Effects of individual quality, reproductive success and environmental variability on survival of a long-lived seabird

Amélie Lescroël[1,2]*, Katie M. Dugger[3], Grant Ballard[4,5] and David G. Ainley[1]

[1]H. T. Harvey & Associates, 983 University Avenue, Bldg. D, Los Gatos, CA 95032, USA; [2]CEBC-CNRS, UPR 1934, 79360 Villiers en Bois, France; [3]Department of Fisheries and Wildlife, Oregon State University, 104 Nash Hall, Corvallis, OR 97331-3803, USA; [4]PRBO Conservation Science, 3820 Cypress Drive #11, Petaluma, CA 94954, USA; and [5]School of Biological Sciences, University of Auckland, Auckland 1142, New Zealand

Summary

1. Heterogeneity in individual quality (i.e. individuals having different performance levels that are consistent throughout life) can drive the demography of iteroparous species, but quality in the context of environmental variability has rarely been evaluated.

2. We investigated the demographic responses of a long-lived seabird, the Adélie penguin (*Pygoscelis adeliae*), to contrasting environmental conditions as a function of reproductive success, breeding quality (BQ) and experience. A continuous index of BQ (BQI) was developed to reflect an individual's ability, relative to others, to produce viable offspring.

3. First, we assessed the relative importance of costs of reproduction vs. heterogeneity in quality by comparing survival and reproductive probabilities among deferred, successful and unsuccessful breeders under 'demanding' conditions using multistate capture–mark–recapture modelling. Then, we quantified the influence of BQI on adult survival among experienced breeders vs. the whole study population under both 'normal' and 'demanding' conditions.

4. Higher survival rates were exhibited by successful (74–76%) compared to unsuccessful breeders (64%); the former also more frequently reproduced successfully at year $t + 1$.

5. From 1997 to 2006, adult survival ranged from 64–79%, with BQI accounting for 91% of variability in the entire study population, but only 17% in experienced breeders. The weakened relationship between BQI and survival in experienced breeders supports the theory that selection during the first reproductive event accounts for a more homogeneous pool of experienced breeders.

6. No significant effect of environmental covariates on survival was evident, suggesting that what appeared to be demanding conditions were within the range that could be buffered by this species.

7. For the first time in seabirds, a quadratic relationship between adult survival and BQI showed that adult survival is shaped by both heterogeneity in quality and reproductive costs. Our study confirms that population demographic patterns are affected by factors at the individuals' level (e.g., individual quality) that are obscured at population-scale levels.

Key-words: costs of reproduction, breeding experience, breeding quality, multistate mark–recapture models, trade-offs

Introduction

Life-history theory is founded on the 'Principle of Allocation', i.e. an increase in the energy allocated to one process must result in a decrease to another, thus giving rise to 'trade-offs' (Cody 1966; Stearns 1992), e.g. between reproduction and survival (e.g. Siefferman & Hill 2008; Weladji *et al.* 2008). This prin-

ciple predicts decreased survival and future reproduction as a function of increased current reproductive effort (Williams 1966), i.e. a demographic cost of reproduction, assuming that rate of energy acquisition is constant among individuals.

Within a population, some individuals can acquire more energy than others and therefore reproduce more successfully, often without exhibiting costs (e.g. Cam *et al.* 2002). This differential could be accounted for by (i) individual heterogeneity in quality, i.e. some individuals consistently

*Corresponding author: lescroel@cebc.cnrs.fr

outperform others in breeding success and longevity, and (ii) age- or experience-related processes, i.e. older, more experienced individuals may exceed those younger and less experienced in breeding or foraging competence (see Forslund & Pärt 1995 for a review). These processes may also interact (e.g. Weladji *et al.* 2006). In particular, the first reproductive event may select among the highly heterogeneous class of inexperienced individuals, possibly leading to a more homogeneous pool of experienced breeders as a result of lower-quality individuals experiencing higher costs and higher mortality associated with their first breeding event (Cam & Monnat 2000; Barbraud & Weimerskirch 2005; Beauplet *et al.* 2006; Nevoux, Weimerskirch & Barbraud 2007).

Differences in individual capability may or may not be expressed depending on environmental conditions. Under favourable conditions, cost of reproduction may not be evident among individuals varying in quality, age or experience (Tavecchia *et al.* 2005), and only under demanding conditions do they become apparent (Barbraud & Weimerskirch 2005). However, individual heterogeneity is seldom considered in investigations of population response to environmental variability.

The goal of our study was to investigate the demographic response of breeding individuals of a seabird, the Adélie penguin (*Pygoscelis adeliae* Hombron & Jacquinot), to contrasting environmental conditions, considering individual heterogeneity in quality and experience. Ainley & DeMaster (1980) showed that individuals breeding at an early age tended to be better breeders throughout their lifetime, but the effect of individual quality per se on survival and its interaction with experience was not evaluated.

First, we assessed the relative importance of costs of reproduction vs. heterogeneity in quality in our study population by comparing survival and reproductive probabilities among deferred, successful and unsuccessful breeders during a period of 'demanding' conditions (2002–06). If reproduction is costly ('cost of reproduction' hypothesis), we expected deferred breeders to have highest survival, and higher subsequent probabilities of reproducing than successful or unsuccessful breeders. On the other hand, if individual quality mitigates cost of reproduction ('heterogeneity in quality' hypothesis), then we expected successful breeders to have higher survival, and higher probability of reproducing successfully in the future.

Second, using individual breeding quality (BQ: an individual's ability to produce offspring compared to others in the same population at the same time) as a surrogate for individual quality, we quantified the influence of BQ on the survival of experienced breeders (i.e. individuals that survived their first reproductive event) vs. the whole study population during a period of contrasted environmental conditions (1997–2006). We predicted that demanding conditions would have a stronger negative impact on survival of lower BQ than higher BQ individuals. However, if the first breeding event selects against lower BQ and leads to a more homogeneous pool of experienced breeders, then we expect BQ to have less influence on the survival of experienced breeders compared to the whole population. On the other hand, if no filtering occurs following the first breeding event, BQ should have the same influence on survival regardless of experience.

Materials and methods

SPECIES AND STUDY SITE

Adélie penguins are pagophilic birds, which spend only 10% of their life on land, where they form breeding colonies distributed around the Antarctic coast and offshore islands (Ainley 2002). Our study colony, Cape Crozier (77°27′S, 169°12′E), Ross Island, is one of the largest for this species (*c.* 140 000 breeding pairs). Adélie penguins exhibit delayed maturity, with age at first breeding ranging 3–7 years for females and 4–8 years for males. Breeders arrive in late October, lay (usually two) eggs in mid-November, and feed their chicks between mid-December and early February. Mortality of adult Adélie penguins is related mainly to activities at sea, and banding studies have shown that some individuals reach at least 20 years of age (Ainley 2002).

