

Age-specific survival and reproductive performances in fur seals: evidence of senescence and individual quality

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Life history theory hypothesises that breeding events induce reproductive costs that may vary among individuals. However, the growing number of studies addressing this question are taxonomically biased, therefore impeding the generalisation of this hypothesis, especially with regard to marine top predators. This study investigated age-related survival and breeding performances in subantarctic fur seal (*Arctocephalus tropicalis*) females from Amsterdam Island, southern Indian Ocean. Using multistate capture–recapture models on data obtained from known-age tagged females over eight consecutive years, we tested for evidence of senescence, individual quality, and reproductive costs in terms of future survival and fecundity. Adult female yearly survival appeared high and constant throughout time. While a two age-class model was preferred in non-breeders, breeding females exhibited three age classes with a maximum survival for the prime-age class (7–12 years). Survival and reproductive probabilities decreased from 13 years onward, suggesting senescence in this population. Survival was lower for non-breeders than for breeders, among both prime-aged (0.938 vs 0.982) and older (0.676 vs 0.855) females. Furthermore, non-breeders exhibited higher probabilities of being non-breeders the following year than did breeders (0.555 vs 0.414). Such results suggest consistency in female breeding performance over years, supporting the hypothesis that non-breeding tend to occur among lower quality individuals rather than representing an alternative strategy to enhance residual reproductive value. However, the high proportion of females that did not breed during two consecutive years, and the lower probability of being a successful breeder after a greater reproductive effort confirmed the existence of reproductive costs, especially during the second half of the lactation. These results also suggest that younger age-classes included a higher proportion of lower quality individuals, which are likely to face higher costs of reproduction. Such hypotheses lead to consider the first breeding event as a filter generating a within-cohort selection process in females.

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Past developments of population dynamics in long-lived species have permitted to estimate the relative importance of demographic parameters contributing to variation in individual lifetime reproductive success (Clutton-Brock 1988, Newton 1989). Studies of large

long-lived mammals have shown that population growth is consistently more affected by a given variation in adult survival than by the same variation in any other vital rate (Goodman 1981, Gaillard et al. 2000). Although a recent study (Gaillard and Yoccoz 2003) thoroughly

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reported variability in mammals' adult survival, this has been underestimated in many studies that assume a constant adult survival rate (Promislow and Harvey 1990, Promislow 1991). Further knowledge of survival variability is therefore required to better understand patterns of life-history evolution (Stearns 1992). In particular, age-related variations in survival are susceptible to influence the evolution of reproductive tactics, and consequently affect the size and dynamics of a given population (Stearns 1992). Hence precise estimates of age-specific survival are needed to improve the accuracy of demographic models in long-lived mammals (Eberhardt 1985). However, many past studies have been based on transversal life-table analyses, which require assumptions (i.e. random sampling, age structure stability) that are commonly not met in the wild (Caughley 1977, Seber 1982). In practice, accurate measurements of age-specific survival are difficult to obtain in the field because they require long-term longitudinal monitoring of known-aged individuals (Lebreton et al. 1992).

Similarly, the influence of parental age on the reproductive performance of long-lived species is a central point of animal life history (Stearns 1992), and age-specific breeding performance has been described in many mammal species (Clutton-Brock 1988, Sydeman et al. 1991, Lunn et al. 1994, Hewison and Gaillard 2001). Indeed, the life history of large mammals is commonly split into three age classes represented by the young, prime-aged and senescent stages when considering survival and reproductive patterns (Caughley 1966, Gaillard et al. 1998b, 2000). In addition, life-history theory commonly reports that some tradeoffs occur between current reproduction and future survival and/or reproductive opportunities (Williams 1966, Stearns 1989). For example, during unfavourable environmental conditions, increased reproductive effort may be associated with an age-related decrease in parental ability to exploit, acquire and allocate resources to the offspring (Trivers 1974, Evans 1990). This would ultimately lead to expose such breeders to face a steep recovery of body reserves, resulting in a decrease in their future survival and/or fecundity (Clutton-Brock 1984, Gustafsson and Pärt 1990, Festa-Bianchet et al. 1998). The survival costs of reproduction in several mammal species have been shown to be different between and within populations (Clutton-Brock et al. 1983, Reiter and LeBoeuf 1991), and reproduction skipping or abortion has been considered to be a means of avoiding such potential costs (Gaillard and Yoccoz 2003). Two main strategies were consequently reported in females, consisting in either (a) early reproduction and high reproductive rates associated with a short life span or (b) late reproduction and low reproduction rates associated with a long life span (Stearns 1983, Boyd et al. 1995). In this context, some studies have considered the non-breeding state as an

alternative strategy allowing higher future survival and reproductive probabilities, which could increase the individual's residual reproductive value and thus its lifetime reproductive success (Drent and Daan 1980, Coulson 1984, Pugesek and Wood 1992). Alternatively, an energetically demanding process like reproduction is not always associated with some form of costs, as some breeding individuals may exhibit a higher level of allocation where resources are abundant, and therefore increase their resource acquisition compared with non-breeders (Tuomi et al. 1983, Partridge 1987). Hence the effects of variation in individual quality has been demonstrated in several species (Clutton-Brock 1991, Harris and Wanless 1995, Cam et al. 1998, Reznick et al. 2000): some individuals may have phenotypes that are better adapted to their environment (Coulson and Porter 1985) and exhibit higher survival rates (Bérubé et al. 1999, Gaillard et al. 2000) and/or reproductive performances (Pomeroy et al. 1999, Beauplet et al. 2004) than those with poorer phenotypes. In this instance, the proportion of "good" individuals within an age class would be greater in older animals. The resulting increase in breeding success with age would then be counter-balanced by senescence, here defined as a concomitant decrease in age-specific reproductive and survival rates with age (Eberhardt 1985, Promislow 1991).

