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Population dynamics in a long-lived seabird: I. Impact of breeding activity on survival and breeding probability in unbanded king penguins

CÉLINE LE BOHEC*, MICHEL GAUTHIER-CLERC†,
DAVID GRÉMILLET*§, ROGER PRADEL‡, ARNAUD BÉCHET†,
JEAN-PAUL GENDNER* and YVON LE MAHO*

**Département d'Écologie, Physiologie et Éthologie, Institut Pluridisciplinaire Hubert Curien (IPHC), Strasbourg, France; †Centre de Recherche de la Tour du Valat, Arles, France; ‡Centre d'Écologie Fonctionnelle et Évolutive, Montpellier, France; and §Percy FitzPatrick Institute of African Ornithology, NRF/DST Centre of Excellence, University of Cape Town, Rondebosch, South Africa*

Summary

1. Understanding the trade-off between current reproductive effort, future survival and future breeding attempts is crucial for demographic analyses and life history studies.

2. We investigated this trade-off in a population of king penguins (*Aptenodytes patagonicus*) marked individually with transponders using multistate capture–recapture models.

3. This colonial seabird species has a low annual proportion of non-breeders (13%), despite a breeding cycle which lasts over 1 year. To draw inferences about the consequences of non-breeding, we tested for an effect of reproductive activity on survival and on the probability of subsequent breeding.

4. We found that birds non-breeding in year t show the same survival rate as breeders (two-states analysis: breeding and non-breeding). However, breeders had a lower probability of breeding again the following year. This negative phenotypic correlation suggests the existence of reproductive costs affecting future breeding probability, but it might also be strengthened by late arrival for courtship in year t.

5. A three-state analysis including breeding success revealed that failed breeders in year t have a lower probability to reproduce successfully in year $t + 1$ than non-breeders in year t, providing some evidence for the existence of reproductive costs. Moreover, successful breeders showed higher survival probability. This positive phenotypic correlation between current reproduction and subsequent survival supports the hypothesis of an heterogeneity in individual quality.

6. Males breeding in year t had a lower probability to breed again in year $t + 1$ than females, suggesting higher reproductive costs for this sex. Such additional costs might be due to higher male parental investment in the final phase of chick-rearing, which also delays the arrival of males in year $t + 1$, and decreases their breeding probability.

7. Our study is the first to explore the breeding biology and the demography of penguins without the disturbance of flipper-bands.

Key-words: heterogeneity hypothesis, intermittent breeding, multistate mark–recapture models, prudent parent hypothesis, transponder tags.

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Correspondence: Céline Le Bohec, IPHC, 23 rue Becquerel, 67087 Strasbourg Cedex 02, France (e-mail: celine.lebohec@c-strasbourg.fr).

Introduction

Survival and reproduction are two functions competing for the same resources. The resulting trade-off holds a central place in life history theory which predicts how animals should optimize lifetime reproductive success (Roff 1992; Stearns 1992; McNamara & Houston 1996). Similarly, the trade-off between current and future reproduction conditions reproductive costs and may be an important selective agent within the evolution of life history strategies (Williams 1966; Reznick 1985; Stearns 1989). Because long-lived species typically have low annual reproductive output (relative to their potential life span) they have relatively little to gain, and much to lose, in terms of fitness, from investigating too heavily in any one reproductive event. Even small increases in their mortality rates can lead to large reductions in lifetime reproductive success. Consequently, long-lived species should minimize risks linked to reproduction (Goodman 1974; Pugesek 1990; Wooller *et al.* 1992), and will be unwilling to trade their own survival for that of their offspring (Sæther *et al.* 1993).

The prudent parent hypothesis (Goodman 1974; Drent & Daan 1980; Cam *et al.* 1998) predicts that non-breeders avoiding the costs of reproduction show higher survival and higher future breeding probabilities than breeders. For an individual, taking sabbaticals is therefore an efficient way to increase its residual reproductive value (Wooller *et al.* 1989; Aebischer & Wanless 1992), i.e. the expected number of offspring produced by an individual in a particular age class after the current reproductive event (Stearns 1992), and for long-lived animals confronted with a stochastic environment, non-breeding ensures survival until the next favourable year (Schaffer 1974; Harris & Wanless 1995). Such reproductive sabbaticals might be triggered by the fitness costs accumulated during successive breeding events or by an unusually high reproductive effort the previous year.

Few studies have focused on the relationship between non-breeding and demographic parameters such as survival probability or future reproduction (Orell *et al.* 1994; Mougin *et al.* 1997; Cam *et al.* 1998). However, population growth rate is affected strongly by the proportion of potential breeders that actually breed (Cam *et al.* 1998). Non-breeding is therefore an important regulation mechanism (Hémery *et al.* 1986; Nichols *et al.* 1994), particularly at high population densities causing intraspecific competition for food (Hémery *et al.* 1986; Mougin *et al.* 1997; Tavecchia *et al.* 2005).

According to the 'individual heterogeneity in quality hypothesis' (Vaupel & Yashin 1985; Nur 1988; Cam *et al.* 1998; Cam & Monnat 2000; Golet *et al.* 2004; Barbraud & Weimerskirch 2005) intermittent breeding might also be linked to individual quality. This hypothesis is supported by empirical studies which indicate that non-breeders are lower-quality individuals in terms of lower survival (Mills 1989; Harris & Wanless 1995; Beauplet *et al.* 2006). Indeed, the fittest individuals might show high reproductive and survival rates, whereas low-quality individuals breed less well and die sooner. Cumulative experience might, none the less, have a positive impact upon individual reproductive performances (Nur 1984; Forslund & Pärt 1995).

