, McNamara and Houston 1996). Two different processes can be distinguished within this heterogeneity hypothesis. The selection process, which operates at the population level, is based on a progressive change in the proportion of individuals with different survival: some individuals perform well in both reproduction and survival, whereas low-quality individuals die sooner, resulting in an age-related decrease in the proportion of lower quality individuals in cohorts (selection and recruitment hypotheses; Curio [1983], Forslund and Pärt [1995]). In contrast, the optimization process, which operates at the individual level, is based on the improvement in individual reproductive performances across young age classes due to cumulative experience (Nur 1984, Newton 1986, Bradley and Wooller 1991, Forslund and Pärt 1995). To date, the contributions of individual- vs. population-level processes to the variation in performance observed at the population level remains uncertain (Saether 1990, Forslund and Pärt 1995, Reid et al. 2003).

Second, there could be variations in resource availability affecting energy acquisition and allocation. Species often live in fluctuating environments, which may affect both reproductive performance and survival and may interact with the selection and individual processes just described (Boyce and Perrins 1987). Theoretical models examining the optimal phenotypic balance between reproduction and survival under variable breeding conditions have investigated the influence of environmental stochasticity on the cost of reproduction in birds (Erikstad et al. 1998, Orzack and Tuljapurkar 2001). For long-lived species with low fecundity, these models predict that, during poor breeding conditions, maximum fitness is achieved by not breeding at all, or by abandoning the offspring, and that when breeding conditions become favorable, the reproductive effort increases at the expense of survival. However, there is little empirical evidence supporting these theoretical models.

The purpose of this paper is to analyze simultaneously the influence of experience (first reproduction vs. subsequent breeding attempts) and of the differential effects of environmental variation (linked to resource availability) on survival and future breeding probability, which rarely has been done. We address the question of the costs of reproduction in a long-lived species of seabird that has delayed maturation: the Blue Petrel (*Halobaena caerulea*).

Our first objective is to test the hypothesis of an effect of experience on survival and on the probability of breeding in the following occasion. We examine possible covariation between survival and future reproduction, taking experience into account. Previous

studies on the Blue Petrel have shown that individuals with no breeding experience are in poorer body condition, are less likely to breed, and have a lower breeding success than experienced breeders (Chastel et al. 1995*b*). Consequently, we predict that inexperienced breeders will exhibit lower survival and probability of breeding than experienced breeders, i.e., inexperienced breeders pay immediate and future costs of reproduction. Our second objective is to examine whether environmental variation affects the costs of reproduction. Based on theoretical models, we predict that under poor environmental conditions (i.e., low resource availability), the costs of reproduction will be greater, particularly for inexperienced breeders. Our third objective is to draw inference about consequences of nonbreeding by testing for an effect of reproductive activity on survival and the probability of breeding in the next year. Again, we examine the effect of environmental conditions on survival probability and future breeding probability of nonbreeders, with the prediction that inexperienced nonbreeders should be more affected than experienced nonbreeders. Finally, we examine the effect of state-dependent body condition on survival and breeding probabilities. Based on previous findings for the Blue Petrel (Chastel et al. 1995*a*, *b*), we make the prediction that breeding probability will increase with increasing body condition.

METHODS

Study species, field methods, and data selection

The Blue Petrel is a small (190-g) long-lived seabird breeding at six subantarctic islands (Warham 1990). It forages over oceanic waters and preys mainly on small crustaceans and fishes from antarctic waters south of the Antarctic convergence (Cherel et al. 2002). Blue Petrels remain between the Antarctic convergence and the northern limit of the pack ice throughout the year. The birds are burrowers and start frequenting the breeding colonies in September. A single egg is laid in late October and the chick fledges in early February.

Data were collected on Mayes Island, a 5-km uninhabited island in the Kerguelen archipelago (48°38′ S, 68°38′ E), Indian Ocean, from 1986 to 2001. Each year, between 71 and 238 individually marked burrows, fitted with an observation window above the nest chamber, were inspected from early-to-mid November just after laying to check for eggs and to record marked adults, and in late January just before fledging. Each year, new individuals found in monitored burrows were marked with stainless steel bands. Birds were captured by hand in their burrows, marked, measured, weighed, and replaced in their burrow. Handling time usually took less than 2–3 minutes. Bands for which numbers had started to wear off were replaced to avoid band loss. The breeding status of marked birds resighted at each sampling period was determined. Individuals were considered as breeders if they laid an egg or raised a

chick. Individuals never observed with an egg or a chick were considered as nonbreeders. These birds were occupying the burrows alone or in pairs, sometimes showing courtship behavior. Given that the first sampling period occurred just after laying, it is very unlikely that nonbreeders represented failed breeders. The number of nests monitored in the study colony increased between 1985 and 1990 and then stabilized at 200 nests. Thus, new individuals that entered the capture–recapture study between 1985 and 1990 may have bred previously; only data collected from 1992 onward were retained for the analyses. Using this restricted data set, we classified new individuals that were observed for the first time in the monitored nests as either nonbreeders that had never previously bred or as first-time breeders, depending on their breeding status the first time they were observed. The data consisted of capture–recapture histories from 1100 individuals, starting at first observation, either as nonbreeders that had never previously bred or as first-time breeders. Among these, 431 individuals bred at least once between 1992 and 2001.