The senescence effect is largely acknowledged in large mammals (Eberhardt 1985, Promislow 1991, Gaillard et al. 1994, 2003), and usually explained by degenerative changes occurring in older organisms (Promislow 1991), and/or related to the cumulative effects of reproductive activities (Sydeman et al. 1991). However, this has only rarely been demonstrated statistically (Gaillard et al. 1993, Jorgenson et al. 1997), especially in pinnipeds (Pistorius and Bester 2002). Previous studies on fur seals have detected an age-specific decrease in either reproductive (Lunn et al. 1994, Dabin et al. 2004) or survival (Boyd et al. 1995) rates, but to our knowledge no longitudinal evidence of either senescence component has been demonstrated (Boyd et al. 1995, Pistorius and Bester 2002). The shortage of such studies is mainly due to the difficulty in estimating survival patterns in older age-classes, which requires long-term monitoring studies of marked individuals (Gaillard et al. 1994).

In 1994, a long-term marking study was initiated to investigate the population ecology of subantarctic fur seals (*Arctocephalus tropicalis*) in Amsterdam Island (Georges and Guinet 2000), requiring the tagging of 100–200 pups each year (Chambellant et al. 2003), as well as a large number of known-aged adult females (Dabin et al. 2004). The objectives of this paper were two-fold. First, we sought to determine the existence of an age-related pattern in survival probabilities of subantarctic fur seal females. As was found for the proportion of breeding females (Dabin et al. 2004), we expect to observe a bell-shaped relationship with age, with a

prime-age class occurring at 8–13 years old and lower survival probabilities exhibited by the older age classes, demonstrating the existence of a senescence effect in females. The second purpose of this paper was to investigate possible reproductive costs in subantarctic fur seal females by examining the co-variation between a breeding event and future survival and reproduction probabilities. In addition, the sign of this co-variation permits to draw inferences regarding the respective magnitude of individual heterogeneity and reproductive costs within the female population (Van Noordwijk and DeJong 1986). The recent developments in mark–recapture modelling allowed us to integrate individual covariates (White and Burnham 1999, Hall et al. 2001) and temporary emigration (Fujiwara and Caswell 2002) into our survival estimates.

Methods

Study site and species

This study was carried out at “La Mare aux Eléphants” breeding colony, on the northeast side of Amsterdam Island, southern Indian Ocean (37°55'S, 77°30'E), where one of the largest breeding colonies of the island can be found (Guinet et al. 1994). The topographic unit representing the breeding colony was delimited with visual reference markers, allowing us to sample the same portion of the rookery each year from 1995 to 2004.

In subantarctic fur seals, births occur from late November to early January, and the nursing period is carried out by the female alone during about 10 months (Georges et al. 1999, Georges and Guinet 2000), after which newly weaned pups leave their native island to acquire nutritional independence (Ofstedal et al. 1987, Bowen 1991). Juvenile females first return to their native rookery mainly occurs from 3 to 6 years of age (Beauplet et al. in press), and usually start reproduction after that period (Dabin et al. 2004).

Individual tagging and resightings

During the 1994–1997 breeding seasons, 130 adult females of unknown age received the same type of tag (Georges and Guinet 2000), as well as 110 adult females during the 1999 breeding season. The tagging procedure did not vary among years (Georges and Guinet 2000), and all animals received an individually numbered plastic tag (Dalton Rototags, Dalton Supply, Nettlebed, UK) in the connective tissue on the trailing edge of both fore flippers. Morphometric data and tooth samples (i.e. for age determination) were collected from 108 of the 240 above-mentioned tagged females during autumn–winter 1999 (Dabin et al. 2004). The breeding colony was surveyed every day during the parturition period in

order to determine the breeding status of the tagged females observed on the rookery during the 1995–2004 breeding seasons. Depending on the breeding season, between 100 and 200 newborn pups were sexed, weighed (± 0.1 kg) and marked each year (Chambellant et al. 2003). At about one month of age, each marked pup was tagged using a similar tagging procedure as that for adults (Georges and Guinet 2000, Chambellant et al. 2003).

Searches for tagged seals were then conducted every two days on the colony throughout the lactation period during the breeding seasons of 1995 to 2004. Each searching session consisted of a 5-hour continuous scan in the delimited rookery section and adjacent areas corresponding to non-breeding/juvenile haul-out sites. Tag number and colour were recorded for each re-sighted individual, and in cases where tags were found to be missing, adult females were recaptured and given new ones, so that tag loss could be considered as negligible in this study. During these surveys, all tagged pups found were weighed using a rope attached to a spring scale (± 0.1 kg), which permitted us to obtain the weaning mass and to calculate individual growth rates for each pup (Chambellant et al. 2003). This allowed us to obtain both the age and breeding performance of the tagged adult females, as well as of any female marked as a pup and returning to the rookery (Beauplet et al. in press).

Modelling female survival and costs of reproduction

This 10-year study of subantarctic fur seal females resulted in capture–recapture histories including information regarding their presence and breeding state in a given year. We analysed data using multistate capture–recapture models, which included three kinds of parameters: recapture probability P_t^w , survival rate S_t^w , and conditional transition probability ψ_t^{wx} (Nichols et al. 1994).

P_t^w = probability that a female is resighted at time t in state w , given that it is present on the colony at time t .