From the 1996–97 (hereafter referred as 1996) to the 2006–07 austral summers, 430 known breeders were banded on the left flipper with a numbered stainless steel band in two adjacent subcolonies (see Dugger *et al.* 2006 for details on band design). Banded birds were resighted from 15 December to 25 January in 1996 to 2001, and from 15 November to 25 January beginning in 2002. During this period, the entire colony was surveyed once every week.

ENVIRONMENTAL CONDITIONS

In March 2000, two giant icebergs, called B-15 and C-16, calved from the Ross Ice Shelf. B-15 measured 295×40 km and, with C-16 (50×25 km), eventually settled against Ross Island, just west of Cape Crozier in January 2001. These icebergs, present until July 2006, restricted the normal drift of pack ice, resulting in higher spring/summer ice cover (ice per unit area), a 40% reduction in regional primary productivity (Arrigo *et al.* 2002), and reduced penguin access to food by requiring more walking on foraging trips (Ainley 2002). Iceberg effects included (i) longer foraging trips (D.G. Ainley, G. Ballard & K. Dugger, unpublished); (ii) disorientation of foraging penguins (i.e. rapid movements of the icebergs could change access pathways to the colony from day to day); and (iii) an average productivity of <0.20 chick pair^{-1} compared to 0.80–1.36 chicks pair^{-1} during pre-iceberg years (1997 to 2000; Ainley *et al.* 2004; D.G. Ainley, G. Ballard & K. Dugger, unpublished). Hereafter, 1996 to 2000 and 2006 were considered 'normal', while 2001 to 2005 were considered summers of 'demanding' environmental conditions.

To construct a covariate for use in modelling, we used monthly mean gridded sea-ice concentration (SIC) derived from passive microwave imagery (http://nsidc.org/data/; Cavalieri *et al.* 1996) to quantify ice cover. From these data, the mean percentage of SIC for all 25-km cells in the Cape Crozier colony foraging area (76°00′–77°30′S, 166°50′–170°00′E; Ainley *et al.* 2004) was calculated for each breeding season (October to February). We hypothesized that high SIC would lead to decreased prey accessibility and increased foraging effort. We also considered conditions experienced while penguins wintered in the pack ice by using values of the Antarctic Oscillation Index (AAOI, http://www.cpc.ncep.noaa.gov/products/precip/CWlink/daily_ao_index/aao/monthly.aao.index.b79.current.ascii.table) averaged during May to August. A high AAOI (see Gong & Wang 1999 for a definition) correlates to the cooling and drying of the Ross

Table 1. Models used for the calculation of the BQI (generalized linear models with logit link, using a binomial distribution)

Model	LogLik	K	n	AICc	ΔAICc	Lik	AICc weight
yearF + n_yrs	−384.15	12	702	792.73	0.00	1.00	0.43
yearF + n_yrs + bd_yearF	−374.02	22	702	793.53	0.78	0.68	0.29
yearF + bd_yearF	−375.13	21	702	793.62	0.87	0.65	0.28
yearF	−388.98	11	702	800.34	7.60	0.02	0.01
Intercept only	−475.58	1	702	953.17	160.42	0.00	0.00

LogLik, log-likelihood; K, number of estimated parameters; n, number of observations; AICc, second-order Akaike's information criterion; ΔAICc, difference between the current and the lowest AICc model; Lik, Likelihood; yearF, the breeding year treated as a factor; n_yrs, the number of years that the individual was in the study; bd_yearF, the year of banding treated as a factor.

Sea region (van den Broeke & van Lipzig 2004), the intensification of surface westerlies over the circumpolar ocean, more intense circumpolar current, and an expansion in large-scale sea-ice extent and cover (Hall & Visbeck 2002; Liu, Curry & Martinson 2004). The latter appears to be detrimental to Ross Sea Adélie penguins, or at least juveniles, in winter (Wilson *et al.* 2001).

The use of flipper bands probably reduced individual apparent adult survival and, therefore, could accentuate or emulate 'demanding' conditions. We were able to quantify this effect in a previous study (Dugger *et al.* 2006) during a period (2000 to 2003) that overlaps the present one. Flipper bands could have decreased apparent annual survival up to 12%, representing a significant influence.

BREEDING SUCCESS AND QUALITY

Once chicks leave nests and assemble into 'crèches' (Ainley 2002), mortality becomes very low (Davis & McCaffrey 1986). Breeding birds were considered 'successful' when they were seen feeding a chick after mean crèche date each year (about the first week of January). Adult banded birds seen during a given season but never with an egg or a chick were classified as 'deferred breeders'. Birds seen with at least one egg or chick but which failed before mean crèche date were classified as 'unsuccessful'.

Individuals varied in the frequency of being successful. A BQI was calculated as the mean per individual of the difference between the actual breeding success (0 for unsuccessful or deferred breeders, 1 for successful breeders) and the predicted breeding success (a numeric value between 0 and 1) for every year. This led to a unique value per individual. The predicted breeding success was modelled from actual breeding success (0 or 1), using three independent variables (breeding year, year of banding and number of years that the individual was in the study = number of years since banding minus number of years bird had not been seen) incorporated into generalized linear models with a logit link (Table 1). We verified that the independent variables were not cross-correlated and that the most general model fit the data. Then, an information theoretic approach and model averaging (Burnham & Anderson 2002) were used to derive a probability of success for each year and individual. Here, our definition of BQ corresponds to the relative performance of an individual compared to others of similar characteristics (same banding year and 'seniority' in the study) over the same time span.

COSTS OF REPRODUCTION AND HETEROGENEITY IN INDIVIDUAL QUALITY

Multistate capture–mark–recapture (MCMR) modelling was used to estimate apparent survival, recapture probabilities and probabilities of transitioning among reproductive states (deferred breeder, state D; unsuccessful breeder, state U; successful breeder, state S) between consecutive years. We used the conditional Arnason–Schwarz (CAS) multistate model (Brownie *et al.* 1993) in program MARK to generate estimates and model selection output (White & Burnham 1999). Before 2002, our relatively late arrival at the colony (during hatching) may have lead to the misclassification of unsuccessful breeders (those that failed with eggs early) as deferred breeders. To avoid this problem, we analysed encounter histories of 242 breeders seen between 2002 and 2006 only.