Until now, the respective importance of reproductive cost and the individual quality hypothesis has not been studied thoroughly. The purpose of this paper is to address this question using a long-lived seabird, the king penguin (*Aptenodytes patagonicus*), by testing for the impact of non-breeding and breeding on survival and future breeding probabilities. The evaluation of selective pressure that reduces survival, such as reproductive costs, requires accurate information on adult survival. Survival probabilities are calculated via an analysis of capture–recapture data (Lebreton *et al.* 1992), and the quality of the data obviously influences the validity of the model output. The main problem is that our present knowledge on the population biology of penguins is based on the use of flipper bands, and several recent publications reported long-term effects of banding in penguins (Froget *et al.* 1998; Ainley 2002; Jackson & Wilson 2002; Gauthier-Clerc *et al.* 2004). In particular, for king penguins, the latter study demonstrated that banded birds have a later arrival at the colony for courtship, a lower breeding probability and a lower breeding success. Recent data suggest that they also have lower survival probabilities (Ribic *et al.* unpublished data). In the present study, we have therefore monitored a population of king penguins using an automatic passive integrated transponder (PIT) tag identification system. This eliminates potential biases due to the detrimental effects of external marks, the loss of flipper bands over the years (Weimerskirch *et al.* 1992; van Heezik *et al.* 1994; Froget *et al.* 1998) and the presence of human observers at the colony that could stress the birds and modify their behaviour (Culik & Wilson 1991; Regel & Pütz 1997). Another major asset of this system is a standardized and ceaseless recapture effort.

The king penguin has an unusual breeding cycle because it needs more than 1 year to fledge a chick (around 14–16 months including moult; Stonehouse 1960; Barrat 1976; Weimerskirch *et al.* 1992; Descamps *et al.* 2002). After successful reproduction, a new breeding attempt starts considerably later than in the previous year. If the arrival for courtship occurs later than mid-March the adult skips the breeding year. First, we tested the hypothesis that individual king penguins show variable breeding probabilities during their life span. We predict that birds occasionally take a year off under certain conditions. For instance, the reproductive cost of a successful breeding event might lead to breeding failure, birds being not in sufficiently good condition to ensure regular attendance at the colony. In addition, their later arrival for courtship might have a cumulative, negative effect.

Secondly, we examined the possible covariation between non-breeding and two key components of fitness: survival probability and the probability of breeding the following year. Our aim was to draw inferences about consequences of reproductive output by testing for an effect of a breeding success in year t on future fitness, in particular on survival and on the probability of breeding in year $t + 1$. We tested four predictions to evaluate the relative importance of the 'reproductive cost hypothesis' (predictions 1, 2 and 3) and the 'individual heterogeneity in quality hypothesis' (prediction 4) for reproductive strategies.

1. Birds taking a sabbatical non-breeding year have higher survival probabilities and a higher probability of reproducing in subsequent years than breeding birds.

2. A successful reproduction affects survival probability negatively the following year.

3. Successful birds in year t have a higher probability of breeding unsuccessfully or of skipping breeding in year $t + 1$ than failed breeders or non-breeders. Such a negative correlation would suggest the existence of reproductive costs, but it might also be strengthened by the breeding delay linked to the particular king penguin breeding cycle.

4. In contrast, assuming that individual quality influences success, successful individuals should exhibit the highest survival and lowest probability of non-breeding in the following year. Such positive association would suggest variations in individual quality. Variability in individual breeding performances and birds with high frequency of breeding success should corroborate this hypothesis all the more.

Finally, several studies have provided evidence of an influence of sex on survival (e.g. Aebischer & Coulson 1990; Tavecchia *et al.* 2001; Olsson & van der Jeugd 2002) and breeding probabilities in birds (e.g. Cézilly *et al.* 1996; Cam & Monnat 2000). Classically asymmetric reproductive costs are expected in polygamous species but they also occur in monogamous species because of the costs of egg-laying, which are covered by females only (Tavecchia *et al.* 2001). Sex-biased mortality may also differ as a result of sexual dimorphism (Promislow *et al.* 1992). Parental investment is shared equally between the sexes in king penguins. The female invests in the egg formation but the male takes over most of the incubation duties (Olsson 1996). We predict that reproductive costs, in terms of survival and breeding probability, are the same for females and males because of similar parental investment and low sexual dimorphism.

Materials and methods

STUDY SITE AND DEMOGRAPHIC SURVEY

This study was carried out on Possession Island (46°25′ S, 51°45′ E), Crozet Archipelago, where a part of the colony 'La Grande Manchotière' has been monitored from 1998 to 2005. Two antennas are buried permanently on each of the three pathways to the study area and connected to a computerized reading system that logs data automatically. The small PIT tags, implanted under the bird's skin between the leg and tail, are activated electromagnetically by the antennas and allow individual identification of the fitted birds throughout their lifetime. The sequence of signals from the antennas reveals whether a bird is entering or leaving the breeding site. This tag has no known adverse effect (Michard *et al.* 1995; Froget *et al.* 1998). Detailed information on the study site, field methods and breeding populations are provided in Gendner *et al.* (2005).

The breeding cycles of the birds were established by interpreting their movements between the breeding area and the sea, and confirmed by analysis of video recordings of body and plumage conditions (see details in Descamps *et al.* 2002; Gendner *et al.* 2005). The duration of their sojourns ashore or at sea informed us about their status and their activities during each stage of their breeding cycle. Our analysis excluded animals that had not reached reproductive age. We used the following notation for states: (1) the animal is alive and does not breed; (2) the animal is alive and fails to reproduce; and (3) the animal is alive and breeds successfully. Birds were considered as being successful (i) if they alternated several short trips at sea and sojourns ashore later than mid-October (Jouventin & Lagarde 1995), thereby showing that they are provisioning a chick (van Heezik *et al.* 1994), and (ii) if they started their premoult foraging trip after the end of October (Descamps *et al.* 2002; Gendner *et al.* 2005). The sex of the birds was determined by analysing the chronology of the sex-specific incubating shifts (Gauthier-Clerc *et al.* 2001). Indeed, at the beginning of the breeding cycle, males are ashore for approximately 1 month to display and take the first long shift of incubation, whereas females leave the colony a few hours after laying, once their males have begun to incubate the egg (Barrat 1976). This procedure allowed us to sex 90% of the individuals. Data from the first year were excluded from the breeding analysis because the birds were transponded during incubation or brooding, and therefore hatching dates could not be determined precisely.