S_t^w = probability that a female in state w at time t survives until $t+1$.

ψ_t^{wx} = probability that a female in state w at time t is in state x at time $t+1$, given that the seal survived from time t to $t+1$.

In order to test the respective effects of time, age, and breeding performance simultaneously, we would ideally have to start with the following global model [$S_{t^*a10}^{\text{state}}$, $P_{t^*a10}^{\text{state}}$, $\psi_{t^*a10}^{\text{state}}$]. However, the high number of parameters for this model led to numerical convergence problems associated with incorrect parameter estimations (Kendall

and Nichols 2002), and we therefore had to divide this study into three successive steps.

First, time dependence on female survival and capture probabilities was tested on the 1999–2004 period in the 110 females tagged during the 1999 breeding season. As has been found in juveniles (Beauplet et al. in press), our field observations showed that some individuals absent on the rookery during a given year were seen again during the next breeding season, leading us to suspect that adult females temporarily emigrated (Fujiwara and Caswell 2002) from the studied population. In order to take into account the individual temporary emigration, we used a multistate model (Arnason 1973, Schwarz et al. 1993) containing two states: an observable (O) state for individuals present in a given year at the colony, and an unobservable (U) state (Kendall and Nichols 2002). First, we started with a multistate model [S_t^{state} , P_t^{state} , ψ_t^{state}], which assumed survival, recapture and transition probabilities dependent on time (t) and state. This starting model, however, requires to be constrained in order to estimate all parameter values (Kendall and Nichols 2002). Thus, state transition probabilities (ψ^{OU} for temporary emigration and ψ^{UO} for temporary immigration, respectively) were constrained to be constant over time, survival probabilities to be the same for observable and unobservable animals (model 43 in Table 2 in Kendall and Nichols 2002), and capture probabilities for the unobservable state were fixed at 0. This led us to start with the multistate model [S_t , P_t^{state} , ψ_t]. The presence of interaction between the effects is noted as “*” whereas a “.” represented a constant pattern of the parameter tested. As no goodness-of-fit (GOF) test is available for multistate models containing an unobservable state, we tested the ability of the simpler nested model [S_t , P_t] to describe the data using U-CARE software (Choquet et al. 2002).

Secondly, when taking into account both the age and breeding status of each female, we also used a conditional multistate model containing three states: 1 = individuals present but not breeding, 2 = breeding females, and 3 = females not present throughout the breeding season. Considering the high-site fidelity exhibited by female fur seals (Gentry and Kooyman 1986, Beauplet et al. in press), we assumed that unobservable females did not breed in another colony, and therefore constrained survival rates of our starting model to be the same for non-breeding and unobservable individuals. We first considered the complete age-dependent model, defined as 10-age-classes representing each year of age from 6 to 14 years old and also including the 15 plus class. However, because of numerical convergence problems associated with incorrect state transition probability estimations (Kendall and Nichols 2002), we initially applied the 3-age-class model in state transition probabilities. It was determined using the prime-age class of 8–13 years old, when reproductive rates were found to

be significantly higher (Dabin et al. 2004). We therefore started with the model [S_{a10}^{st} , P_{a10}^{st} , ψ_{a3}^{st}], which assumed both survival and recapture probabilities dependent on both the complete 10-age-classes (a10) and the breeding status (st), while state transition probability depended on both 3-age-classes (a3) and breeding status. We then tested whether our starting global model was compatible with our biological knowledge and provided an adequate description of our data, using the same method as described above. We built the global GOF test of this model by adding each component of the monostate GOF tests of the CJS model applied to both age and breeding status separately.

We finally tested the importance of breeding performance at year Y on future survival and breeding performance at year Y+1. From 1999 to 2003, breeding performances (bp) of 131 females were classified in four different categories during the 10-month lactation period: (1) non-breeders (nb) represented females that were not seen with a pup throughout the breeding season; (2) early failure (ef) represented females breeding a pup that died before 30 April (i.e. less than five months of age); (3) late failure (lf) represented females breeding either a pup that died beyond five months of age, or a pup weaned with an insufficient growth rate to allow postweaning survival chances (pup growth rate $< 0.03 \text{ kg d}^{-1}$, Beauplet et al. in press); (4) successful breeding (sb) represented females succeeding in taking their pup to the weaning process with a sufficient growth rate and weaning mass to allow good postweaning survival probabilities (Beauplet et al. in press). We then tested whether our starting global model [S^{bp} , P^{bp} , ψ^{bp}] provided an adequate description of our data, using the GOF test for multistate models (Pradel et al. 2003) implemented in U-CARE software (Choquet et al. 2002).

The model selection procedure was then performed following the parsimony principle, based on the Akaike information criterion corrected for small sample sizes (AIC_C , Lebreton et al. 1992). The lower the AIC_C value, the more parsimonious the model (Burnham and Anderson 1998), and we considered two models to be significantly different when the ΔAIC_C was greater than two (Anderson and Burnham 1999). All estimates and AIC_C values were computed using program MARK (White and Burnham 1999), and unless otherwise stated, values are reported as means \pm SE.

Results

Effect of time

The CJS model fitted the data poorly ($\chi^2 = 9.234$, $df = 3$, $p = 0.03$), and a large part of this statistic was explained by the test 2.Ct, indicating a ‘trap dependence’ effect on capture (Pradel 1993). Nevertheless, the unobservable

state implemented in our multistate model permitted to take into account this ‘trap happiness’ effect in the capture probabilities. Indeed, the low transition probabilities ($\psi^{OU} = 0.124 \pm 0.026$ and $\psi^{UO} = 0.127 \pm 0.075$, respectively) showed a non-random pattern of temporary emigration, indicating the existence of a Markovian temporary emigration effect (Schaub et al. 2004). There was no evidence of an effect of time (year) on either recapture (Table 1, model 2 vs 3) or survival (model 1 vs 2) probabilities, which led us to select the constant model [S., P^O., ψ].

