

Interannual variation in the post-weaning and juvenile survival of subantarctic fur seals: influence of pup sex, growth rate and oceanographic conditions

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Summary

1. A major hypothesis of life history theory is that early development conditions affect future survival and reproductive success. However, although a growing number of studies have addressed this question, many of them are taxonomically biased, thereby impeding the generalization of this hypothesis.

2. This study examines the factors influencing post-weaning survival in five weaned cohorts of subantarctic fur seal pups from Amsterdam Island, southern Indian Ocean. It used mark–recapture data from 7 consecutive years of different environmental conditions.

3. The cohort return rate varied from 45% to 74% of weaned pups, depending on the year of weaning. In each cohort, 96% of weaned pups returned between 3 and 6 years of age, and none of the factors examined seemed to influence this timing pattern. The probability of survival to this first return was negatively related to sea-surface temperature anomalies (SSTa) of the 6 months following the weaning process. It increased with pup preweaning growth rate and differed between the sexes. Females' survival rate was significantly higher than males', except during years of extreme SSTa, where no difference was detected.

4. The juvenile state represented young individuals after their first return on their native island. Annual juvenile tag loss rate was constant at 0.217 (SE = 0.027), whereas temporary emigration rate varied over cohorts and was higher in males 0.423 (SE = 0.035) than in females 0.170 (SE = 0.012). This dispersion pattern may be prolonged in some cases, as the yearly immigration probability was constant at 0.290 (SE = 0.065).

5. Taking into account tag loss and temporary emigration, the estimated yearly survival probability of juveniles was 0.964 (SE = 0.022). This value was unrelated to any tested oceanographic or individual parameter including sex.

6. Results support the hypothesis that early development traits affect short-term post-weaning survival. However, no long-term effect of maternal postnatal investment was detected after the first return to the native island. Results also indicate that the effect of early development traits on survival interacts with environmental conditions encountered shortly after independence of individuals.

Key-words: early development, multistate mark–recapture models, post-lactating survival, sea surface temperature anomalies, temporary emigration.

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Introduction

Past developments of population dynamics in long-lived species have permitted the estimation of the relative importance of parameters contributing to variation in individual lifetime reproductive success (Clutton-Brock 1988; Newton 1989). Any change in population

growth rate appeared to be determined by the relative influence of its fitness components, which depends directly on both their elasticity and temporal variation features (Pfister 1998; Gaillard *et al.* 2000). Studies in large mammal populations have shown that offspring survival can represent a significant contributor to variation in population dynamics, as well as a potential indicator of the population status (Eberhardt 1981; Clutton-Brock 1988; Sinclair 1996). Increase in population size was indeed found to be related to an enhancement in the reproductive output of surviving offspring into the next generation, while low juvenile survival periods caused the population to decline (Stearns 1992; Gaillard, Festa-Bianchet & Yoccoz 1998a). Hence, a precise assessment of the factors affecting offspring survival is crucial for the understanding of population dynamics. In contrast with preweaning survival, which is generally dependent on maternal care (Gaillard *et al.* 2000), factors such as birth timing, birth weight and maternal dominance status appear to have less impact on offspring post-weaning survival (Clutton-Brock *et al.* 1987; Clutton-Brock, Price & Albon 1991). In fact, most reported causes of post-weaning mortality are more related to the environmental context, such as climatic and environmental conditions, as well as density-dependence (Clutton-Brock *et al.* 1991; Singer *et al.* 1997).

Although commonly acknowledged, there have been few studies of how postnatal maternal investment may influence offspring post-weaning survival, and ultimately fitness (Lindström 1999). Hence, evidence for an effect of resource transfer to offspring fitness has been documented only recently (Merilä & Svensson 1997; Festa-Bianchet, Jorgenson & Reale 2000; Hall, McConnell & Barker 2001). In pinnipeds, offspring remain on the breeding island depending upon maternal milk until they are weaned (Trillmich 1996), which allows a precise assessment of preweaning survival rates (Boltnev, York & Antonelis 1998; Bradshaw *et al.* 2003) and the factors that could influence this demographic parameter (Pomeroy *et al.* 1999; Chambellant *et al.* 2003). The pups exploit the maternal milk to accumulate fat stores, which represent an excellent insulator (Bryden 1964; Blix, Grav & Ronald 1979), and also provide essential nutrients to sustain them from weaning to nutritional independence (Bryden 1968; Hindell, Bryden & Burton 1994). Such an abrupt interruption of parental care is thus a crucial step in the life history of the animal (Oftedal, Boness & Tedman 1987; Bowen 1991), as newly weaned pups must face a number of critical challenges, including escaping predators and learning to locate and capture accessible prey.