The proportion of non-breeders was calculated each year. To estimate breeding frequencies and proportions of individuals according to their successful breeding attempts, we considered only birds whose records were available for at least 3 successive years. The breeding frequency of the population was calculated as the mean of all individual breeding frequencies (see Jiguet & Jouventin 1999).

STATISTICAL METHODS

We relied on the multistate capture–recapture modelling approach (Lebreton *et al.* 1992; Brownie *et al.* 1993; Schwarz *et al.* 1993) that allows for estimation of survival and resighting probabilities, as well as probabilities of transitioning to an alternate reproductive state, given that the individual is alive (Nichols *et al.* 1994; Nichols & Kendall 1995). We used the conditional Arnazon–Schwarz model (Schwarz *et al.* 1993) as available in program M-SURGE (Choquet *et al.* 2004). Three types of parameters can be estimated with these models: apparent survival probability: S_t^r, conditional transition probability Ψ_t^{rs} and capture probability p_t^r. Definitions are as follows:

S_t^r = probability that a bird in breeding state r ($r = 1, 2, 3$) at time t survives until period $t + 1$. It is a local survival probability: even if scarce, permanent emigration might be possible (Weimerskirch *et al.* 1992) and could not be distinguished from death.

Ψ_t^{rs} = probability that a bird in breeding state r at time t is in breeding state s ($s = 1, 2, 3$) at time $t + 1$, given that the individual survived until $t + 1$.

p_t^r = probability that a bird in state r at time t is resighted, given that it is alive and present at time t.

The recapture period lasts from November t to May $t + 1$, excluding the deadly winter months. All adults detected during a given summer had been detected the previous summer. We therefore considered the probability p_t^r of detecting a bird (breeding or non-breeding) was 1·0, provided that it remained alive. Consequently, the reliability of survival estimates should be high (Pollock *et al.* 1990; Lebreton *et al.* 1992), and this automatic identification system complies with the assumptions of the known-fate model.

Following Nichols *et al.* (1994), capture history data were used to estimate time- and state-specific survival probabilities and time-specific transition probabilities between states. This method allowed us to test hypotheses about whether reproductive costs affect future survival, future reproduction (probability of breeding in the following year), or both factors.

In addition, we investigated the sex effect on survival and transition probabilities. Indeed, sex specificity is a common source of variation in survival probability of some birds, and it was necessary to determine whether we needed to incorporate this variable into our models. However, sex determination using breeding cycle was not possible for some birds ($n = 46$), either because their incubation shifts were not sufficiently well defined, because they showed the same amount of female- and male-type breeding cycles, or because they did not breed again and/or died. Thus, the determination of sex is not independent from capture histories and survival. From a statistical viewpoint, it is consequently not possible to analyse the capture histories of individuals of known sex separately from those of individuals of unknown sex without running the risk of overestimating survival probabilities. We first estimated the sex ratio of our population to be 1·18 males per female (218 males, 185 females). Following Oro & Pradel (2000), we used a ‘sex’ covariate based upon this sex ratio, thus coding 1 for males, 0 for females and 0·54 for unsexed individuals. In models containing the ‘sex’ covariate, a logit link function was used.

To draw inferences about the evolutionary consequences of non-breeding, we investigated two complementary fitness components and proceeded as follows: (i) we estimated and compared the survival probabilities of non-breeders ($s = 1$) and breeders ($s = 2$), and the respective probabilities that a non-breeder and breeder will breed again in the following season, given that they are alive (two-states analysis). We also tested whether both state-specific survival and transition probabilities varied over time and between sexes (independently, in interaction or in parallel). (ii) We repeated the same analysis while including the reproductive output (failed breeder, $s = 2$; and successful breeder, $s = 3$) in order to evaluate the fitness costs of a successful breeding activity (three-states analysis).

For all data sets, the most general model had time- (t), state- (r, s) and sex-specific (g) parameters ($p_i S^r_{t*g*} \Psi^{rs}_{t*g*}$). An asterisk between terms indicates that an interaction is included, and a plus sign indicates an additive model without interactions.

GOODNESS-OF-FIT AND MODEL SELECTION

One prerequisite of our analysis is that the most general model fits the data adequately. We fulfilled this requirement by using the goodness-of-fit tests (GOF) made available recently for multistate mark–recapture models (Pradel *et al.* 2003) and computed in the program U-CARE (Choquet *et al.* 2005). Because we wanted to investigate possible effects of sex on survival and transition probabilities, we fitted the Arnason–Schwarz model for each sex separately and then pooled the results to obtain the overall fit. When the lack of fit was significant, we calculated a variance inflation factor ($\hat{c}$) to account for extra-binomial variation present in our data and adjust model selection criteria. This coefficient was then computed as the ratio of the GOF statistic for our global model to the degrees of freedom ($\hat{c} = \chi^2$/d.f.; Lebreton *et al.* 1992). Burnham & Anderson (1998) recommend using quasi-likelihood in situation where $1 \leq \hat{c} \leq 4$; a higher value indicates the remaining structural failure of the general model (Cam *et al.* 2004).

Model selection was based on the estimation of an information-theoretic criterion (Akaike’s information criterion) adjusted for small sample size (AICc; Burnham & Anderson 2002). This criterion allowed us to select the best model in terms of both parsimony (fewest model parameters) and adequate description of the data. Models with the lowest AICc values were retained as good candidate models (Burnham & Anderson 1998). AICc values are interpretable only in terms of ‘relative value’ (Lebreton *et al.* 1992; Burnham & Anderson 1998). When the difference between the AICc values of two models was lower than 2, we considered that they were statistically indistinguishable. In this case, the more interpretable or biologically meaningful model was usually retained (Tavecchia *et al.* 2001). With the variance inflation term, the quasi-Akaike information criterion (QAICc = deviance/$\hat{c}$ + 2 × np; Lebreton *et al.* 1992; Pradel *et al.* 2003) improves on conventional AICc because it incorporates corrections for small sample size and overdispersion (Burnham & Anderson 1998).