Effect of age and breeding status

Of the 310 known-age tagged females that were resighted, 238 individuals had their breeding status recorded from 1999 through 2004 and were thus included in the analysis. The overall GOF test was marginally significant ($\chi^2 = 25.73$, $df = 16$, $p = 0.06$), indicating that the global model [S_{a10}st, P_{a10}st] poorly fitted the data. The main part of this χ^2 statistic was explained by test 2.Ct ($\chi^2 = 18.88$, $df = 11$, $p = 0.06$), and this Markovian temporary emigration effect has been taken into account using the non observable state in the model (Schaub et al. 2004). We can therefore reasonably suppose that our starting model (Table 2, model 12) fitted the data well, since it was more complex than the tested one, and thus probably captured more heterogeneity in the capture–recapture dataset.

Starting with the general model (Table 2, model 12), we found no effect of age on transition probabilities from breeding and unobservable states (model 10 vs 11 and 12). However, an age effect (i.e. prime-age class at 8–13 years) was found on the transition probabilities from a non-breeding to a breeding state (model 9 vs model 10). Notably, the proportion of seals that were non-breeders at year Y and breeders at year Y + 1 was lower in younger and older females compared with the prime-age class individuals (Fig. 1). Interestingly, the probability for a breeding female at year Y to breed again the next year Y + 1 was constant in all age classes (0.586, SE = 0.052), and higher than in non-breeders at year Y (Fig. 1). We found no age effect on recapture rates (model 8 vs 9), and AICc values were nearly

identical for models in which capture probability was modelled either as a function of breeding state or as a constant parameter (model 7 vs 8). We therefore applied objective biological criteria (Burnham and Anderson 1992, Lebreton et al. 1992) and selected the [S_{a10}st, Pst, ψ_{a3} ¹, ψ^2 , ψ^3] model, because field records showed that long-lactating breeding females have higher chances to be observed when present on the rookery (1.000, CI_{95%} = [0.933–1.000]) than non-breeders (0.896, CI_{95%} = [0.827–0.939]). We then tested for age dependence in survival probabilities using all possible pertinent models (not shown in Table 2), and found that breeding females exhibited three categories of survival probabilities (model 5 and 6 vs 8), with a maximum value for the prime-age class (i.e. 7–12 years, Fig. 2). A model with two age classes for non-breeding individuals (model 2 vs 3 and 5) was preferred, and also indicated a lower survival in females older than 12 years old (Fig. 2). Interestingly, the younger age class of both breeding and non-breeding females exhibited similar survival probabilities (model 1 vs 2, Fig. 2).

We then simultaneously considered the age-related survival (this study) and reproductive (Dabin et al. 2004) rates of a theoretical initial cohort of four year old females (i.e. modal age at first return on native colony; Beauflet et al. in press). The maximum productive period occurred for prime-aged females, as nearly half of the initial cohort was breeding during that period (Fig. 3). Only 37.8% of the individuals would survive to the age of 14 years old, with only 15.1% of the initial cohort breeding at that age (Fig. 3). Only 14.0% of the initial cohort survived after 16 years of age, among which none was breeding (Fig. 3).

Effect of breeding performance

Of the 238 known-age tagged females with a recorded breeding status, 184 individuals had their breeding performances recorded from 1999 through 2003 and were thus included in the analysis. The overall GOF test revealed that the global model [S^{bp}, P^{bp}, ψ^{bp}] did not fit the data satisfactorily ($\chi^2 = 95.65$, $df = 75$, $p = 0.05$), and this result was mainly due to the test MITEC ($\chi^2 = 48.93$, $df = 6$, $p < 0.001$), indicating a short-term ‘trap

Table 1. Description of constraints, AICc, dAICc, Akaike weights (AICw), and number of estimated parameters (No. par.) for various models testing an effect of time on recapture and survival probabilities in 110 breeding-age female subantarctic fur seals tagged in Amsterdam Island during the 1999 breeding season and resighted during the 1999–2004 breeding seasons. Models are ranked according to their AICc.

Model ¹	Description of constraint	AICc	dAICc	No. par.
1 S, P ^O , ψ_t^{wx}	absence of time effect on survival	327.950	0	4
2 S, P ^O , ψ_t^{wx}	absence of time effect on recapture	332.285	4.33	7
3 S, P ^O , ψ_t^{wx}	starting model	333.964	6.01	10

¹: See Methods section for model nomenclature.

Table 2. Description of constraints, AICc, dAICc, and number of estimated parameters (No. par.) for various models testing an effect of age and breeding state on recapture, survival and transition probability in 238 known-age subantarctic fur seal tagged females resighted in in Amsterdam Island during the 1999–2004 breeding seasons. Models are ranked according to their AICc.