A goodness-of-fit (GOF) test was performed to check whether the full state- and time-dependent CAS model, $S(f \times t) p(f \times t) \Psi(f \times to \times t)$ fit our data. In this model, state refers to reproductive state in a given year. Survival probabilities (S) and recapture probabilities (p) vary by state of departure (f; initial reproductive state) and time interval (t), and transition probabilities (Ψ) vary by state of departure, state of arrival (to; subsequent reproductive state) and time interval. Currently, no optimal GOF test exists for the CAS model (Choquet *et al.* 2005). Therefore, a GOF test for the more general JollyMoVe (JMV) model (Pradel, Wintrebert & Gimenez 2003), $S(f \times t) p(f \times to \times t) \Psi(f \times to \times t)$, which allows the recapture probabilities to also vary by state of arrival, was performed using U-CARE (Choquet *et al.* 2005). Our data failed to pass the Where Before, Where After (WBWA; Pradel 2005) test subcomponent ($\chi^2 = 24.22$, d.f. = 12, $P = 0.02$), indicating some kind of memory pattern in our data structuring that to date can only be accommodated by use of an overdispersion factor (Choquet *et al.* 2005). This factor ($\hat{c}$) was calculated by dividing the overall GOF test statistic ($\chi^2 = 65.56$) by the degrees of freedom (d.f. = 42, Lebreton *et al.* 1992), in this case: $\hat{c} = 1.56$.

To minimize the number of models in the set, we determined the best structure for recapture, transition and survival parameters in stages. We modelled recapture probabilities first, maintaining a fully time- and state-dependent structure on survival and transition probabilities. Once the best recapture structure was chosen, it was retained for modelling transition probabilities; the best of the latter was included with the best recapture probability structure into a base model that was then used to model survival.

QUANTIFYING THE INFLUENCE OF INDIVIDUAL BREEDING QUALITY ON SURVIVAL

We used 11 years (1996 to 2006) of resighting data to quantify the influence of individual BQ on survival among experienced breeders under contrasted environmental conditions. In contrast to the analysis investigating the specific annual costs of reproduction associated

with reproductive state, we determined whether there was a direct relationship between survival and BQ measured as a continuous variable (BQI).

Our study birds were banded as breeding adults of unknown age. However, by suppressing the first encounter from each capture history and working only with resighted birds (i.e. 1997 to 2006), we identified individuals that survived at least one (if not their first) reproductive event and the subsequent winter, classified as 'experienced breeders'. According to Ainley (2002), one and sometimes two (but usually not more) years of previous breeding increased breeding success. Effects of four covariates on apparent survival were compared for experienced birds only (1997 to 2006, 152 birds) contrasted with the entire study population during the same period (197 birds). Apparent survival and recapture probabilities were estimated starting with a Cormack–Jolly–Seber (CJS) capture–mark–recapture (CMR) model using MARK. Covariates included BQI, a categorical index of summer environmental conditions ('normal' or 'demanding'), summer SIC and winter AAOI.

In the event that the relationship between survival and BQI was not linear, we developed models that included linear, log-linear (pseudo-threshold), and quadratic transformations of BQI. For quadratic models, we mean-centred them, in order to decrease the penalty associated with the extra quadratic term $(BQI_i – mean BQI)^2$, where BQI_i is the covariate value for individual i, and mean BQI is the mean of the covariate over all individuals.

The percentage of variation explained by a given covariate was calculated as $\{Dev[\Phi(covariate)]-Dev[\Phi(.)]\}/\{Dev[\Phi(t)]-Dev[\Phi(.)]\}$, where Dev was the deviance for the survival model with covariate effect $\Phi(covariate)$, for the constant survival model $\Phi(.)$ and for the survival model with time effect $\Phi(t)$ (Skalski, Hoffmann & Smith 1993).

The GOF test performed under U-CARE indicated that the general, time-dependent CJS model $[\Phi(t)p(t)]$ (see Lebreton *et al.* 1992) fit both data sets (all birds: $\chi^2 = 8.16$, d.f. = 12, $P = 0.77$; experienced birds: $\chi^2 = 3.49$, d.f. = 9, $P = 0.94$).

Similar to MCMR analysis, we determined the best model structure for recapture rates while maintaining a time- and strata-dependent structure on apparent survival. Once the best recapture structure was chosen, it was retained for all subsequent survival models.

MODEL SELECTION

An information theoretic approach (Burnham & Anderson 2002) was used to select the best models and determine the strength of evidence supporting specific effects. Model selection criteria used to rank and select our best model included the corrected version of Akaike's information criterion for small sample sizes (AICc or QAICc when including the overdispersion factor, Lebreton *et al.* 1992), the difference in AICc between each candidate model and the model with the lowest AIC*c* value (ΔAICc or ΔQAICc) and Akaike weights (Burnham & Anderson 2002).

Additionally, we used the analysis of deviance test (ANODEV; Skalski *et al.* 1993), implemented in MARK, for selecting pertinent individual or environmental covariates (Grosbois *et al.* 2008). The ANODEV test compares the amount of deviance explained vs. not explained by a covariate: it was retained only when the amount of deviance explained was significant ($P < 0.05$).

All calculations other than CMR or MCMR modelling were performed using R (http://r-project.org/) and parameter estimates ± the standard error are given unless otherwise noted.
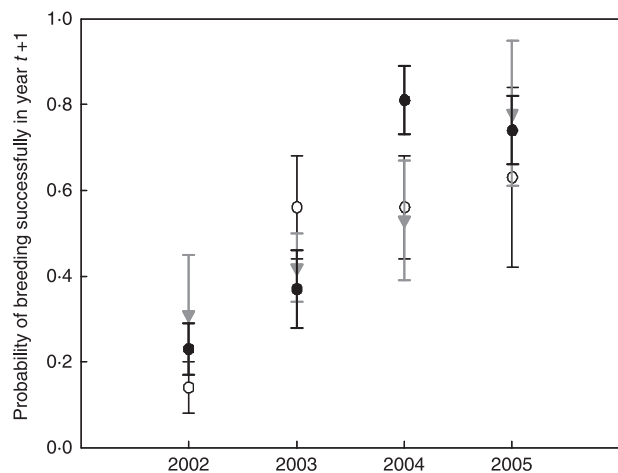

Fig. 1. Probability of breeding successfully in year *t* + 1 given a bird was a ▼ deferred breeder, ○ unsuccessful breeder or ● successful breeder in year *t* for Adélie penguins at Cape Crozier, Ross Island, 2002–2005. Estimates from best model $[S\,(D=U,S)\,p\,(.)\,\Psi\,(f \times to \times t)]$; Table 2, model 10] are (± 1 SE).