Results

PRELIMINARY TESTS

Between summer 1997/1998 and summer 2004/2005, a total of 449 adult king penguins were marked and their reproductive activities were monitored. For the two-states analysis, the overall GOF test showed that the general model $[p^{r}_{t*g*}S^{r}_{t*g*}\Psi^{rs}_{t*g*}]$ fitted the data satisfactorily ($\chi^2_{23} = 31{\cdot}96$, $P = 0{\cdot}101$), so no adjustment to model selection or variance estimation was required (Buckland *et al.* 1997). For the three-states analysis, the GOF test indicated a lack of fit of our global model ($\chi^2_{44} = 80{\cdot}94$, $P = 0{\cdot}001$). All deviations from expected values laid in TEST 3G.Sm of the group 'male' ($\chi^2_{18} = 31{\cdot}67$, $P = 0{\cdot}024$). Given that this component has not yet been identified as biologically meaningful, that it concerns only one of the studied groups and that the lack of fit is moderate, we opted to apply a variance inflation factor. In the absence of any obvious explanation for this particular departure, elaboration of a corresponding model would amount to overfitting. The relatively small value of the variance inflation factor from the global model test ($\hat{c} = 1{\cdot}84$) was perfectly compatible with overdispersed count data (Burnham *et al.* 1987). Subsequent three-states analysis started from model $[p^{r}_{t*g*}S^{r}_{t*g*}\psi^{rs}_{t*g*}]$ and made use of this overall overdispersion factor estimate $\hat{c}$ to correct for the lack of fit.

OCCURRENCE AND TEMPORAL VARIABILITY OF NON-BREEDING EVENTS

In our study, recapture probabilities did not depend on breeding state. Consequently, it was possible to compute the proportion of non-breeders using equation 7 from Nichols *et al.* (1994). Our population is characterized by a low proportion of non-breeders, with non-significant interannual variability (13% [7–19%]; $\chi^2_6 = 11{\cdot}07$, $P = 0{\cdot}086$; Fig. 1). For the 355 adult birds observed for at least 3 successive years, the breeding frequency was 0·87. Over the 7 years of the study, 48% of the birds bred each year. Among the 52% of the birds that took at least 1 year off, 39% took only 1 year off of 6 years (Table 1). Reproductive performances were not similar between individuals. Indeed, some birds succeeded in less than half their breeding attempts (52%), whereas others performed well in reproduction (34%) and might be considered as high-quality birds (Fig. 2).

COST OF REPRODUCTION: IS IT BENEFICIAL TO SKIP A BREEDING YEAR?

Effect of time, sex and breeding activity on survival probabilities

Reducing the number of model parameters by eliminating non-supported effects or interactions is crucial to obtain good estimates of survival and transition probabilities, and to increase the power of main effect tests (Cézilly *et al.* 1996). Starting with the two-states analysis, we reduced the 46 parameters of the initial model $[p_iS^{r}_{t*g*}\psi^{rs}_{t*g*}]$ to 25 in the model $[p_iS_i\psi^{rs}_{t*g*}]$ through regressive model selection. The model in which survival probability depends only upon time $[p_iS_t\psi^{rs}_{t*g*}]$ rated better than all other models (AICc = 2462·80; Table 2).

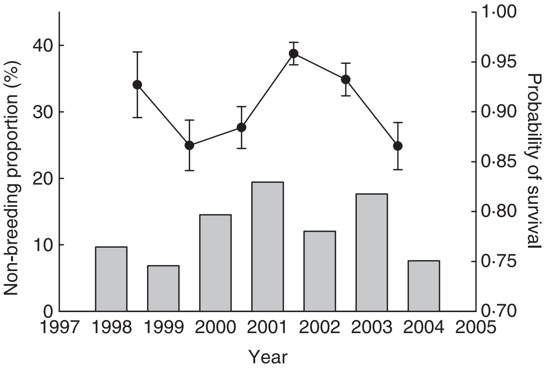

Fig. 1. Annual variations of the estimated non-breeding proportion (bars) and of the estimated survival probability (S_t obtained with the best model $[p_iS_t\psi^{rs}_{g*t+}]$ of the two-states analysis; symbols and line) for king penguins on Crozet Island.

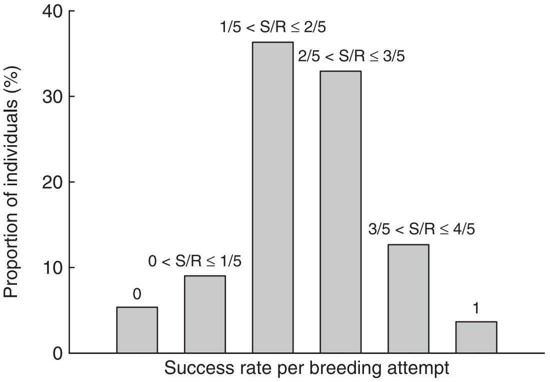

Fig. 2. Proportion of individuals according to their successful breeding attempts in king penguins.

Table 1. Proportion of individuals according to their frequency of non-breeding years for king penguins that take at least 1 year off (52% of the population)

Frequency of non-breeding years	% (*n*)
2 years off/3	1% (2)
1 year off/2	5% (10)
1 year off/3	22% (40)
1 year off/4	10% (18)
1 year off/5	21% (39)
1 year off/6	39% (73)
1 year off/7	2% (4)

The second-best model $[p_iS^{r}_{t+}\psi^{rs}_{t*g*}]$ bore an additive effect of state and time, meaning that the effects of time and state are parallel on a logit scale. This model remained insufficiently supported by the data compared to the model with the lowest AICc $[p_iS_t\psi^{rs}_{t*g*}]$ (ΔAICc = 2·20; Table 2). We detected no state and sex influence on the survival probability. Estimates of annual survival are given in Fig. 1, according to the last best model $[p_iS_t\psi^{rs}_{g*t+}]$.