Model	Description of constraint	AIC	dAICc	No. par.
1	$S_{a2/13}^1 S_{a3/7-12}^2 P^{st} \psi_{a3}^{12} \psi_{a3}^{13} \psi_{a3}^2$ $\psi_{a3}^3/S_{a3}^1 < 13 = S_{a3}^2 < 7$	1535.618	0	14
2	$S_{a2/13}^1 S_{a3/7-12}^2 P^{st} \psi_{a3}^{12} \psi_{a3}^{13} \psi_{a3}^2 \psi_{a3}^3$	1535.788	0.17	15
3	$S_{a3/8-13}^1 S_{a2/13}^2 P^{st} \psi_{a3}^{12} \psi_{a3}^{13} \psi_{a3}^2 \psi_{a3}^3$	1537.172	1.55	16
4	$S_{a2/13}^1 S_{a2/13}^2 P^{st} \psi_{a3}^{12} \psi_{a3}^{13} \psi_{a3}^2 \psi_{a3}^3$	1539.691	4.07	14
5	$S_{a10}^1 S_{a3/7-12}^2 P^{st} \psi_{a3}^{12} \psi_{a3}^{13} \psi_{a3}^2 \psi_{a3}^3$	1550.921	15.30	26
6	$S_{a10}^1 S_{a3/7-13}^2 P^{st} \psi_{a3}^{12} \psi_{a3}^{13} \psi_{a3}^2 \psi_{a3}^3$	1555.225	19.61	26
7	$S_{a10}^{st} P_{a3} \psi_{a3}^{12} \psi_{a3}^{13} \psi_{a3}^2 \psi_{a3}^3$	1563.446	27.83	35
8	$S_{a10}^{st} P_{a3}^{st} \psi_{a3}^{12} \psi_{a3}^{13} \psi_{a3}^2 \psi_{a3}^3$	1563.668	28.05	36
9	$S_{a10}^{st} P_{a10}^{st} \psi_{a3}^{12} \psi_{a3}^{13} \psi_{a3}^2 \psi_{a3}^3$	1599.855	64.24	60
10	$S_{a10}^{st} P_{a10}^{st} \psi_{a3}^1 \psi_{a3}^2 \psi_{a3}^3$	1603.737	68.12	62
11	$S_{a10}^{st} P_{a10}^{st} \psi_{a3}^1 \psi_{a3}^2 \psi_{a3}^3$	1611.729	76.11	66
12	$S_{a10}^{st} P_{a10}^{st} \psi_{a3}^1 \psi_{a3}^2 \psi_{a3}^3$	1616.364	80.75	70

Note: “.” represented a constant pattern of the parameter tested, and st represented the non-breeding (1), breeding (2) and unobservable (3) states. a10 represented the complete age-class-dependent model, while a3 and a2 represented a 3 and a 2 age-class model, respectively.

dependence’ on capture (Pradel 1993). As the starting model did not contain an unobservable state, we fitted $[S^{bp}, P_m^{bp}, \psi^{bp}]$ model to account for this ‘trap happiness’ in the capture probabilities (Table 3, model 9), following Pradel (1993).

While capture probabilities were found similar in all breeding females regardless of their performance (model 5 vs 9), they were higher than in non-breeding individuals (model 9 vs 10). Moreover, the ‘trap happiness’ effect had to be taken into account for both breeding and non-breeding females (model 5 vs 7 and 8). The survival probability of females failing in their breeding attempt (0.933, SE = 0.023; model 2 vs 5) did not depend on the timing of failure, but differed from survival probability of successful (0.980, SE = 0.016; model 2 vs 3) or

non-breeding (0.843, SE = 0.024; model 2 vs 6) individuals. Although no significant difference in model fit ($\Delta AIC_c < 2$) was observed between model 2 and model 4, the least number of parameters led us to consider model 4 to be a better fitting model, suggesting that non-breeding and early failure females showed similar transition probabilities. Individuals exhibiting such breeding performance at year Y had significantly higher chances to be non-breeders (0.555, SE = 0.026) than to become successful breeders (0.239, SE = 0.021) at year Y + 1 (Fig. 4). Interestingly, transition probabilities to non-breeding state at year Y + 1 were also found to be similar in breeding and late failure females (0.376, SE = 0.030; model 1 vs 4), and lower than in

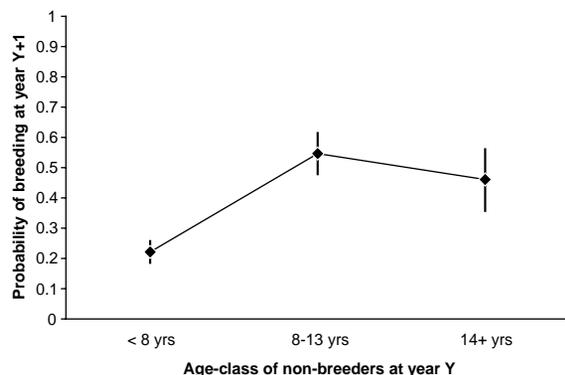


Fig. 1. Influence of age in non-breeding subantarctic fur seal females on the breeding probability in the following year. Data are presented as mean \pm SE, and were estimated from model 1, Table 2.

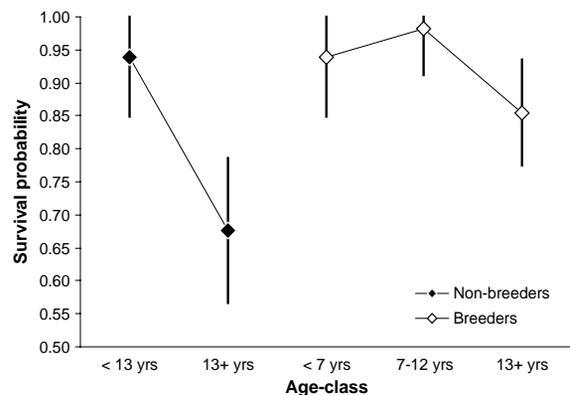


Fig. 2. Influence of breeding state and age in subantarctic fur seal females on the survival probability in the following year. Breeders and non-breeders at year Y are represented by open and filled diamonds, respectively. Data are presented as mean \pm SE, and were estimated from model 1, Table 2.