Statistical methods

Data were analyzed using multistate capture–recapture models (Brownie et al. 1993, Schwarz et al. 1993). These models include three kinds of parameters (Nichols et al. 1994): recapture probability p_t^r, defined as the probability that a bird is resighted at time t in state r, given that it is alive and present at time t; survival probability S_t^r, defined as the probability that a bird in state r at time t survives until time $t + 1$; and conditional transition probability ψ_t^{rs}, defined as the probability that a bird in state r at time t is in state s at time $t + 1$, given that the individual survived from time t to time $t + 1$. Nichols et al. (1994) generalized the concept of individual states, and described a statistical method for estimation of time- and state-specific survival and recapture probabilities and time-specific transition probabilities between states. This method permits one to address the influence of experience on survival and the probability of breeding in the following year. The effect of external covariates on survival and transition parameters can be taken into account (Nichols and Kendall 1995). The most general model that we started with was the conditional Arnason-Schwarz model (Schwarz et al. 1993). We used the following notation for states: 1, inexperienced nonbreeder, for an individual that had never bred previously; 2, first-time breeder, for an individual breeding for the first time; 3, experienced breeder, for an individual with at least one previous breeding attempt; and 4, experienced nonbreeder, for a nonbreeding individual with at least one previous breeding attempt.

In our case, some transition probabilities are unidirectional. Once an individual has been a first-time breeder, it remains an experienced breeder or an experienced nonbreeder for the rest of its life. Thus, tran-

sition probabilities from state 2 to 2 and 1 are fixed at 0. Similarly, experienced individuals cannot return to states 1 or 2. Transition probabilities from state 3 and 4 to states 1 and 2 are thus fixed at 0. Experienced individuals must be first-time breeders before becoming experienced breeders or nonbreeders, and transition probabilities from state 1 to states 3 and 4 are fixed at 0. Finally, because there is no recapture probability for first-time breeders, we set the recapture probabilities equal for first-time and experienced breeders. Using matrix notation, the parameters just defined can be summarized in matrices of survival, transition, and recapture probabilities:

$$\mathbf{S}_t = \begin{pmatrix} S_t^1 \\ S_t^2 \\ S_t^3 \\ S_t^4 \end{pmatrix} \qquad \boldsymbol{\Psi}_t = \begin{pmatrix} \psi_t^{11} & \psi_t^{12} & 0 & 0 \\ 0 & 0 & \psi_t^{23} & \psi_t^{24} \\ 0 & 0 & \psi_t^{33} & \psi_t^{34} \\ 0 & 0 & \psi_t^{43} & \psi_t^{44} \end{pmatrix}$$

$$\mathbf{P}_t = \begin{pmatrix} p_t^1 \\ p_t^3 \\ p_t^3 \\ p_t^4 \end{pmatrix}.$$

This most general model was denoted as $(S_t^r, p_t^r, \psi_t^{rs})$. Preliminary analysis using this approach indicated that the estimated recapture probability for breeders was extremely close to 1.0, suggesting that it is very unlikely that fieldworkers missed first-time breeders established in the study colony.

Because breeding starts at the end of the calendar year and ends at the beginning of the next calendar year, survival, recapture, and transition probabilities were defined (see next section) from the first capture session during the 1991–1992 breeding season.

Environmental and individual covariates

We examined the effect of two covariates that were suspected to affect survival and breeding probabilities: sea surface height (representing oceanographic conditions at a regional scale) and body mass of birds during breeding. Compared to sea surface temperature, sea surface height has the advantage of integrating three-dimensional oceanographic variations.

We used the change in sea surface height (SSH) between January and October of year t ($\Delta\text{SSH} = \text{SSH}_{\text{Jan}} - \text{SSH}_{\text{Oct}}$) as a covariate for adult survival in year t and state transition probabilities between year t and $t + 1$, because we have shown in a previous study that most of the annual adult mortality occurred outside the breeding period (Barbraud and Weimerskirch 2003). This allowed us to avoid the recapture period. We assumed that this SSH gradient was a better indicator of the changes in oceanographic conditions during winter than single monthly SSH values, because it has been shown that abrupt changes in SSH may correspond to large-scale climate changes (Park 2001). SSH was used

as a regional indicator of biophysical oceanographic conditions around the Kerguelen Islands. Oceanic phytoplankton and zooplankton productivity in the Southern Ocean is primarily limited by light and nutrients (phosphate, nitrate, silicate, and iron), and is affected by vertical mixing processes that deliver nutrients to the surface (Lewis et al. 1986, Uz et al. 2001). Primary productivity is impacted by the depth of the thermocline, a shallower thermocline increases the vertical flux of nutrients to the surface. Because an increase in SSH reflects an increase in the thermocline depth, SSH values are negatively correlated with the primary productivity at a global scale, but also in the Kerguelen region (Le Quéré et al. 2002, Wilson and Adamec 2002). SSH was thus used as a proxy, because data on primary productivity, prey availability, or thermocline depths are temporally short or scarce. The Blue Petrel is a macrozooplankton and micronekton feeder, with crustaceans and fish forming the bulk of its food (Cherel et al. 2002); thus, SSH variations may indirectly affect, through the food web, food availability for Blue Petrels and, hence, their survival and reproductive success. SSH were obtained from the TOPEX/Poseidon (T/P) altimeter satellite (launched in August 1992; joint mission of NASA/CNES) measurements at the CLIOKER 1 station (50°46′ S, 68°52′ E) south of the Kerguelen archipelago (Topex information available online).[2] SSH data are obtained by removing the tidal and meteorological (wind and pressure) effects on sea level. Initial data were low-pass-filtered at 365 days so as to eliminate seasonal variability and to obtain the interannual variations (Park 2001).