Effect of time, sex and breeding activity on state transition probabilities

The model with an additive effect of time on state × sex interaction for breeding transition probabilities $[p_iS_t\psi^{rs}_{g*t+}]$ had the lowest AICc value (2450·57; Table 2). Nevertheless,

Table 2. Effect of breeding activity on king penguin survival (S) and transition probability (ψ) obtained with a two-states analysis (breeding or non-breeding). Non-supported effects were removed from the initial state-, time- and sex-dependent model. The AICc with the lowest value indicates the best model (shown in bold type)

Model	DEV	NP	AICc	ΔAICc
Modelling survival probabilities				
$[p_i S^r_{t*g*} \psi^{rs}_{t*g*}]$	2386·40	46	2489·16	26·36
$[p_i S^r_{t+g+} \psi^{rs}_{t*g*}]$	2398·22	32	2467·29	4·50
$[p_i S^r_{t+} \psi^{rs}_{t*g*}]$	2398·24	31	2465·00	2·20
$[p_i S^r_{g+} \psi^{rs}_{t*g*}]$	2434·82	27	2492·41	29·61
$[p_i S^r \psi^{rs}_{t*g*}]$	2434·83	26	2490·15	27·36
$\boldsymbol{[p_i S_t \psi^{rs}_{t*g*}]}$	**2398·35**	**30**	**2462·80**	**0**
$[p_i S_g \psi^{rs}_{t*g*}]$	2435·23	26	2490·56	27·76
$[p_i S_i \psi^{rs}_{t*g*}]$	2435·24	25	2488·31	25·51
Modelling transition probabilities				
$[p_i S_t \psi^{rs}_{t+g+}]$	2422·05	14	2451·02	0·45
$\boldsymbol{[p_i S_t \psi^{rs}_{g*t+}]}$	**2419·46**	**15**	**2450·57**	**0**
$[p_i S_t \psi^{rs}_{t+}]$	2428·38	13	2455·22	4·66
$[p_i S_t \psi^{rs}_{g*}]$	2445·85	10	2466·35	15·79
$[p_i S_t \psi^{rs}]$	2454·23	8	2470·56	20·00
$[p_i S_t \psi_t]$	2972·74	12	2997·46	546·89
$[p_i S_t \psi_g]$	2967·71	8	2984·04	533·47
$[p_i S_t \psi_i]$	2978·93	7	2993·18	542·61
$[p_i S^r_{t+} \psi^{rs}_{t+g+}]$	2421·94	15	2453·05	2·48
$[p_i S^r_{t+} \psi^{rs}_{g*t+}]$	2419·35	16	2452·61	2·04

Model subscripts: i = constant; t = time-dependence; rs = state-dependence; g = sex effect; + = additive model; * = model with interaction. DEV: deviance; NP: number of estimated parameters; AICc: Akaike's information criterion corrected for small sample bias; ΔAICc: difference in value between AICc of the most parsimonious model and the model in question.

the constrained model with time-specific survival probability and additive effects of time, sex and state for transition probabilities $[p_i S_t \psi^{rs}_{t+g+}]$ had ΔAICc < 2 (Table 2). Non-breeders had a higher probability of breeding the following year than breeders ($\psi^{12} > \psi^{22}$; Table 3a). Breeding females at time t had a higher probability of breeding again at time $t + 1$ than breeding males ($\psi^{22}_F > \psi^{22}_M$; Fig. 3). The probability to remain a non-breeder was higher for males than for females ($\psi^{11}_M > \psi^{11}_F$; Fig. 3). Any annual fluctuations in breeding transition probability occurred synchronously among states and sexes (parallel on a logit scale).

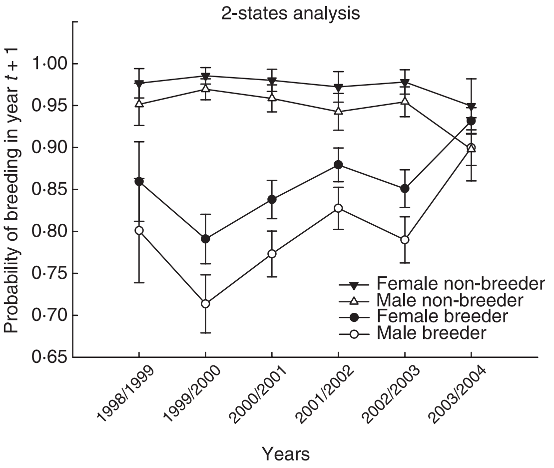

Fig. 3. Estimates of the probability that king penguin males or females are breeders at time $t + 1$ conditional on breeding decision at time t and on survival until $t + 1$ (two-states analysis). The probabilities were estimated from a model including the additive effect of time $[p_i S_t \psi^{rs}_{g*t+}]$.

COST OR QUALITY HYPOTHESIS?

We conducted the same type of analysis for the survival and transition probabilities of individuals breeding in year $t + 1$, conditioned by their breeding decision and output in year t (three-states analysis).