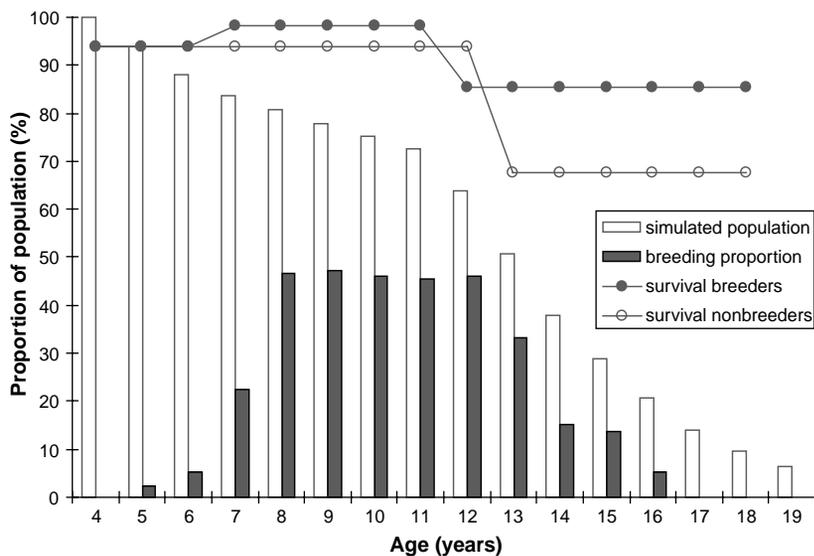


Fig. 3. Distribution in proportion (%) of a simulated cohort (white histogram) of female subantarctic fur seals starting at four years old (i.e. age at first return on native colony; Beauplet et al. in press), and based on age-specific survival rates of breeders and non-breeders (black dotted and white dotted lines, respectively). The black histogram represents age-specific reproduction rates of the initial female cohort, calculated from Dabin et al. (2004).

non-breeding and early failure females (Fig. 4a). However, the probability to be a successful breeder at year $Y+1$ was significantly higher in successful breeders at year Y than in late failure females at year Y (Fig. 4c).

Discussion

Effect of time

It is noteworthy that a recent study (Schaub et al. 2004) demonstrated that models containing a Markovian temporary emigration pattern provide precise estimates of parameters especially when no time dependence occurs, which is also the case in this study. Our results indeed indicated that recapture probability was constant through time, suggesting no active avoidance behaviour from females, and no major differences between field-worker observation skills. This confirms an homogeneous effort of recapture accomplished from one year to another (Beauplet et al. in press), allowing us to consider an absence of bias in our survival estimates (Prévot-Julliard et al. 1998). Consistent with what has been found in juveniles (Beauplet et al. in press), adult female survival was also constant over time, confirming the minor impact of environmental conditions on adult survivorship in long-lived mammals (Gaillard et al. 2000). The contrasting result found in Antarctic fur seals (Boyd et al. 1995) may be due to the greater environmental variability experienced by this species (Gentry and Kooyman 1986) in conjunction with the higher energetic requirements necessary to reach sufficient pup weaning conditions over a shorter lactation period (Oftedal et al. 1987).

Age-specific survival and reproductive features

Relationships between age-specific survival and reproduction need to be further explored to understand life-history strategies (Stearns 1992), and this longitudinal study is particularly relevant for assessing senescence in a large mammal species. The adult female survival probabilities estimated in this study were much higher than those estimated in phocid species (Testa and Siniff 1987, Pistorius and Bester 2002), but the range (i.e. 0.85–0.98) was similar to that observed among other female fur seal (Payne 1977, Lander 1981, York 1987, Boyd et al. 1995), and large herbivore (Gaillard et al. 1998b, 2000) species. Consistent with previous studies in ungulates (Gaillard et al. 1993, Jorgenson et al. 1997), this result suggests low variability of adult female survival rates among fur seal species despite marked differences in population dynamics (Wickens and York 1997). Nevertheless, unlike previous results described in Antarctic fur seal females (Boyd et al. 1995), individual age was found to influence annual survival (Fig. 2). Similarly to ungulate populations (Loison et al. 1994, Gaillard et al. 1998b), survival of breeding females was best illustrated with a bell-shaped 3-age class model with prime-age individuals exhibiting the highest value. In contrast, non-breeders exhibited a 2-age class pattern with significantly lower and more variable survival probability in animals older than 12 years of age (Fig. 2).

Similar to what has been found previously in survival features of long lived mammals, some aspects of reproductive performance typically have a quadratic relationship with age, in which performance increases and then declines with age (Clutton-Brock et al. 1992, Gaillard et al. 2000). This study population also exhibited such a pattern, with an observed peak of breeding rate in the 8–13 year old age classes (Dabin et al. 2004). This result

Table 3. Description of constraints, AICc, dAICc, and number of estimated parameters (No. par.) for various models testing an effect of breeding performance on recapture, survival and transition probability in 184 subantarctic fur seal females breeding in Amsterdam Island during the 1997-2003 breeding seasons. Models are ranked according to their AICc.