Results

COSTS OF REPRODUCTION AND HETEROGENEITY IN INDIVIDUAL QUALITY

Capture probability for this population was both constant and very high over the study period (Table 2; Model 1): $p = 0.99 \pm 0.01$ (95% CI: 0.95–1.00). We retained this best capture probability model for modelling transition probabilities and survival.

The reproductive state of an Adélie penguin in any given year varied in relation to its reproductive state in the previous year and time (model 1, Fig. 1). As predicted by the 'heterogeneity in quality hypothesis', more often than not, successful breeders exhibited a higher probability of reproducing successfully in subsequent years than unsuccessful breeders (Fig. 1). The probability of remaining a successful breeder also tended to be less variable (mean SE = 0.08) than the probability of transitioning from an unsuccessful or a deferred breeder in the previous year to a successful breeder (mean SE = 0.13). The probability of breeding successfully increased from 2002 to 2005 for all three reproductive states (range: 0.20 in 2002 to 0.70 in 2005), but differences within years varied by reproductive state (Fig. 1).

Among models designed to address our hypotheses regarding the effect of individual quality and costs of reproduction (models 10 and 11, Table 2), the 'heterogeneity in quality' hypothesis was best supported: successful breeders exhibited higher survival compared to deferred breeders and unsuccessful breeders (model 10; $S_S = 0.76 \pm 0.03$ vs. $S_{D=U} = 0.67 \pm 0.03$). This model received five times more weight than the next best, which tested the 'cost of reproduction' (model 11). This model tested whether deferred breeders had higher, survival than unsuccessful and successful breeders (in fact, the model output gave $S_D = 0.70 \pm 0.05$ vs. $S_{U=S} = 0.71 \pm 0.03$). Time

Table 2. Modelling capture (p), transition (Ψ) and survival (S) probabilities according to time (t) and reproductive state (f, 'departure' state; to, 'arrival' state; D, deferred breeder; U, unsuccessful breeder; Succ, successful breeder) for Adélie penguins at Cape Crozier, Ross Island, 2002–06

No.	Model	QAICc	ΔQAICc	QAICc weight	No. par.	Dev
Modelling capture probabilities						
1	$S\,(f \times t)\,p\,(.)\,\Psi\,(f \times to \times t)$	1038.72	0.00	0.80	37	179.80
2	$S\,(f \times t)\,p\,(f)\,\Psi\,(f \times to \times t)$	1042.72	4.00	0.11	39	179.23
3	$S\,(f \times t)\,p\,(t)\,\Psi\,(f \times to \times t)$	1043.22	4.50	0.08	39	179.73
4	$S\,(f \times t)\,p\,(f + t)\,\Psi\,(f \times to \times t)$	1048.82	10.10	0.01	41	180.73
5	$S\,(f \times t)\,p\,(f \times t)\,\Psi\,(f \times to \times t)$	1055.88	17.16	0.00	45	178.47
Modelling transition probabilities						
1	$S\,(f \times t)\,p\,(.)\,\Psi\,(f \times to \times t)$	1038.72	0.00	1.00	37	179.80
6	$S\,(f \times t)\,p\,(.)\,\Psi\,(f \times to + t)$	1071.86	33.14	0.00	22	246.23
7	$S\,(f \times t)\,p\,(.)\,\Psi\,(t)$	1072.67	33.95	0.00	17	257.75
8	$S\,(f \times t)\,p\,(.)\,\Psi\,(f \times to)$	1079.62	40.90	0.00	19	260.43
9	$S\,(f \times t)\,p\,(.)\,\Psi\,(.)$	1087.92	49.20	0.00	14	279.33
Modelling survival probabilities						
10	$S\,(D{=}U,\text{Succ})\,p\,(.)\,\Psi\,(f \times to \times t)$	1021.93	0.00	0.75	25	189.78
11	$S\,(D, U{=}\text{Succ})\,p\,(.)\,\Psi\,(f \times to \times t)$	1025.29	3.36	0.14	25	193.14
12	$S\,(.)\,p\,(.)\,\Psi\,(f \times to \times t)$	1027.48	5.55	0.05	26	193.14
13	$S\,(f)\,p\,(.)\,\Psi\,(f \times to \times t)$	1027.51	5.58	0.05	28	188.76
14	$S\,(f + t)\,p\,(.)\,\Psi\,(f \times to \times t)$	1031.22	9.29	0.01	31	185.83
15	$S\,(t)\,p\,(.)\,\Psi\,(f \times to \times t)$	1032.13	10.20	0.00	29	191.18
16	$S\,(f \times t)\,p\,(.)\,\Psi\,(f \times to \times t)$	1038.72	16.79	0.00	37	179.80

QAICc, quasilikelihood second-order Akaike's information criterion; ΔQAICc, difference between the current and the lowest QAICc model; No. par., number of parameters; Dev, deviance defined as the difference in $-2\log(\text{Likelihood})$ of the current model and $-2\log(\text{Likelihood})$ of the saturated model.

Table 3. Modelling capture (p), and survival (Φ) probabilities according to time (t), environmental conditions (SIC, iceberg, AAOI) and individual BQ (BQI, lnBQI and BQI_mc) for Adélie penguins at Cape Crozier, Ross Island, 1997–2006

No.	Model	AICc	ΔAICc	AICc weight	No. par.	Dev	P-ANODEV
Modelling capture probabilities							
1	$\Phi\,(t)\,p\,(.)$	749.55	0.00	0.98	10	729.17	
2	$\Phi\,(t)\,p\,(t)$	757.12	7.56	0.02	17	722.05	
Modelling survival probabilities							
3	$\Phi\,(t + \text{BQI\_mc})\,p\,(.)$	735.85	0.00	0.61	11	713.39	
4	$\Phi\,(\text{BQI\_mc})\,p\,(.)$	736.89	1.04	0.36	3	730.84	<0.01
5	$\Phi\,(t \times \text{BQI\_mc})\,p\,(.)$	742.66	6.82	0.02	19	703.33	
6	$\Phi\,(t)\,p\,(.)$	749.55	13.71	0.00	10	729.17	
7	$\Phi\,(\text{AAOI})\,p\,(.)$	750.44	14.60	0.00	3	744.40	0.32
8	$\Phi\,(.)\,p\,(.)$	750.90	15.05	0.00	2	746.87	
9	$\Phi\,(\text{lnBQI})\,p\,(.)$	751.36	15.51	0.00	3	745.32	0.44
10	$\Phi\,(\text{SIC})\,p\,(.)$	751.96	16.11	0.00	3	745.92	0.55
11	$\Phi\,(\text{BQI})\,p\,(.)$	752.78	16.93	0.00	3	746.73	0.82
12	$\Phi\,(\text{iceberg})\,p\,(.)$	752.90	17.05	0.00	3	722.05	0.94

lnBQI, the natural logarithm of BQI plus 1; BQI_mc, mean-centred quadratic BQI; SIC, sea-ice concentration averages for the breeding season; iceberg, 'normal' vs. 'demanding' environmental conditions.

effects on survival were not supported (models 14, 15 and 16), nor was a model including survival variation across all three different reproductive states (model 13) or constant survival across reproductive state and time (model 12).