Effect of time, sex and breeding activity on survival probabilities

We reduced the number of parameters explaining survival probability in the initial model $[p_i S^r_{t*g*} \psi^{rs}_{t*g*}]$ by eliminating all interactions between the effects of sex, time and state simultaneously, i.e. $[p_i S^r_{t+g+} \psi^{rs}_{t*g*}]$ (Table 4). This model had a markedly lower QAICc = 2034·48, indicating the absence of parameter interactions on survival probability. Removing the effects of sex, time and state alternatively favoured the model with an additive effect of time and state on survival rates $[p_i S^r_{t+} \psi^{rs}_{t*g*}]$. It indicates that any annual fluctuations in survival probability occurred synchronously among states (QAICc = 2031·63; Table 4). Again, no sex effect on the survival probability was detected (ΔQAICc = 2·85). Successful

Table 3. Mean parameter estimates for survival and breeding transition probabilities obtained with (a) the two-states analysis (from model $[p_i S_t \psi^{rs}_{g*t+}]$) and (b) the three-states analysis (from model $[p_i S^r_{t+} \psi^{rs}_{t+}]$) in king penguins

	Survival to $t + 1$	Non-breeding at $t + 1$ ($s = 1$)	Breeding at $t + 1$ ($s = 2$)	Breeding at $t + 1$	
				Breeding failure ($s = 2$)	Breeding success ($s = 3$)
State at t	Mean ± SE	Mean ± SE	Mean ± SE	Mean ± SE	Mean ± SE
(a) Two-states analysis					
Non-breeder ($r = 1$)	–	0·040 ± 0·018	0·960 ± 0·018	–	–
Breeder ($r = 2$)	–	0·171 ± 0·029	0·829 ± 0·029	–	–
(b) Three-states analysis					
Non-breeder ($r = 1$)	0·902 ± 0·027	0·058 ± 0·021	–	0·340 ± 0·033	0·602 ± 0·035
Failed breeder ($r = 2$)	0·844 ± 0·029	0·020 ± 0·005	–	0·472 ± 0·045	0·508 ± 0·044
Successful breeder ($r = 3$)	0·971 ± 0·009	0·359 ± 0·020	–	0·594 ± 0·021	0·047 ± 0·013

Table 4. Effect of breeding output on king penguin survival (*S*) and transition probability (ψ) obtained with a three-states analysis (successful breeding, failed breeding or non-breeding). Non-supported effects were removed from the initial state-, time- and sex-dependent model. The QAICc with the lowest value indicates the best model (shown in bold type)

Model	DEV	NP	QAICc	ΔQAICc
Modelling survival probabilities				
$[p_i S^r_{t*g*} \psi^{rs}_{t*g*}]$	3369·22	103	2099·58	67·95
$[p_i S^r_{t+g+} \psi^{rs}_{t*g*}]$	3388·98	79	2034·48	2·85
$[p_i S^r_{t+} \psi^{rs}_{t*g*}]$	**3389·16**	**78**	**2031·63**	**0**
$[p_i S^r_{g+} \psi^{rs}_{t*g*}]$	3422·63	74	2038·19	6·56
$[p_i S^r \psi^{rs}_{t*g*}]$	3422·72	73	2035·37	3·74
$[p_i S_t \psi^{rs}_{t*g*}]$	3464·71	76	2066·85	35·22
$[p_i S_g \psi^{rs}_{t*g*}]$	3501·59	72	2075·10	43·76
$[p_i S_i \psi^{rs}_{t*g*}]$	3501·65	71	2072·59	40·96
Modelling transition probabilities				
$[p_i S^r_{t+} \psi^{rs}_{t+g+}]$	3508·44	20	1949·12	2·19
$[p_i S^r_{t+} \psi^{rs}_{t+}]$	**3508·44**	**19**	**1946·93**	**0**
$[p_i S^r_{t+} \psi^{rs}_{g+}]$	3536·51	15	1953·53	6·60
$[p_i S^r_{t+} \psi^{rs}]$	3536·53	14	1951·40	4·46
$[p_i S^r_{t+} \psi_t]$	4385·02	14	2412·63	465·70
$[p_i S^r_{t+} \psi_g]$	4404·13	10	2414·55	467·62
$[p_i S^r_{t+} \psi_i]$	4405·37	9	2413·14	466·20
$[p_i S^r_{t+g+} \psi^{rs}_{t+}]$	3508·26	20	1949·03	2·09

Model subscripts: *i* = constant; *t* = time-dependence; *rs* = state-dependence; *g* = sex effect; + = additive model; * = model with interaction. DEV: deviance; NP: number of estimated parameters; QAICc: Akaike's information criterion based on quasi-likelihood and corrected for small sample bias. Our estimated of overdispersion ($\hat{c}$) was 1·84; ΔQAICc: difference in value between QAICc of the most parsimonious model and the model in question.

breeders had a higher mean survival probability than non-breeders which in turn had a higher survival than failed breeders (Fig. 4).

Effect of time, sex and breeding activity on state transition probabilities

Starting from the model $[p_i S^r_{t+} \psi^{rs}_{t*g*}]$ as selected above, selection led to the model $[p_i S^r_{t+} \psi^{rs}_{t+g+}]$, with all main effects on transition probability but without interaction terms. Thus, breeding transition probability appeared unaffected by sex. An additive effect of state and time $[p_i S^r_{t+} \psi^{rs}_{t+}]$ was retained (QAICc = 1946·93; Table 4). It indicates that transition probabilities to a state at time $t + 1$ according to the state at time *t* occurred synchronously throughout the years (the probability to retain the same status was calculated as the complement to 1 of the sum of the probabilities to move to any other status). Breeding probabilities were estimated using model $[p_i S^r_{t+} \psi^{rs}_{t+}]$. Non-breeders had a higher probability of breeding successfully the following year than failed breeders and successful breeders ($\psi^{13} > \psi^{23} \gg \psi^{33}$; Table 3b). Failed breeders had a higher probability of breeding again the year after and to manage this reproduction with success than to take a year off ($\psi^{23} \gg \psi^{21}$; Table 3b). Successful breeders at time *t* had a higher probability of breeding unsuccessfully or non-breeding at time $t + 1$ than failed breeders or non-breeders (failed breeding at time $t + 1$: $\psi^{32} > \psi^{22} > \psi^{12}$; non-breeding $t + 1$: $\psi^{31} \gg \psi^{11} > \psi^{21}$; Table 3b).