Model	Description of constraint	AICc	dAICc	No. par.
1	$S^{nb} S^{ef/ff} S^{sb} P^{nb} P^{ef/ff/sb} \psi^{nb/ef} \psi^{ff} \psi^{sb}/\psi^{linb} = \psi^{sb/b}$	2792.061	0.00	15
2	transition to nonbreeding state equals for breeding and late failing animals	2792.334	0.27	19
3	similar survival in early and late failing breeders	2793.457	1.40	18
4	breeders survival different from failing breeders	2793.967	1.91	16
5	transition equals for nonbreeding and early failing animals	2794.288	2.23	20
6	nonbreeders recapture different from breeders	2796.342	4.28	18
7	nonbreeders survival different from failing breeders	2797.552	5.49	19
8	trap dependence effect on nonbreeders	2798.169	6.11	19
9	starting model	2805.635	13.57	24
10	capture different in nonbreeding and early failing females	2808.142	16.08	20

Note: “.” represented a constant pattern of the parameter tested, and a model with immediate trap dependence on capture was denoted P_m , bp represented the following four states of breeding performance: nb represented non-breeding females, ef represented females breeding a pup that died at less than 5 months of age, if represented females breeding either a pup that died older than 5 months of age or a pup weaned with an insufficient growth rate to allow postweaning survival chances, and sb represented females breeding a pup successfully.

is somewhat consistent with other fur seal species (York and Hartley 1981, Lunn et al. 1994, Arnould et al. 2003), although the maximum breeding rate was much lower in our study population (i.e. 0.63 vs >0.80). Interestingly, older breeding Antarctic fur seal females were more likely to pup again the next season than younger breeding females (Lunn et al. 1994), whereas age did not seem to influence such breeding decisions in our study. No age-specific costs of reproduction in terms of future reproduction were therefore detected in our study population. Interestingly, the probability for a non-breeder at year Y to become a breeder at year Y+1, was similar to the survival features exhibited by the three age classes (Fig. 1).

Senescence

Our longitudinal data showed that a decline in survival with age occurred in both breeding and non-breeding females (Fig. 2). Moreover, these results were concomitant with the age-related decrease in reproductive performances observed in the female population (Dabin et al. 2004), showing support for the hypothesis of individual senescence. While reproductive senescence has been proposed in a few marine mammal species using transversal data (Sydeman et al. 1991, Trites 1991), the statistical demonstration of individual senescence was still lacking (Boyd et al. 1995, Pistorius and Bester 2002). To our knowledge, this is the first longitudinal study reporting a senescence effect of a pinniped species in terms of both reduced survival and breeding performances. Nevertheless, such result is consistent with what has been commonly described in large herbivores (Gaillard et al. 1993, Jorgenson et al. 1997), although the age-simultaneity of survival and reproductive senescence needs to be further explored in these species.

Reproductive costs and individual quality hypotheses

In contrast with what has been found in Antarctic fur seals (Boyd et al. 1995), non-breeding females of any age class exhibited lower chances of survival to the next season than breeding females (Fig. 2). Moreover, breeders at year Y showed a higher probability of breeding during the next season than did non-breeders of any age at year Y. We therefore found no evidence that non-breeding status may lead to an increase in future survival or reproduction probabilities. Hence, these results do not confirm the hypothesis considering the non-breeding state as an alternative strategy to enhance residual reproductive value (Coulson 1984, Wooller et al. 1990, Orell et al. 1994). On the contrary, the age-related increase of non-breeders' mortality led to a decline in residual reproductive value with age, and therefore provided selective pressure for increasing reproductive

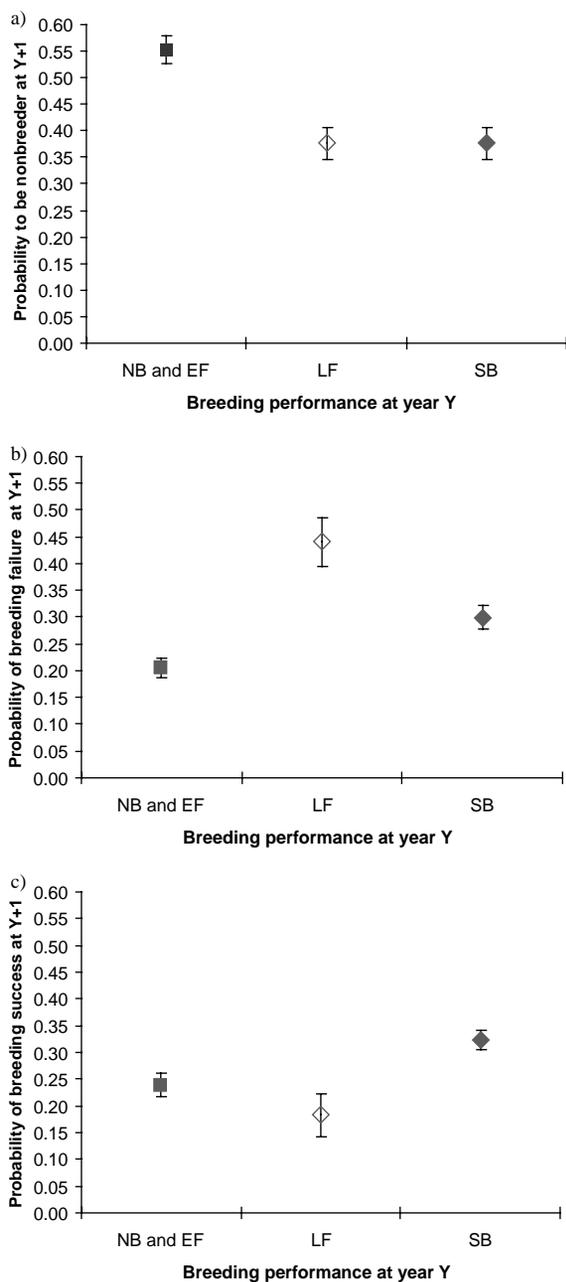


Fig. 4. Influence of the breeding performance of subantarctic fur seal females at year Y on the breeding performance in the following year. Black squares represents both non-breeders (NB) and early failure breeders (EF) at year Y, while filled and open diamonds represents successful breeders (SB) and late failure breeders (LF) at year Y, respectively. Data are presented as mean \pm SE, and were estimated from model 1, Table 3. (a) Probability to be nonbreeder at year Y+1. (b) Probability of breeding failure at year Y+1. (c) Probability of successful breeding at year Y+1.