A precise estimate of post-weaning survival is often difficult to obtain in pinnipeds, particularly as weaned offspring spend considerable time at sea where they cannot be studied easily. Moreover, individual factors such as body mass and condition can affect first-year survival more extensively under conditions of fluctuating food availability (Coulson *et al.* 1997). Previous

studies in phocids have shown that first-year survival probability increased with increasing body mass and condition at weaning (McMahon, Burton & Bester 2000; Hall *et al.* 2001). We expect to observe such a relationship in otariid seals, which should confer some selective advantages in the heavier-at-weaning individuals. For example, as individual birth weights of subantarctic fur seal (*Arctocephalus tropicalis* Gray) pups are correlated positively with their probability of early preweaning survival (Chambellant *et al.* 2003), it seems likely that higher weaning mass could also enhance their probability of post-weaning survival. To our knowledge, very few studies have evaluated fur seal post-weaning survival, and such a hypothesis was demonstrated only on male Northern fur seal (*Callorhinus ursinus* Linnaeus) pups (Baker & Fowler 1992). However, this is difficult to confirm in other fur seal species, mainly because of the high level of pup dispersion at sea after weaning, as well as the delay until first reproduction exhibited by those species (Wickens & York 1997; Dabin *et al.* 2004). This led us to expect that environmental factors such as food availability may also influence pup post-weaning survival. In 1994, a long-term marking study was initiated to investigate the population ecology of subantarctic fur seals in Amsterdam Island (Georges & Guinet 2000), which necessitated 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). Moreover, recent developments in mark–recapture modelling now allow the integration of individual covariates (White & Burnham 1999; Hall *et al.* 2001) and immature temporary emigration (Fujiwara & Caswell 2002) into survival estimates.

The aims of the present study, therefore, were to determine (1) the resighting pattern of weaned pups in their native island; (2) the post-weaning survival rate; (3) the juvenile tag loss, emigration and survival rates; and (4) the factors influencing post-weaning and juvenile survival in subantarctic fur seals born at Amsterdam Island, taking into account tag loss and temporary emigration.

Materials and methods

STUDY SITE AND SPECIES

The study was carried out at 'La Mare aux Eléphants' breeding colony, on the north-east side of Amsterdam Island, southern Indian Ocean (37°55' S, 77°30' E), where one of the largest breeding colonies can be found (Guinet, Jouventin & Georges 1994). The breeding colony was delimited with visual reference markers, allowing us to sample the same portion of the rookery each year from 1995 to 2003.

In subantarctic fur seals, births occur from late November to early January, with a mean parturition date in mid-December (Georges & Guinet 2000). The nursing period lasts about 10 months (Georges, Sevot & Guinet 1999), after which newly weaned pups leave

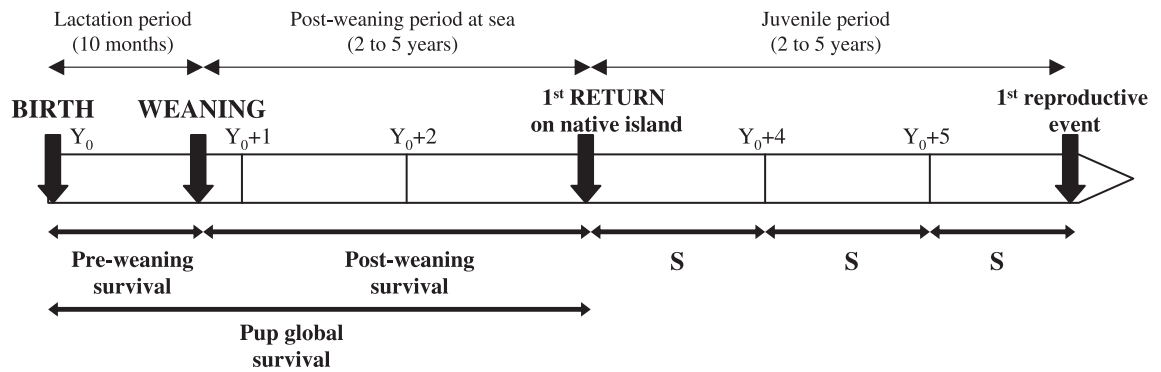


Fig. 1. Schematic representation of the main events occurring during the life of a subantarctic fur seal pup from birth to first reproduction. In this example, the post-weaning (spent exclusively at sea) and juvenile periods last 2 and 3 years, respectively. Post-weaning survival represents the proportion of weaned pups surviving until their first return at Amsterdam Island. Pup global survival (GbS) represents the proportion of pups surviving from birth to this first return. Juvenile survival (S) represents the yearly survival probability of young individuals between their first return and their first reproductive event.

their native island to acquire nutritional independence (Ofteidal *et al.* 1987; Bowen 1991). In this study, pup post-weaning and global survival, as well as yearly juvenile survival, represented the proportion of individuals surviving during the respective periods defined in Fig. 1.