QUANTIFYING THE INFLUENCE OF INDIVIDUAL BQ ON SURVIVAL

Similar to MCMR modelling, we observed high resighting probabilities and no variation in resighting rates from 1997 to 2006: $p = 0.98 \pm 0.01$ (95% CI: 0.96–0.99) (model 1, Table 3). Retaining this best capture probability structure, we modelled the effect of environmental conditions and individual BQ on apparent survival in the entire study population. The quadratic structure of BQI (BQI_mc) was the only covariate to have a significant effect on survival (ANODEV test: $F = 67.19$, $P < 0.01$, model 4, Table 3), accounting for 90.6% of the survival variability. Two additional models, both including BQI_mc, were competitive (<2 AICc), accounting for 98% of the total model weight (models 3 and 4). Variation in survival
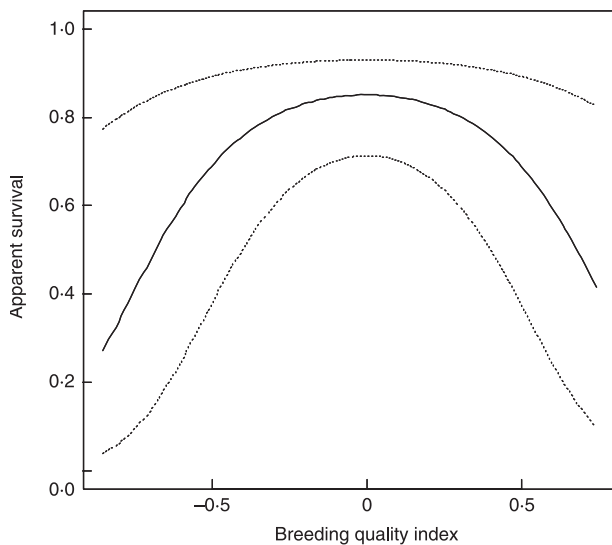
Fig. 2. Estimates of apparent adult survival with 95% confidence limits for Adélie penguins at Cape Crozier, Ross Island, 1997–2005 from the best model Φ (*t* + BQI_mc) *p* (.) (Table 3, model 3).
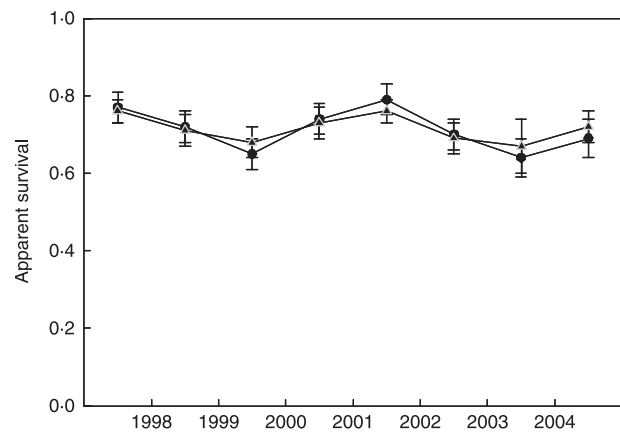

Fig. 3. Model-averaged estimates (± 1 SE) of apparent survival for Adélie penguins at Cape Crozier, Ross Island, 1997–2005 from two data sets including 1) the entire study population (●) and 2) experienced birds only (▲).

related to BQI was also consistent through time as our top model included an additive general time-dependent effect (i.e. both BQI and time had an effect on survival but they did not interact). The model including the interaction between time and BQI_mc (model 5) received very low support (AICc weight = 0.02), so we rejected the hypothesis that BQI influence on survival was dependent upon breeding season.

The 95% CI's surrounding the estimate of the quadratic effect of BQI from our best model did not include zero (model 3: β_{BQI_mc} = −3.78 ± 0.97; 95% CI: −5.68 to −1.88), and the negative sign indicates that survival was highest for individuals of average breeding performance and decreased for both low- and high-breeding-performance individuals (Fig. 2). Annual survival estimates from model averaging over the whole model set (for BQI = 0) varied between 0.64 and 0.79 depending on year (Fig. 3).

However, when considering experienced breeders only, none of the covariates explained a significant amount of variability in survival probabilities (Table 4). Accordingly, the amount of variability in survival explained by BQI_mc (model 4) dropped from 90.6% to 17.4% (ANODEV test: F = 1.47, P = 0.26). Although this model was competitive (<2 AICc), the 95% CIs for the estimate of the BQI_mc effect on apparent survival from this model included zero (β_{BQI_mc} = −2.45 ± 1.34; 95% CI: −5.07 to 0.17). For experienced breeders, survival varied primarily by time only (model 3) and this model received 1.7 times more support than the second best model containing the effect of BQI (model 4). Survival for experienced breeders showed a pattern similar to the entire population but with less overall annual variation (0.67 to 0.76 depending on years, Fig. 3). Consistent with our modelling results, both the range and the variance of BQI was reduced for experienced breeders compared to the entire population (range = −0.70 to 0.57 vs. −0.85 to 0.74, var = 0.062 vs. 0.088, respectively, $F_{196, 151}$ = 1.42, P = 0.02).

Discussion

Our study confirms that individual quality can mitigate costs of reproduction in long-lived vertebrate species (Weladji *et al.* 2008) but also highlighted for the first time in seabirds a quadratic relationship between adult survival and BQ, with survival highest for individuals with average BQI. Surprisingly, no significant effect of environmental conditions – as we chose to measure them – on apparent adult survival was evident, but our results tend to refute the hypothesis that the influence of individual quality varies annually.