Each year when burrows were checked to determine the breeding status of occupying birds, individuals were captured and weighed to the nearest 2 g with a 300-g Pesola scale. For each year, an average body mass was calculated for each breeding state. Body mass was considered as a surrogate of physical body condition (i.e., the amount of body reserves) because structural measurements of body size such as culmen, tarsus, or wing length were not correlated with body mass (Pearson's correlation coefficients: $r = 0.081$, $P = 0.276$ for culmen; $r = 0.087$, $P = 0.387$ for tarsus; $r = 0.121$, $P = 0.035$ for wing; all P's Bonferroni corrected, $n = 523$ birds). The effects of experience, breeding state, and year on changes in body mass were tested using a mixed-model ANOVA with the maximum likelihood method (procedure MIXED, SAS version 8.02; SAS Institute 1999). Because some individuals were weighed on several occasions, "individual" was declared as a random effect.

Covariates were tested through ultrastructural models in which survival probability is a function of SSH and/or body mass, following a linear-logistic function (Clobert and Lebreton 1985):

$$\text{logit}(\phi) = \log\left[\frac{\phi}{(1 - \phi)}\right] = \alpha + \beta \times \text{covariate}.$$

Here α is the intercept parameter and β is a slope parameter. The confidence intervals around β provide evidence of an effect. We concluded that covariates had an effect when their 95% confidence intervals did not include 0. The percentage of explained variation in survival of the full model that is explained by a covariate (r^2) was estimated based on the ratio of differences in relative deviance (Dev) of constant, covariate- and time-dependent models (Schemper 1990):

$$r^2_{\text{QDdev}} = \frac{\text{Dev(covariate)} - \text{Dev(constant)}}{\text{Dev}(t) - \text{Dev(constant)}}.$$

Here covariate, t, and constant are the covariate-dependent, time-dependent, and constant survival rates, other things being equal.

Model selection and goodness of fit

Our selection of models for estimation was based on model goodness-of-fit (GOF) tests and a second-order Akaike's Information Criterion, which is a small-sample bias adjustment (AIC$_c$; Burnham and Anderson 2002). The GOF test of the most general model was performed to determine whether this model provided an adequate description of the data. AIC$_c$ selects the model that is best in terms of both parsimony and quality of fit to the data. The model in which AIC$_c$ is minimized is selected as best for describing the data. Evidence for each of the alternative models was evaluated using change in AIC$_c$, calculated as $\Delta_i\text{AIC}_c$ (Δ_i) values (Anderson et al. 2000). As a general guideline, Δ_i values >2 are a good indication that the model with the lower AIC$_c$ is preferable, whereas Δ_i values <2 indicate that models are fairly similar in their abilities to describe the data (Lebreton et al. 1992). The likelihood of a model, given the data, was estimated with a likelihood-based inference approach with AIC$_c$ weights (w_i) calculated following Anderson et al. (2000):

$$w_i = \frac{\exp\left(-\frac{1}{2}\Delta_i\right)}{\sum_{r=1}^{R} \exp\left(-\frac{1}{2}\Delta_r\right)}.$$

Here, for a set of R models, Δ_i is the AIC$_c$ difference between model i and the lowest AIC$_c$ model. The relative likelihood of model i vs. j is w_i/w_j.

To verify whether our most general model (S_t^r, p_t^r, ψ_t^{rs}) reasonably fits the data, we used a GOF test recently made available for multistate mark–recapture models (Pradel et al. 2003). We used program U-Care (Choquet et al. 2003a) to assess the fit of our general model. Because we detected significant lack of fit (see *Results: Goodness-of-fit tests*), we calculated a variance inflation factor ($\hat{c}$) to account for that extra-binomial variation. The inflation factor was calculated as the

TABLE 1. Selection among models of state-dependent survival probability (S), recapture probability (p) and transition probability (ψ) on Blue Petrels at Kerguelen Islands.

Model	np	Dev	QAIC$_c$	Δ_i	w_i
Modeling capture probabilities					
$(S_t^r, p_t^r, \psi_t^{rs})$	90	6699.851	5345.051	89.957	0.000
$(S_t^r, p_t, \psi_t^{rs})$	76	7076.431	5604.819	349.725	0.000
$(S_t^r, p_t^{14}, \psi^{rs})$	85	6699.851	5334.246	79.152	0.000
$(S_t^r, p_{t+}^{14}, \psi_t^{rs})$	78	6709.016	5326.256	71.162	0.000
$(S_t^r, p^r, \psi_t^{rs})$	71	6743.980	5338.221	83.127	0.000
Modeling survival probabilities					
$(S_t, p_{t+}^{14}, \psi_t^{rs})$	52	6745.725	5299.446	44.352	0.000
$(S, p_{t+}^{14}, \psi_t^{rs})$	46	6762.701	5299.986	44.892	0.000
$(S_{t+}^r, p_{t+}^{14}, \psi_t^{rs})$	56	6730.239	5295.915	40.821	0.000
$(S_{t+}^{2=3}, p_{t+}^{14}, \psi_t^{rs})$	55	6745.239	5305.362	50.268	0.000
$(S_{t+}^{1=2}, p_{t+}^{14}, \psi_t^{rs})$	55	6733.866	5296.606	41.512	0.000
$(S_{t+}^{3=4}, p_{t+}^{14}, \psi_t^{rs})$	55	6736.230	5298.426	43.332	0.000
Modeling transition probabilities					
$(S_{t+}^r, p_{t+}^{14}, \psi^{rs})$	27	6863.572	5338.395	83.301	0.000
$(S_{t+}^r, p_{t+}^{14}, \psi_t)$	31	7580.973	5898.874	643.780	0.000
$(S_{t+}^r, p_{t+}^{14}, \psi_{t+}^{rs})$	34	6749.806	5265.198	10.104	0.006
$(S_{t+}^r, p_{t+}^{14}, \psi_{t+}^{24=34})$	34	6756.545	5270.385	15.291	0.000
$(S_{t+}^r, p_{t+}^{14}, \psi_{t+}^{11=24})$	35	6826.792	5326.525	71.431	0.000
$(S_{t+}^r, p_{t+}^{14}, \psi_{t+}^{34=44})$	35	6776.181	5287.563	32.469	0.000
Modeling covariates					
$(S_{\Delta SSH}^r, p_{t+}^{14}, \psi_{t+}^{rs})$	32	6742.031	5255.094	0	0.964
$(S_{mass}^r, p_{t+}^{14}, \psi_{t+}^{rs})$	32	6753.940	5264.262	9.168	0.010
$(S_{\Delta SSH+mass}^r, p_{t+}^{14}, \psi_{t+}^{rs})$	37	6738.805	5262.919	7.825	0.020
$(S_{\Delta SSH}^r, p_{t+}^{14}, \psi_{\Delta SSH}^{rs})$	25	7033.339	5464.993	209.899	0.000
$(S_{\Delta SSH}^r, p_{t+}^{14}, \psi_{mass}^{rs})$	25	6866.492	5336.550	81.456	0.000