effort with age. Nevertheless, our results are consistent with the hypothesis of variation among individuals regarding their intrinsic quality (Curio 1983, Newton 1989, Morris 1998). The lower survival of younger

breeders (Fig. 2) suggests that younger age-classes included a higher proportion of lower quality individuals, which are likely to face higher costs of reproduction (Curio 1983, Nur 1988, Cam and Monnat 2000). Consequently, younger animals of lower quality would exhibit a lower breeding success (Newton 1989) and/or higher mortality rates following their first reproduction (Promislow 1991, Clutton-Brock et al. 1996), which would consecutively lead to a within-cohort selection process (Curio 1983, Vaupel and Yashin 1985, Cam and Monnat 2000). The lower survival exhibited by females failing in their breeding attempt compared with successful breeding females also tends to confirm the good phenotype selection hypothesis. Such a concept of individual quality is also supported by the contrasting effects of the breeding performance at year Y to the reproductive performance at year Y+1 (Fig. 4). Indeed, females exhibiting a poor breeding performance in a given year tended to remain in the same breeding performance category the following year. Furthermore, we also found significant differences between late failure and successful breeders (i.e. similar reproductive effort) in the probability to exhibit a successful breeding performance in the following year. These results suggest consistency in female breeding performance over years. Moreover, the positive correlation detected between survival and reproduction supports the hypothesis that females of this population vary more in their individual quality than in the way they allocate energy between survival and reproduction (Van Noordwijk and DeJong 1986).

Interestingly, the probability of being a successful breeder at year Y+1 was higher in early failure and non-breeding individuals than in late failure females, suggesting that significant higher costs of reproduction occurred particularly during the second half of the pup-rearing period. This result is not surprising, as this period corresponds to a decline in prey availability and subsequent extension of maternal foraging trips (Beauplet et al. 2004) coupled with both the moulting process and the end of the embryonic diapause (Bester 1995), leading to decreasing maternal performances and, consequently pup growth (Beauplet et al. 2004). However, this confirms that fur seal females may be able to tolerate depletion of individual capabilities (i.e. body reserves) up to some physiologically determined threshold level (Guinet et al. 1998), and costs of reproduction become apparent only when this individual level is exceeded (Tuomi et al. 1983, Loison et al. 2004). This hypothesis is also supported by the high proportion of females (i.e. 41.4%) that did not breed during two consecutive years. We therefore suggest that reproductive costs occurred in the successful breeding females that did not breed during the next season, while females failing in their breeding attempt exhibited both future survival and fecundity costs. However, females failing in their breeding

attempt during a given year cannot be simply categorised as low quality individuals. The high magnitude of individual heterogeneity observed within the females (Van Noordwijk and DeJong 1986) makes it necessary to analyse individual life breeding success throughout the longest possible period of their reproductive life in order to dispose of a good measure of individual quality.

As has been found in previous studies of long-lived birds (Harris and Wanless 1995, Cam et al. 1998, Cobley et al. 1998), our estimates showed that successful mothers have the highest survival and future breeding probabilities, which suggests that most individuals exhibiting such performance were higher-quality individuals. Yet to our knowledge, previous studies in large mammals (Clutton-Brock et al. 1983, Trillmich 1986, Boyd et al. 1995) have not allowed for such a conclusion. Nevertheless, Pomeroy et al. (1999) stated that half of the study females produced 74% of the pups, and a few other studies on ungulates (Gaillard et al. 1998a) provided substantial evidence for individual variation in female quality. Moreover, Dobson et al. (1999) suggested that the expression of individual quality could depend on genotypes that code simultaneously for reproductive and longevity potentials. Cam et al. (1998) hypothesised differences in methodology to interpret such discrepancies between species. Alternatively, it is possible that studies have led to different interpretations because they were carried out in distinct demographic situations. In particular, density-dependence was found to affect juvenile survival (Clutton-Brock et al. 1987), and it is possible that higher population density (Beauplet et al. 2004) may also increase individual heterogeneity (Toigo et al. 2002), and thus make individual quality patterns more conspicuous. Consequently, population parameters may have been diversely influenced by intrinsic differences between individuals, such as age, fecundity or phenotypic characteristics. Recent developments in life-history theory have allowed for the assessment of the influence of heterogeneity on life-history traits as a determinant of individual quality (McNamara and Houston 1992). The nature of individual quality in female subantarctic fur seals needs to be further explored, as it seems essential for determining whether a state variable could be viewed as an objective predictor of this quality. This will allow us to explore whether individual quality is a dynamic or a constant variable over time (Houston and McNamara 1992, McNamara and Houston 1992). Furthermore, it could be interesting to explore to what extent individual quality could be determined by characteristics related to either individual phenotypic patterns (Festa-Bianchet 1998, Pomeroy et al. 1999, Crocker et al. 2001) or foraging tactics during the pup-rearing process (Beauplet et al. 2004).

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