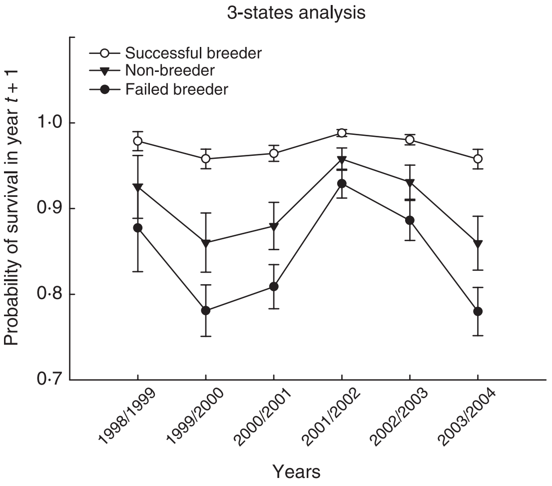

Fig. 4. Estimates of survival probability of successful breeders (white circles), non-breeders (black triangles), and failed breeders (black circles) in king penguins using the model with parallelism $[p_i S^r_{t+} \Psi^{rs}_{t+}]$ (three-states analysis).

Discussion

Our aim was to draw inferences about fitness consequences of non-breeding by testing for an effect of reproductive activity on survival and on the probability of subsequent breeding in unbanded king penguins. We focused on two central hypotheses that might explain such sabbatical years: the costs of reproduction and/or heterogeneity in individual quality. More generally, our state-dependent approach of life history mechanisms allowed us to examine the adaptive significance of intermittent breeding in long-lived birds.

BREEDING IN KING PENGUINS: INFREQUENT SABBATICALS AND HIGH SURVIVAL RATES

Our analysis revealed high, variable survival probabilities, with an average annual survival of 90·6% [77·5–98·4%] (Fig. 1). These results are in line with the very high, yet variable survival rates of king penguins previously evaluated on Crozet and Marion Islands (90% [75–97%], Weimerskirch *et al.* 1992; Olsson & van der Jeugd 2002). Similar variable survival rates were also recorded in yellow-eyed penguins (*Megadyptes antipodes*, 74–96%, Richdales 1957) and in emperor penguins (*A. forsteri*, 60–100%, Barbraud & Weimerskirch 2001). Interannual variability in survival probability, just as within breeding probability, is common among long-lived seabirds (Wooller *et al.* 1989; Chastel *et al.* 1995). Several variables have been proposed to explain these features, including food availability (Coulson 1984; Aebischer & Wanless 1992; Chastel *et al.* 1993) or the access to breeding sites (Chastel *et al.* 1993). We found no difference between years in the proportion of non-breeding king penguins. Environmental stochasticity, and its impact on food availability, is particularly stronger while birds raise their chicks throughout the subAntarctic winter, a time period during which food resources are low, less predictable and more distant from the breeding site (Cherel *et al.* 1993; Olsson & van der Jeugd 2002; Gauthier-Clerc *et al.* 2004). Thus, in this species, winter conditions do not influence the proportion of birds attempting to breed during the ongoing season, but it might impact their reproductive success, with consequences for their future breeding probabilities. Beyond the high survival rate specific to long-lived seabirds, king penguins have low fecundity despite their annual breeding frequency being close to one breeding attempt per year. Consequently, the cost of a breeding attempt might be small for king penguins as, compared to several Procellariiformes, they do not reproduce every second or third year even if they are subject to the same seasonally fluctuating environment.

INTERMITTENT BREEDING IN KING PENGUINS: COST OR QUALITY HYPOTHESIS?

King penguins do not breed as often as they could in theory, although they are physiologically capable of breeding every year (van Heezik *et al.* 1994; Jiguet & Jouventin 1999). Beyond the impact of environmental forcing on king penguin breeding schedules, (1) this itself implies that reproduction has a cost (Goodman 1974; Drent & Daan 1980; Cam *et al.* 1998; Barbraud & Weimerskirch 2005) and that birds are not capable of meeting this cost upon every possible breeding attempt; and (2) additionally, the 'individual heterogeneity in quality hypothesis' (Vaupel & Yashin 1985; van Noordwijk & de Jong 1986; Stearns 1992) predicts that the fittest birds reproduce more often and show the highest breeding success.

Our study shows that successful breeders have a higher probability to become non-breeders or failed breeders the following year (Table 3). This corroborates the former hypothesis, i.e. the existence of reproductive costs. After several successive reproductive phases (successful or unsuccessful), king penguins may accumulate small yet additive reproductive costs such as loss of body mass or depression of the immune system (Gustafsson *et al.* 1994). van Heezik *et al.* (1994) and Gauthier-Clerc *et al.* (2001) suggested the existence of a body condition threshold for breeding in king penguins. In their opinion, failure to breed occurs if birds are not in sufficiently good condition to attend the colony regularly and secure a mate. Similarly, Chastel *et al.* (1995) observed that body condition had a significant influence on the breeding probabilities and on the reproductive success of blue petrels (*Halobaena caerulea*). Beauplet *et al.* (2006) showed that costs of reproduction become apparent only when a physiological threshold is reached. They suggested that reproductive costs occurred in the successful breeding fur seal (*Arctocephalus tropicalis*) that did not breed during the next season, while individuals failing their breeding attempt exhibited costs both in terms of future survival and of fecundity. As king penguins reach such a threshold body condition (Olsson 1997; Gauthier-Clerc *et al.* 2001; Robin *et al.* 2001), especially after a breeding success, they are predicted to invest less heavily in reproduction, or skip a breeding year, to avoid facing reduced survival. Intermittent breeding might allow the individual to recover good body condition, which contributes to high foraging performance and high breeding success the following year. A sabbatical can therefore be interpreted in king penguins as a way of preserving residual reproductive value, as proposed by Coulson (1984), Aebischer & Wanless (1992) and Pugesek & Wood (1992).