Notes: Model subscripts include: ΔSSH, variation in sea surface height; mass, body mass; t, a year effect with interaction; $t+$, an additive effect of year (i.e., no interaction). Model superscripts include: r and s, state-specific parameters; 1, inexperienced nonbreeders; 2, first-time breeders; 3, experienced breeders; 4, experienced nonbreeders. Abbreviation are: np, number of parameters; Dev, relative deviance; QAIC$_c$, Akaïke Information criterion corrected for $\hat{c}$; Δ_i, the QAIC$_c$ difference between the current and lowest QAIC$_c$ model; w_i, the current model weight.

GOF statistic for our global model divided by the degrees of freedom of the model (Pradel et al. 2003). With the inflation factor, the AIC$_c$ becomes the quasi-likelihood AIC$_c$ (QAIC$_c$, Lebreton et al. 1992). We used program M-SURGE (Choquet et al. 2003b) for model selection and parameter estimation.

RESULTS

Goodness-of-fit tests

The GOF test of our general model indicated a lack of fit (Test3G + TestM + LRT: $\chi^2 = 223.49$, df = 172, $P = 0.005$). The relatively small value of the variance inflation factor from the global test ($\hat{c} = 1.299$) was compatible with overdispersed data. To correct for overdispersion, we used $\hat{c} = 1.299$ in the remaining analysis.

Effect of time, breeding activity, and experience

Recapture probabilities.—We first examined whether recapture probabilities varied with state. A model with no state effect on p (Table 1; $[S_t^r, p_t, \psi_t^{rs}]$) was not preferred to the general model ($S_t^r, p_t^r, \psi_t^{rs}$). Because nests were checked two to three times during the incubation period to ensure that both partners who al-

ternate incubation shifts were identified, we suspected that the recapture probabilities of breeders were high and constant. A model with capture rates constant over time for breeders and varying for nonbreeders ($S_t^r, p_t^{14}, \psi_t^{rs}$) was much better in terms of QAIC$_c$ than the general model ($S_t^r, p_t^r, \psi_t^{rs}$). Recapture probability for breeders was close to 1.0 (0.999; deviance profile confidence interval: 0.984–1.000). A model in which temporal variations of recapture probabilities of experienced nonbreeders and of inexperienced nonbreeders were parallel on a logit scale ($S_t^r, p_{t+}^{14}, \psi_t^{rs}$) was preferred over a model with an interaction between state and year ($S_t^r, p_t^{14}, \psi_t^{rs}$) or a model with no year effect (S_t^r, p^r, ψ_t^{rs}). This indicated that recapture probabilities of inexperienced and experienced nonbreeders varied synchronously over time. For all remaining models, recapture probabilities were modeled as in model ($S_t^r, p_{t+}^{14}, \psi_t^{rs}$).

For nonbreeders, there was an effect of experience on recapture probabilities, because experienced individuals had higher recapture probabilities than inexperienced ones in all years ($\hat{p}^4 = 0.527 \pm 0.032$ and $\hat{p}^1 = 0.364 \pm 0.019$ from model $[S_t^r, p_t^{14}, \psi_t^{rs}]$). Estimated probabilities of recapture increased until 1996 for experienced birds, whereas they remained constant for
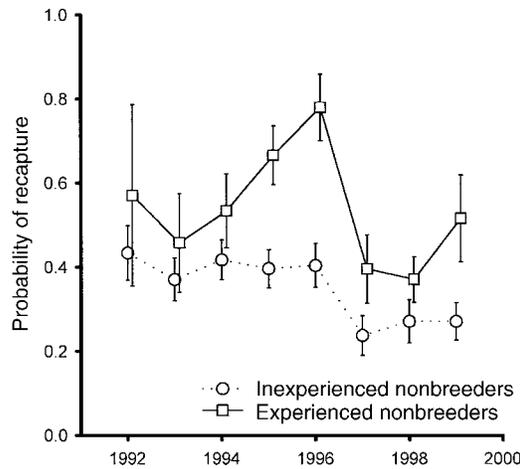
FIG. 1. Estimates (± 1 SE) of recapture probability of inexperienced and experienced nonbreeders, 1992–1999 (no estimates are available for the first year of the study because there were no experienced individuals) under model (S_t^r, p_{t+}^{14}, ψ_t^{rs}). Because of identifiability problems, no estimate is available for the year 2000.

inexperienced birds (Fig. 1). For nonbreeders, recapture probabilities sharply decreased in 1997 (Fig. 1).