COST OF REPRODUCTION AND HETEROGENEITY IN INDIVIDUAL QUALITY

In our study, successful breeders sustained no detectable reproduction cost and exhibited higher probability of reproducing successfully in year *t* + 1 than unsuccessful breeders in most years (although error measures overlapped substantially between groups). Thus, on an annual basis, individual reproductive success and survival were positively correlated. This suggests the existence of interindividual heterogeneity in quality that can mitigate costs of reproduction in our study population. Such demographic pattern is likely to be a feature common to long-lived species (Cam & Monnat 2000; Weladji *et al.* 2008). Although the pattern of heterogeneity in individual quality is often detected, the process producing this effect on a population's demographic response to environmental variability has rarely been precisely quantified.

MEASURING QUALITY

Individual heterogeneity in quality refers to differences in performance that are consistent throughout life (Stopher *et al.* 2008). When the performances considered are fertility and survival, it becomes a concept very similar to individual

Table 4. Modelling capture (*p*), and survival (Φ) probabilities according to time (*t*), environmental conditions (SIC, iceberg, AAOI) and individual BQ (BQI, lnBQI and BQI_mc) for experienced Adélie penguins at Cape Crozier, Ross Island, 1997–2006

No.	Model	AICc	ΔAICc	AICc weight	No. par.	Dev	*P*-ANODEV
	Modelling capture probabilities						
1	Φ (*t*) *p* (.)	547.94	0.00	1.00	10	527.44	
2	Φ (*t*) *p* (*t*)	558.88	10.94	0.00	17	523.45	
	Modelling survival probabilities						
3	Φ (*t*) *p* (.)	547.94	0.00	0.32	10	527.44	
4	Φ (BQI_mc) *p* (.)	549.05	1.11	0.18	3	543.00	0.26
5	Φ (AAOI) *p* (.)	550.10	2.15	0.11	3	544.04	0.36
6	Φ (SIC) *p* (.)	550.25	2.30	0.10	3	544.19	0.38
7	Φ (.) *p* (.)	550.30	2.36	0.10	2	546.27	
8	Φ (lnBQI) *p* (.)	550.60	2.65	0.08	3	544.54	0.43
9	Φ (BQI) *p* (.)	551.13	3.19	0.06	3	545.08	0.51
10	Φ (iceberg) *p* (.)	552.14	4.19	0.04	3	546.08	0.80

fitness. We defined BQI as an individual's ability to produce offspring compared to the success of others, which is much closer to individual fitness, a relative concept, than absolute measures such as lifetime reproductive success (LRS), which averages environmental variability (Coulson *et al.* 2006; Metcalf & Pavard 2007). In our study, working with individuals of unknown age and previous experience (because they were marked as breeding adults), we could not include longevity as part of BQI. So it is possible that BQI was partially confounded with an age effect if reproductive performance improves with age through mechanisms other than the 'selection' hypothesis (i.e. low-quality individuals are counter-selected with time), like increasing foraging ability. The increase in breeding probabilities over all three reproductive states might reflect an age (or experience) effect, but the strong relationship between BQI and apparent survival supports heterogeneity in quality as well. By necessity, we focused on individuals that attempted to breed at least once and ignored individuals that never attempted to breed, including those that will remain nonbreeders for life (Ainley 1978) and those that will die before expressing a phenotype (i.e. 'the invisible fraction'; Sinervo & McAdam 2008); thus, variance in BQ is likely higher than we observed. Nevertheless, in this study, BQI provided a means to investigate important aspects of seabird demography when age is unknown.

QUANTIFYING THE INFLUENCE OF INDIVIDUAL BQ ON SURVIVAL

Apparent survival of breeding Adélie penguins increased with increased BQ up to the average, but decreased with further BQ increase (Fig. 2). At first glance, this quadratic relationship might appear to contradict our MCMR modelling (i.e. successful breeders exhibit higher survival), but these analyses address different scales of quality. The MCMR modelling investigated apparent survival associated with specific breeding states – states which individuals could transition into and out of from year to year. This analysis was important for assessing the relationship between survival and breeding status on an annual basis. In contrast, the additive BQI effect observed in the second analysis reflects a consistent effect of BQI over a multi-year time-scale.

We likely would have observed stronger patterns in BQI if our definition of BQ (see Methods) had been different. Indeed, individuals that bred successfully only once but in years of very low average productivity (notably in 2001) were assigned very high BQIs even though they often did not survive this 'extraordinary' success. Therefore, the second half of the quadratic curve may represent costs of breeding in years of particularly low overall productivity (i.e. presumably bad conditions). The reward of this 'do like the average' strategy in terms of survival implies a stabilizing selection or trade-off, which could explain why the mode of the distribution of the lifetime successful breeding events has not shifted to a higher value. Alternatively, the right tail of the quadratic curve might reflect the fact that very high BQI individuals were birds of high quality at the end of their life or/and senescent birds increasing their reproductive effort before dying (i.e. the terminal investment hypothesis, Velando, Drummond & Torres 2006).

Of potential concern for the validity of our study is the confounding effect that could be caused if flipper bands affected apparent survival based on an individual's quality, sex or age. Working on the same population during an overlapping period, Dugger *et al.* (2006) showed that band effects on apparent survival interacted neither with sex, season nor with 'year since tagging' (related to both age and experience). It is nevertheless possible that survival of low BQ individuals, or even higher BQ birds that bred in years of daunting conditions, was more negatively affected by bands than medium BQ individuals. If so, this may have exaggerated the difference we found in survival rates based on quality. However, we did not detect variability in the effect of BQI on survival. In other words, there was no interaction between BQI and time, so since all individuals were banded and the effect of BQI on survival was constant through time, we believe our conclusions regarding heterogeneity in survival are valid.

The demography of the Adélie penguin, therefore, may be driven by the mixed effects of heterogeneity in quality and costs of reproduction. Such combined influence has also been

suggested in king penguins (*Aptenodytes patagonicus* Miller, Le Bohec *et al.* 2007) but to our knowledge, only two previous studies highlighted a quadratic relationship between survival and a quality correlate in birds (waterfowl: Blums *et al.* 2005; serins: Figuerola & Senar 2007).