However, the unusual breeding cycle of the king penguin that exceeds 1 year mitigates our conclusions, as non-breeding can be considered a standard feature of king penguin biology (as in the shag *Phalacrocorax aristotelis*; e.g. Aebischer & Wanless 1992). The delay linked to the previous success can force individuals to skip a breeding year if they subsequently arrive too late for courtship. Hence, our observation that an individual is less likely to breed in the year $t + 1$ following a breeding attempt might also reflect late arrival for courtship in this second year ('opportunity cost'). Few other bird species have a breeding cycle that lasts more than 1 year. For instance, the breeding cycle of the wandering albatross (*Diomedea exulans*) lasts for up to 375 days (Weimerskirch *et al.* 1986). Jouventin & Dobson (2002) suggested that in this species biennial breeding might be due to physiological (animal body size) and/or ecological (distance to the feeding zone) constraints. However, in contrast with all other biennial or triennial species, a high breeding frequency is observed in the king penguin. Our results also show that failed breeders in year t have a lower probability to reproduce successfully in year $t + 1$ than non-breeders in year t. This difference is once again convincing evidence that reproductive costs do exist, and it suggests that non-breeding is an efficient way to increase residual reproductive value.

In king penguins breeding at the Crozets, we also detected a positive influence of successful breeding on survival probabilities when taking into account the reproductive output component (Fig. 4). This positive phenotypic correlation might be caused by variable individual quality or environmental stochasticity, or by a conjunction of both variables (van Noordwijk & de Jong 1986; Nur 1988; Reznick 1992; Stearns 1992). Jiguet & Jouventin (1999) speculated that individual quality plays a leading role in this process in king penguins, and Harris & Wanless (1995) and Cam *et al.* (1998) for other seabirds. Inter-individual heterogeneities of demographic parameters such as survival or reproduction are very likely to be a feature common to long-lived species (Cam & Monnat 2000). Some individuals are both successful parents and good survivors (Curio 1983; Golet *et al.* 2004; Beauplet *et al.* 2006). In our study the high survival probability of successfully breeding king penguins compared to non-breeders and failed breeders and heterogeneity in the frequency of breeding success (Fig. 2) supports this 'quality hypothesis'. Our findings are consistent with a previous study of long-lived kittiwakes (*Rissa tridactyla*, Cam & Monnat 2000). In this species, Coulson & Porter (1985) found that high-quality birds have a high annual reproductive rate as well as a long life span. In king penguins, Olsson (1996) showed a strong effect of parental quality on breeding success. He explained this feature via the twofold influence of individual quality and food availability on survival probability. The author suggested that high-quality birds have sufficiently high foraging efficiencies to reach the physiological state required for breeding, even though food availability is low. High-quality birds are therefore able to reproduce under suboptimal conditions without jeopardizing their survival. Monaghan *et al.* (1989), following the same idea, speculated that low-quality birds which have a tighter energy balance than birds of higher quality, are more sensitive to environmental change.

FORAGING EFFICIENCY AS THE OVERRIDING FORCE

Long-lived birds breeding in stochastic environments seek a balance between reproductive effort and survival based on varying costs and benefits of reproduction (Erikstad *et al.* 1998). In the subAntarctic area food availability might vary strongly between successive years, with knock-on effects on seabird foraging efficiency (Erikstad *et al.* 1998; Golet *et al.* 2004). This interannual variability in resources is supposed to lead to annual fluctuations in survival probability. As we have seen, these fluctuations in survival and transition probabilities occur synchronously between states (parallel on a logit scale) in king penguins, which means that probabilities follow the same pattern over time. In addition, food abundance fluctuates seasonally and the marine resource availability is at its minimum during the winter (Hindell 1988; Cherel *et al.* 1993). The king penguin breeding cycle includes the winter months when resources are less abundant than during the summer, particularly near the colonies. Birds must expend more energy searching for food (Charrassin & Bost 2001), all the more when rearing a chick. In our study, as in Olsson & van der Jeugd (2002), no adult mortality occurred during the summer months. Adult mortality is generally observed in winter for king penguins, and after a breeding failure (Olsson & van der Jeugd 2002; Gauthier-Clerc *et al.* 2004). Besides the death of the chick, breeding failure might bring the adult close to its lower body condition threshold. Because endotherms, especially birds, are under strong energetic constraints, even a brief period of unfavourable energy balance may be fatal (e.g. Pough 1980). This might explain the low survival probabilities of failed breeders recorded during our study.

SKIPPING A BREEDING YEAR: A SEX-SPECIFIC STRATEGY?

Several studies have shown different breeding frequencies in male and female birds (Coulson & Thomas 1985; Croxall & Rothery 1991; Cézilly *et al.* 1996). There is also some evidence for sex-biased reproductive costs (via reduced breeding propensity of females), at least in monogamous bird species (Pugesek & Wood 1992). However, evidence for a sex-biased cost of reproduction in terms of adult survival of monogamous vertebrates remained elusive (Tavecchia *et al.* 2001). Here we show that king penguin males are more prone than females to skip a breeding season. Males provision their chicks for longer than females towards the end of the chick-rearing phase (Stonehouse 1960; Jouventin & Lagarde 1995) and arrive later in the following breeding season. When arriving late during the breeding season, males face a lower availability of potential partners ('ideal-free mate choice hypothesis'; Olsson 1998; Bried *et al.* 1999). Finding no suitable match, males might prefer to skip reproduction rather than to pair with low-quality individuals. In addition, given that they undertake the final stage of chick-rearing on their own, males might also reach a poorer body condition than females. This is due to the additional energetic costs of late chick-rearing, and to the fact that breeding males do not have sufficient time to replenish their body stores if they try immediately to breed again ('expensive fat storing hypothesis' Olsson 1998). The costs of reproduction might therefore be higher for king penguin males which breed successfully.

This study confirms the importance of state-dependent processes (Mangel & Clark 1988; McNamara & Houston 1996) in the evolution of life history strategies for long-lived species such as the king penguin. As with many seabirds breeding in seasonal environments, the timing of reproduction and its output influence each other both within and between seasons in this species. An important goal for future work will be to add information on breeding phenologies to our state-dependent analysis.

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