Survival probabilities.—Examination of the variation in survival suggested, at first sight, that survival did not vary with state because models with equal survival across states (Table 1; [S_t, p_{t+}^{14}, ψ_t^{rs}] and [S, p_{t+}^{14}, ψ_t^{rs}]) were preferred over model (S_t^r, p_{t+}^{14}, ψ_t^{rs}). However, a model in which temporal variations of survival probabilities of the four states were parallel on a logit scale (S_{t+}^r, p_{t+}^{14}, ψ_t^{rs}) was preferred. This indicated that survival probabilities of all states varied over time (Fig. 2) and that the variations were synchronous, suggesting that a common external factor affected survival.

Model (S_{t+}^r, p_{t+}^{14}, ψ_t^{rs}) was again preferred over a model with equal survival in experienced and inexperienced breeders ($S_{t+}^{2=3}$, p_{t+}^{14}, ψ_t^{rs}), or a model with equal survival in inexperienced nonbreeders and first-time breeders ($S_{t+}^{1=2}$, p_{t+}^{14}, ψ_t^{rs}), or a model with equal survival in experienced nonbreeders and experienced breeders ($S_{t+}^{3=4}$, p_{t+}^{14}, ψ_t^{rs}). Mean survival probabilities estimates indicated that first-time breeders had the lowest survival probabilities (Table 2). Survival estimates from (S_{t+}^r, p_{t+}^{14}, ψ_t^{rs}) indicated that survival of first-time breeders was particularly low in 1996, 1997, and 1999 (Fig. 2).
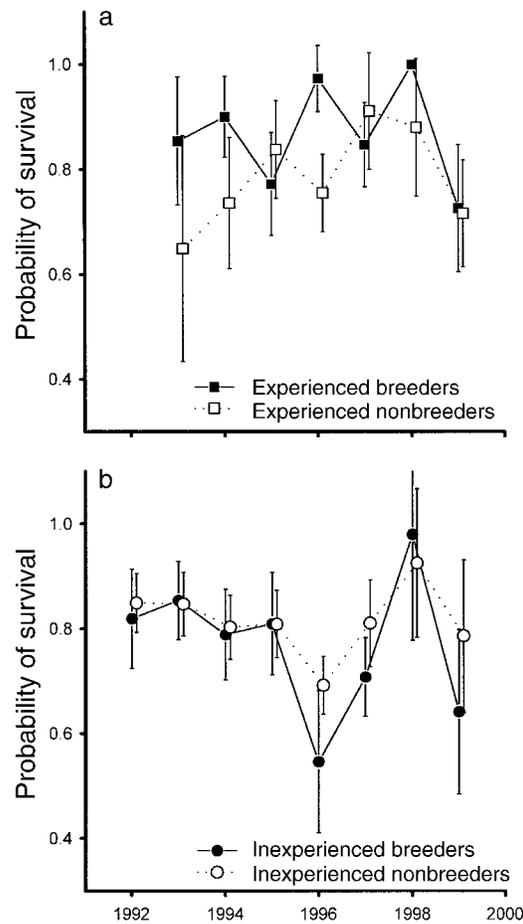

FIG. 2. Estimates (± 1 SE) of survival probability of (a) experienced breeders and nonbreeders (no estimates are available for the first year of the study because there were no experienced individuals), and (b) inexperienced breeders and nonbreeders under model (S_t^r, p_t^{14}, ψ_t^{rs}). Because of identifiability problems no estimate is available for 2000.

State transition probabilities.—Models in which transition probabilities only depend on state (Table 1; [S_{t+}^r, p_{t+}^{14}, ψ^{rs}]) or time (S_{t+}^r, p_{t+}^{14}, ψ_t), were not preferred over model (S_{t+}^r, p_{t+}^{14}, ψ_t^{rs}). A model (S_{t+}^r, p_{t+}^{14}, ψ_{t+}^{rs}) with an additive effect of state and time for breeding transition probabilities was preferred over model (S_{t+}^r, p_{t+}^{14}, ψ_t^{rs}). There was strong evidence for a difference between breeding transition probabilities of first-time

TABLE 2. Mean parameter estimates for survival and breeding transition probabilities for Blue Petrels at Kerguelen Islands.

State in year t	Survival to $t + 1$		Breeding at $t + 1$		Nonbreeding at $t + 1$	
	Mean	1 SE	Mean	1 SE	Mean	1 SE
Inexperienced nonbreeder	0.815	0.044	0.135	0.022	0.865	0.022
First-time breeder	0.750	0.060	0.381	0.050	0.619	0.050
Experienced breeder	0.896	0.043	0.500	0.055	0.500	0.055
Experienced nonbreeder	0.821	0.047	0.317	0.047	0.683	0.047