REDUCED INDIVIDUAL HETEROGENEITY AMONG EXPERIENCED BREEDERS

Compared to the entire study population, the heterogeneity in BQ among experienced breeders was reduced and the explanatory power of the BQI on survival was much weaker (17% in experienced breeders vs. 91% in the entire study population), although sample size and associated power to estimate effect were slightly decreased. The difference between both data sets ('experienced breeders' and 'entire study population') lies in the removal of birds that were seen breeding only once and were never resighted (i.e. they died, or permanently emigrated) from the 'experienced breeders' data set. Those birds are therefore either first breeders that did not survive their first breeding event, or experienced breeders that died from other natural causes. In this latter case, they should behave like individuals from the 'experienced breeders' data set. Thus, differences observed between both data sets should come primarily from the absence of first breeders in the 'experienced breeders' data set. The weakened relationship between BQI and survival and the lower heterogeneity in quality of experienced breeders suggest support for the theory that the first reproductive event can act as a selective process leading to a more homogeneous pool of experienced breeders (Cam & Monnat 2000; Barbraud & Weimerskirch 2005; Beauplet *et al.* 2006; Nevoux *et al.* 2007), while stressing that some heterogeneity in BQ remains among experienced breeders but does not necessarily correlate with interindividual differences in survival.

FACING CHALLENGING EVENTS

We detected no immediate influence of challenging environmental conditions on apparent survival. Indeed, survival was unrelated either to SIC during the breeding season, presence/absence of icebergs, or the AAOI. In contrast, breeding success was much lower during years of concentrated sea ice (iceberg) compared to others (see Methods). Therefore, under 'demanding' environmental conditions, adult survival was apparently favoured over offspring production, as in most other long-lived species (e.g., Erikstad *et al.* 1998; Weimerskirch, Zimmerman & Prince 2001). This implies not only that a trade-off exists between survival and current reproduction at the population level but also that what we judged as 'demanding' conditions were still within the range of conditions whose effects on adult survival Adélie penguins can buffer. It is probable that we witnessed the upper limit of the qualitatively defined 'habitat optimum' model of Smith *et al.* (1999) with respect to SIC. Heavier ice cover, namely fast ice with no cracks, likely would have produced more dramatic patterns in our results (see Emslie *et al.* 2003).

In our study, apparent adult survival of Adélie penguins in 1997–2006 varied 64% to 79% (mean 71%), which is comparable to work at Cape Crozier (58–89%) in 1960–75 (Ainley & DeMaster 1980) and to work in Adélie Land (64–82%) in 1991–98 (Jenouvrier, Barbraud & Weimerskirch 2006). This range of survival rates is relatively low, with a high degree of annual variability compared to other long-lived, slow-to-mature seabirds. Taking the potential flipper band effect into account, the true rate might be higher (76–91%).

This study confirms the importance of taking individual quality into account when investigating the demography of iteroparous species, as the population can be quite heterogeneous in this regard, with significant consequences to reproduction and survival. Important goals for future work are (i) to incorporate age into quantifying heterogeneity in quality, and (ii) to evaluate the influence of individual quality on true rather than apparent survival by incorporating immigration/emigration parameters in a metapopulation context.

Acknowledgements

References

Ainley, D.G. (1978) Activity patterns and social behavior of non-breeding Adélie penguins. *Condor*, **80**, 138–146.

Ainley, D.G. (2002) *The Adélie Penguin: Bellwether of Climate Change*. Columbia University Press, New York.

Ainley, D.G. & DeMaster, D. (1980) Survival and mortality in a population of Adélie penguins. *Ecology*, **61**, 522–530.

Ainley, D.G., Ribic, C.A., Ballard, G., Heath, S., Gaffney, I., Karl, B.J., Barton, K.J., Wilson, P.R. & Webb, S. (2004) Geographic structure of Adélie penguin populations: overlap in colony-specific foraging areas. *Ecological Monographs*, **74**, 159–178.

Arrigo, K.R., van Dijken, G.L., Ainley, D.G., Fahnestock, M.A. & Markus, T. (2002) Ecological impact of a large Antarctic iceberg. *Geophysical Research Letters*, **29**(7), 10.1029/2001 GLO.

Barbraud, C. & Weimerskirch, H. (2005) Environmental conditions and breeding experience affect costs of reproduction in blue petrels. *Ecology*, **86**, 682–692.

Beauplet, G., Barbraud, C., Dabin, W., Küssener, C. & Guinet, C. (2006) Age-specific survival and reproductive performances in fur seals: evidence of senescence and individual quality. *Oïkos*, **112**, 430–441.

Blums, P., Nichols, J.D., Hines, J.E., Lindberg, M.S. & Mednis, A. (2005) Individual quality, survival variation and patterns of phenotypic selection on body condition and timing of nesting in birds. *Oecologia*, **143**, 365–376.

Brownie, C., Hines, J., Nichols, J., Pollock, K. & Hestbeck, J. (1993) Capture-recapture studies for multiple strata including non-markovian transitions. *Biometrics*, **49**, 1173–1187.

Burnham, K.P. & Anderson, D.R. (2002) *Model selection and multimodel inference – A Practical Information-Theoretic Approach*, 2nd edn. Springer-Verlag, New York.

Cam, E. & Monnat, J. (2000) Apparent inferiority of first-time breeders in the kittiwake: the role of heterogeneity among age class. *Journal of Animal Ecology*, **69**, 380–394.

Cam, E., Link, W.A., Cooch, E.G., Monnat, J. & Danchin, E. (2002) Individual covariation in life-history traits: seeing the trees despite the forest. *American Naturalist*, **159**, 96–105.

Cavalieri, D., Parkinson, C., Gloersen, P. & Zwally, H.J. (1996, updated 2006) *Sea Ice Concentrations from Nimbus-7 SMMR and DMSP SSM/I Passive Microwave Data, October 1997 to February 2006*. National Snow and Ice Center, Boulder, Colorado. Digital media.

Choquet, R., Reboulet, A., Lebreton, J., Gimenez, O. & Pradel, R. (2005) *U-CARE 2.2 User's Manual*. CEFE, Montpellier, France. Available from URL: http://ftp.cefe.cnrs.fr/biom/Soft-CR/.

Cody, M. (1966) A general theory of clutch size. *Evolution*, **20**, 174–184.

Coulson, T., Benton, T.G., Lundberg, P., Dall, S.R.X., Kendall, B.E. & Gaillard, J.M. (2006) Estimating individual contributions to population growth: evolutionary fitness in ecological time. *Proceedings of the Royal Society B: Biological Sciences*, **273**, 547–555.

Davis, L.S. & McCaffrey, F. (1986) Survival analysis of eggs and chicks of Adélie penguins (Pygoscelis adeliae). *Auk*, **103**, 379–388.

Dugger, K.M., Ballard, G., Ainley, D.G. & Barton, K.J. (2006) Effects of flipper bands on foraging behaviour and survival of Adélie penguins (*Pygoscelis adeliae*). *Auk*, **123**, 858–869.

Emslie, S.D., Berkman, P.A., Ainley, D.G., Coats, L. & Polito, M. (2003) Late-Holocene initiation of ice-free ecosystems in the southern Ross Sea, Antarctica. *Marine Ecology Progress Series*, **262**, 19–25.