Note: Survival probability estimates were obtained from model (S_{t+}^r, p_{t+}^{14}, ψ_{t+}^{rs}).
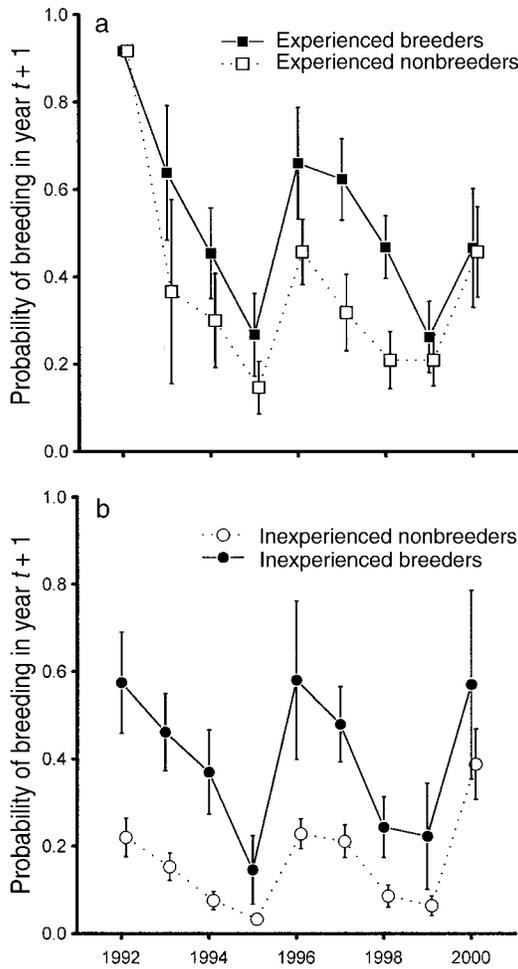
FIG. 3. Estimates (±1 SE) of state transition probability for (a) experienced breeders and nonbreeders in year t (no estimates are available for the first year of the study because there were no experienced individuals), and (b) inexperienced breeders and nonbreeders in year t under model (S^r_{t+}, p^{14}_{t+}, ψ^{rs}_t). Because of identifiability problems, no estimate is available for 2000.

breeders and experienced breeders, because a model in which first-time and experienced breeders had equal probabilities of nonbreeding in the following year was rejected (S^r_{t+}, p^{14}_{t+}, $\psi^{24=34}_t$). First-time breeders had a lower probability of breeding in the following year than experienced breeders (Fig. 3). There was also strong evidence for a difference between breeding transition probabilities of inexperienced nonbreeders and first-time breeders ([S^r_{t+}, p^{14}_{t+}, ψ^{rs}_t] vs. [S^r_{t+}, p^{14}_{t+}, $\psi^{11=24}_t$]). Inexperienced nonbreeders had a lower probability of breeding in the following year than first-time breeders (Table 2). Similarly, a model (S^r_{t+}, p^{14}_{t+}, $\psi^{34=44}_{t+}$) in which experienced breeders and experienced nonbreeders had equal probabilities of nonbreeding in the following year was rejected, and experienced breeders had a higher probability of breeding in the following year than experienced nonbreeders (Table 2).

Environmental and individual effects

From 1992 to 2000, the ΔSSH ranged from -30 mm to 41 mm. Plotting the annual survival of first-time breeders and inexperienced nonbreeders against ΔSSH showed an inverse relationship (Fig. 4), suggesting that mortality of inexperienced Blue Petrels increased when environmental conditions deteriorated. There was no apparent relationship between the survival of experienced breeders and nonbreeders and ΔSSH (Fig. 4). To formally test these relationships, we tested a model in which state survival probabilities were a function of ΔSSH (Table 1; [$S^r_{\Delta\ SSH}$, p^{14}_{t+}, ψ^{rs}_{t+}]), which was preferred over model (S^r_{t+}, p^{14}_{t+}, ψ^{rs}_{t+}) by a wide margin of QAIC$_c$
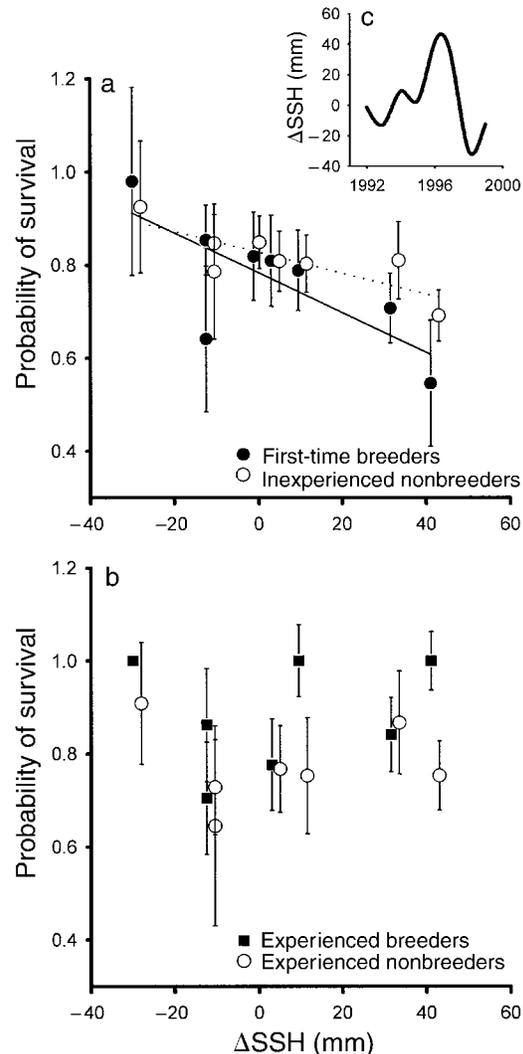

FIG. 4. Relationships between the survival probability in year t and variation in sea surface height (SSH) between January and October of year t for (a) first-time breeders and inexperienced nonbreeders, and (b) experienced breeders and experienced nonbreeders. Survival estimates (±1 SE) were obtained from model (S^r_t, p^{14}_{t+}, ψ^{rs}_{t+}). Inset (c) shows the variation in SSH between January and October as a function of year.