Erikstad, K.E., Fauchald, P., Tveraa, T. & Steen, H. (1998) On the cost of reproduction in long-lived birds: the influence of environmental variability. *Ecology*, **79**, 1781–1788.

Figuerola, J. & Senar, J.C. (2007) Serins with intermediate brightness have a higher survival in the wild. *Oikos*, **116**, 636–641.

Forslund, P. & Pärt, T. (1995) Age and reproduction in birds – hypotheses and tests. *Trends in Ecology & Evolution*, **10**, 374–378.

Gong, D. & Wang, S. (1999) Definition of Antarctic Oscillation Index. *Geophysical Research Letters*, **26**, 459–462.

Grosbois, V., Gimenez, O., Gaillard, J.-M., Pradel, R., Barbraud, C., Clobert, J., Møller, A.P. & Weimerskirch, H. (2008) Assessing the impact of climate variation on survival in vertebrate populations. *Biological Reviews*, **83**, 357–399.

Hall, A. & Visbeck, M. (2002) Synchronous variability in the Southern Hemisphere atmosphere, sea ice and ocean resulting from the annular mode. *Journal of Climate*, **15**, 3043–3057.

Jenouvrier, S., Barbraud, C. & Weimerskirch, H. (2006) Sea ice affects the population dynamics of Adélie penguins in Terre Adélie. *Polar Biology*, **29**, 413–423.

Le Bohec, C., Gauthier-Clerc, M., Grémillet, D., Pradel, R., Bechet, A., Gendner, J. & Le Maho, Y. (2007) Population dynamics in a long-lived seabird: I. Impact of breeding activity on survival and breeding probability in unbanded king penguins. *Journal of Animal Ecology*, **76**, 1149–1160.

Lebreton, J., Burnham, K., Clobert, J. & Anderson, D. (1992) Modeling survival and testing biological hypotheses using marked animals: A unified approach with case studies. *Ecological Monographs*, **62**, 67–118.

Liu, J., Curry, J. & Martinson, D. (2004) Interpretation of recent Antarctic sea ice variability. *Geophysical Research Letters*, **31**, doi:10.1029/2003GL018732.

Metcalf, C.J.E. & Pavard, S. (2007) Why evolutionary biologists should be demographers. *Trends in Ecology & Evolution*, **22**, 205–212.

Nevoux, M., Weimerskirch, H. & Barbraud, C. (2007) Environmental variation and experience-related differences in the demography of the long-lived black-browed albatross. *Journal of Animal Ecology*, **76**, 159–167.

Pradel, R. (2005) Multievent: an extension of multistate capture-recapture models to uncertain states. *Biometrics*, **61**, 442–447.

Pradel, R., Wintrebert, C. & Gimenez, O. (2003) A proposal for a goodness-of-fit test to the Arnason-Schwarz multisite capture-recapture model. *Biometrics*, **59**, 43–53.

Siefferman, L. & Hill, G. (2008) Sex-specific costs of reproduction in Eastern Bluebirds Sialis sialis. *Ibis*, **150**, 32–39.

Sinervo, B. & McAdam, A. (2008) Maturational costs of reproduction due to clutch size and ontogenetic conflict as revealed in the invisible fraction. *Proceedings of the Royal Society B: Biological Sciences*, **275**, 629–638.

Skalski, J.R., Hoffmann, A. & Smith, S.G. (1993) Testing the significance of individual- and cohort-level covariates in animal survival studies. *Marked Individuals in the Study of Bird Population* (eds J.D. Lebreton & P.M. North), pp. 9–28. Birkhäuser-Verlag, Basle, Switzerland.

Smith, R.C., Domack, E., Emslie, S., Fraser, W.R., Ainley, D.G. Baker, K., Kennett, J., Leventer, A., Mosley-Thompson, E., Stammerjohn, S. & Vernet, M. (1999) Marine ecosystem sensitivity to historical climate change: Antarctic Peninsula. *BioScience*, **49**, 393–404.

Stearns, S. (1992) *The Evolution of Life Histories*. Oxford University Press, Oxford, UK.

Stopher, K.V., Pemberton, J.M., Clutton-Brock, T.H. & Coulson, T. (2008) Individual differences, density dependence and offspring birth traits in a population of red deer. *Proceedings of the Royal Society B: Biological Sciences*, **275**, 2137–2145.

Tavecchia, G., Coulson, T., Morgan, B., Pemberton, J., Pilkington, J., Gulland, F. & Clutton-Brock, T. (2005) Predictors of reproductive cost in female Soay sheep. *Journal of Animal Ecology*, **74**, 201–213.

van den Broeke, M.R. & van Lipzig, N.P. (2004) Changes in Antarctic temperature, wind and precipitation in response to the Antarctic Oscillation. *Annals of Glaciology*, **39**, 119–126.

Velando, A., Drummond, H. & Torres, R. (2006) Senescent birds redouble reproductive effort when ill: confirmation of the terminal investment hypothesis. *Proceedings of the Royal Society B: Biological Sciences*, **273**, 1443–1448.

Weimerskirch, H., Zimmerman, L. & Prince, P.A. (2001) Influence of environmental variability on breeding effort in a long-lived seabird, the yellow-nosed albatross. *Behavioral Ecology*, **12**, 22–30.

Weladji, R.B., Gaillard, J., Yoccoz, N.G., Holand, O., Mysterud, A., Loison, A., Nieminen, M. & Stenseth, N.C. (2006) Good reindeer mothers live longer and become better in raising offspring. *Proceeding of the Royal Society B: Biological Sciences*, **273**, 1239–1244.

Weladji, R.B., Loison, A., Gaillard, J., Holand, O., Mysterud, A., Yoccoz, N.G., Nieminen, M. & Stenseth, N.C. (2008) Heterogeneity in individual quality overrides costs of reproduction in female reindeer. *Oecologia*, **156**, 237–247.

White, G. & Burnham, K. (1999) Program MARK: survival estimation from populations of marked animals. *Bird Study*, **46**, 120–139.

Williams, G. (1966) *Adaptation and Natural Selection*. Princeton University Press, Princeton, New Jersey.

Wilson, P.R., Ainley, D.G., Nur, N., Jacobs, S., Barton, K.J., Ballard, G. & Comiso, J. (2001) Adélie penguin population change in the Pacific sector of Antarctica: relation to sea ice extent and the Antarctic Circumpolar Current. *Marine Ecology Progress Series*, **213**, 301–309.