TABLE 3. Estimation of the slope of the relationship between variation in sea surface height (ΔSSH) and annual survival in Blue Petrels at Kerguelen Islands.

Breeding state	Slope	1 SE	95% CI
Inexperienced nonbreeders	−0.0159	0.0049	−0.0255, −0.0062
First-time breeders	−0.0256	0.0074	−0.0401, −0.0111
Experienced breeders	0.0002	0.0081	−0.0156, 0.0160
Experienced nonbreeders	−0.0091	0.0071	−0.0294, 0.0047

Note: Estimates are from model ($S^r_{\Delta SSH}$, p^{14}_{t+}, ψ^{rs}_{t+}).

($\Delta QAIC_c = 10.104$). For first-time breeders and inexperienced nonbreeders, the slope of the relationship was negative, with 95% confidence intervals excluding zero (Table 3). The $|\beta|$ tended to be higher for first-time breeders (although the confidence intervals showed some overlap), perhaps indicating that they might be more sensitive to variations in ΔSSH than nonbreeders. For experienced individuals, the value of β was close to zero (Table 3), indicating that the effect of ΔSSH on the survival probabilities was null or very low; ΔSSH explained 58.5% of the variation in survival over time for all breeding states, and 88.2% of the temporal variation in survival for first-time breeders and inexperienced breeders.

Mean body mass varied with experience, breeding state, and year (all P's < 0.001; Appendix A). Among breeders and nonbreeders, experienced individuals had higher body mass than inexperienced ones (Appendix B). The pattern of variation of body mass across years differed between breeding states (significant interaction, year $\times$ state; Appendix A). However, a model in which survival was a function of body mass (Table 1; [S^r_{mass}, p^{14}_{t+}, ψ^{rs}_{t+}]) was not preferred over model ($S^r_{\Delta SSH}$, p^{14}_{t+}, ψ^{rs}_{t+}). For each state, the 95% confidence intervals for the slopes of the relationships between survival and body mass included zero. This suggested that body mass during breeding did not affect survival estimated during the following year. A model with an additive effect of ΔSSH and body mass on survival ($S^r_{\Delta SSH+mass}$, p^{14}_{t+}, ψ^{rs}_{t+}) was not preferred over model ($S^r_{\Delta SSH}$, p^{14}_{t+}, ψ^{rs}_{t+}).

Using model ($S^r_{\Delta SSH}$, p^{14}_{t+}, ψ^{rs}_{t+}), we tested for an effect of ΔSSH ($S^r_{\Delta SSH}$, p^{14}_{t+}, $\psi^{rs}_{\Delta SSH}$) and body mass ($S^r_{\Delta SSH}$, p^{14}_{t+}, ψ^{rs}_{mass}) on state transition probabilities. Both models were clearly rejected ($w_i < 0.0001$; Table 1).

DISCUSSION

Experience had a significant, positive influence on survival and future breeding probabilities for both breeding and nonbreeding birds, confirming our first hypothesis. This result is consistent with previous findings on the Blue Petrel (Chastel et al. 1995*a*) and other long-lived species (see a review in Cam and Monnat [2000], Ainley [2002]) for which inexperienced breeders had a lower future probability of breeding than experienced breeders. First-time breeders had a lower survival probability than experienced breeders, which is also consistent with several other studies (Promislow 1991, Clutton-Brock et al. 1996, Cam and Monnat

2000). Among nonbreeders, survival probability did not seem to be affected by experience. In addition, we showed that, independently of the costs associated to reproduction, experience per se affected the life history of individuals, because inexperienced nonbreeders had lower future breeding probabilities than experienced nonbreeders.

For experienced individuals, we found evidence of positive phenotypic correlations between the components of fitness: breeders in year t showed a higher probability of surviving and breeding in year $t + 1$ than nonbreeders in year t. Positive covariation among life history traits is a common phenomenon in iteroparous animals (see a review in Cam et al. [1998], Sandercock et al. [2000], Yoccoz et al. [2002]). Positive phenotypic correlations between components of fitness may be caused by variation in resource availability across environments (individuals in better environments should exhibit higher reproductive and survival rates than individuals in poorer environments) or variations in individual quality. Because fitness parameters were estimated from only one colony where both breeders and nonbreeders were observable, and because birds, regardless of their status and experience, were exposed to the same environmental conditions, we suspect that positive correlations were more likely linked to differences in individual quality. In Blue Petrels, body condition may reflect individual quality because there is a positive correlation between reproductive performance and body condition (Chastel et al. 1995*b*). Thus, our findings support the prediction of Nur's (1988) model regarding the question of breeding vs. not breeding.

By contrast, for inexperienced individuals, we found evidence of negative phenotypic correlations: first-time breeders showed a lower probability of surviving than inexperienced nonbreeders, particularly during the years 1996, 1997, and 1999. This was particularly marked in 1996, with an exceptionally low survival probability (0.628 ± 0.068, mean $\pm$ 1 SE) for such a long-lived species. This result strongly supports the hypothesis of a reproductive cost on survival for inexperienced individuals. Nevertheless, first-time breeders in year t showed a higher probability of breeding in year $t + 1$ than inexperienced nonbreeders in year t. Given that we observed a reproductive cost on survival, one may expect a reproductive cost on future breeding probability. This paradox is resolved within

the framework of the selection hypothesis, which is supported by the results. First, there is evidence in the Blue Petrel that first-time breeders have a lower success probability mostly because their body condition is low compared to that of experienced breeders (Chastel et al. 1995a). Secondly, the variations in breeding frequency are partly explained by variations in body condition, individuals in good condition breeding more frequently than those in poor condition (Chastel et al. 1995b). Thus, the higher proportion of failed breeders among first-time breeders might reflect a higher proportion of individuals in poor condition (i.e., low-quality individuals). Given that the survival probability of first-time breeders was lower than the survival probability of inexperienced nonbreeders, these results suggest that selection might be operating on first-time breeders. The selection process on first-time breeders in year t implies that a higher proportion of high-quality individuals is present in year $t + 1$. This is consistent with the low survival probability for first-time breeders during the winter in 1996 and 1997, followed by high probabilities of breeding in 1996 and 1997. Thus, a large fraction of the low-quality individuals was probably removed from the population, and the high-quality individuals that remained had a high probability of breeding during the following summers. Similar patterns were observed for inexperienced nonbreeders and experienced nonbreeders, suggesting that selection also operated to a lesser degree within these portions of the population. The survival probabilities of inexperienced, but not experienced, individuals are negatively affected by poor environmental conditions, which is consistent with the hypothesis of a high proportion of low-quality individuals among the segment of the population that never attempted to breed. The values of the slopes between survival and ΔSSH for each state suggest that selection probably operates strongly on inexperienced individuals and is weak or null on experienced ones.

Because we estimated apparent mortality, which includes mortality and permanent emigration, the low apparent survival of inexperienced birds may also reflect high permanent emigration for individuals caught for the first time. We think that this is unlikely because no Blue Petrels banded in the study colony were captured outside the study colony during surveys on Mayes Island, although we cannot exclude the possibility that birds permanently emigrated to neighboring islands.

Our results support the hypothesis of an influence of environmental conditions on life history traits and on the costs of reproduction as predicted by Erikstad et al. (1998). First, survival probability for inexperienced individuals was correlated with environmental conditions. Second, the decrease in survival for first-time breeders was particularly pronounced during years with poor environmental conditions (1996 and 1997), suggesting that the costs of reproduction were enhanced during these years. In seabirds, the body condition of

individuals deteriorates during breeding due to the energetic costs of incubation (during which individuals fast on the egg) and chick rearing (when individuals forage at sea to feed the young) (Warham 1990). Inexperienced individuals in poor condition that faced poor food conditions during or after breeding probably could not restore their physical conditions and suffered higher mortality. This could be due to poorer foraging efficiency and lower skill of young inexperienced birds, as established for the Herring Gull *Larus argentatus* (Greig et al. 1983). Although our results indicate that survival probabilities for each segment of the population were not related to body condition, we think that this does not necessarily refute our hypothesis. Indeed, our covariate (body condition during breeding) might not have been appropriate, because body condition varies importantly throughout the year (Warham 1990).

The relationships between survival probabilities and ΔSSH were strong and unequivocal (Fig. 4); ΔSSH explained >88% of the variation in survival for first-time breeders and inexperienced nonbreeders. This oceanographic variable seems to be a promising proxy of climate conditions when assessing the ecological effects of climate fluctuations on the population dynamics of seabirds, and perhaps marine mammals. It should be noted that the stratification of the studied population into breeding states clearly improved our understanding of the effect of environmental variability on survival.

In conclusion, our results show that first-time breeders pay a cost of reproduction in terms of survival. Although it is considered difficult to demonstrate a reproductive trade-off using correlative data (Reznick 1985), our results confirm those of Pyle et al. (1997) on the Western Gull *Larus occidentalis*, those of Tavecchia et al. (2001) on the Greater Flamingo *Phoenicopterus ruber roseus*, and those of Tavecchia et al. (2003) on Soay sheep *Ovis aries*, who also found costs of first reproduction for young individuals. It should be noted that age was not taken into account because we did not have information on age of the subjects, but that some of the ''first-time breeder'' effect may be due to age effects, as suggested by other studies (Pyle et al. 1997) in which first-time breeders paid a higher survival cost if they attempted to breed at a young age. First reproduction may act as a filter, selecting individuals of higher quality. The increase in survival with experience would correspond to a progressive disappearance of phenotypes of lesser quality, although the improvement of performance within individuals may contribute marginally to the observed patterns at the population level. Variation in sea surface height, reflecting food availability, in the winter following reproduction is probably a major factor of selection. The mortality among first-time breeders was particularly enhanced when food availability was low, indicating higher costs of reproduction during these years. Following these high-intensity selection events,

a higher proportion of high-quality individuals remained in the population, which resulted in an increase of the probability of breeding during the next summer. More stratified models, accounting for part of the remaining heterogeneity among experienced breeders, would permit estimation of the intensity of selection on experienced individuals.

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APPENDIX A

A table presenting results of a mixed-model ANOVA testing the effects of breeding state (breeder vs. nonbreeder), experience (inexperienced vs. experienced), year, and their interactions on body mass of Blue Petrels is available in ESA's Electronic Data Archive: *Ecological Archives* E086-034-A1.

APPENDIX B

Figures showing variation in the mean body condition (± SE) of (a) experienced breeders and first-time breeders and (b) experienced nonbreeders and inexperienced nonbreeders across years is available in ESA's Electronic Data Archive: *Ecological Archives* E086-034-A2.