INDIVIDUAL TAGGING, WEIGHING AND RESIGHTING

The breeding colony was surveyed every day during the parturition period, and each newborn was sexed, weighed (± 0.1 kg) and identified within 12 h after birth (Georges & Guinet 2000), except in 1998, when field studies began in January (Chambellant *et al.* 2003). At 1 month of age, each marked pup was tagged in the connective tissue on the trailing edge of both fore-flippers with an individually numbered plastic tag (Dalton Rototags, Dalton Supply, Nettlebed, UK). Both tags' male and female components bore a unique three-digit number and were colour-coded by year. All pups received the same type of tag, and the tagging procedure did not vary among years. Depending on the breeding season, from 100 to 200 newborn pups were marked each year, and weighed regularly from birth to weaning. This allowed us to obtain the weaning mass (M_w) and to calculate individual growth rate (GR_G) for as many animals as possible (see Chambellant *et al.* 2003).

Searches for tagged seals were conducted every 2 days on the colony from the 1995–2003 breeding seasons. Each searching session consisted of a 3-h continuous scan in the delimited rookery section and adjacent areas corresponding to non-breeding/juvenile haul-out sites. Tag number, colour and, whenever possible, the number of tags remaining were recorded for each resighted individual.

JUVENILE TAG LOSS, SURVIVAL AND EMIGRATION ANALYSES

Considering the first capture as the year of first return in the native island, estimate of juvenile tag-loss rate

(T) was assessed in individuals that had their number of remaining tags recorded each season from the 1999–2003 breeding seasons. To model and estimate T, we used the conditional multistate model (Arnason 1973; Schwarz, Schweigert & Arnason 1993) with two states: 1 = individuals with only one remaining tag, and 2 = individuals with two tags. Because we did not suspect any effect of number of tags on survival or tag loss, we assumed survival and state transition probabilities to be similar for individuals in states 1 and 2. However, we suspected that the capture probability could be affected by the number of tags (i.e. it may be easier to detect animals with two tags rather than with one single tag). We therefore started with a model $[S_t, p_{t^*tag}, \psi_t]$ which assumed both survival (denoted S) and state transition (ψ) probabilities dependent on time (t), and recapture (p) probability dependent on both number of tags (tag) and time. The presence of interaction between the effects is noted as '*', whereas an additive relationship was represented by a '+' and a '.' denoted a constant pattern of the parameter tested. This model permits the estimation of tag loss as the transition probability from state 2 to state 1, taking into account the survival and recapture probabilities. The transition probability from state 1 to 2 was fixed to 0, as individuals that had lost a tag could not recover it. We then tested whether our starting global model $[S_t, p_{t^*tag}, \psi_t]$ was compatible with our biological knowledge and provided adequate description of our data, using the goodness-of-fit (GOF) test for multistate models (Pradel, Wintrebert & Gimenez 2003) implemented in U-CARE software (Choquet *et al.* 2002). The model-selection procedure then followed 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 & Anderson 1998), considering that two models were significantly different when the ΔAIC_C was greater than 2 (Anderson & Burnham 1999).

To estimate juvenile survival and the factors affecting this survival probability on the whole population of

weaned animals resighted in their native island, we also relied on multistate modelling. Indeed, our field observations showed that some individuals absent on the colony during a given year were seen again during the next breeding season, leading us to suspect that juvenile temporary emigration (Fujiwara & Caswell 2002) occurs in the studied population. We therefore used a multistate model with two states: an observable state for individuals present in a given year at the colony, and an unobservable state (Kendall & Nichols 2002) in order to take into account temporary emigrants. First, we started with the model $[S_{t*sex*coh*state}, P_{t*sex*coh*state}, \Omega_{t*sex*coh*state}]$, which assumed survival (denoted S), recapture (p) and transition (Ω) probabilities dependent on time (t), sex (sex) and cohort (coh). This starting model, however, requires to be constrained to estimate parameter values (Kendall & Nichols 2002). Thus, state-transition probabilities (Ω_{OU} for emigration and Ω_{UO} for immigration, respectively) were constrained to be constant over time, survival probabilities to be the same for observable (O) and unobservable (U) animals (Kendall & Nichols 2002; see their Table 2 model 43), and capture probabilities for the unobservable state were fixed at 0. This led us to start with model $[S_{t*sex*coh}, P_{t*sex*coh*state}, \Omega_{sex*coh*state}]$. As no GOF test is available for multistate models containing an unobservable state, we tested the ability of the simpler nested model $[S_{t*sex*coh}, p_{t*sex*coh}]$ to describe the data using U-CARE software (Choquet *et al.* 2002). We built the global GOF test of this model by adding each component of the GOF tests of the Cormack–Jolly–Seber model (S_t, p_t) applied to each sex and cohort separately. Model selection was then performed following the parsimony principle, as described above. However, when models with similar AIC_C values were observed, we estimated parameter values and standard errors using a model-averaging procedure based on model AIC_C weight (see Burnham & Anderson 1998; Anderson & Burnham 1999). All estimates and AIC_C values were computed using program MARK (White & Burnham 1999).

Survival rate (\hat{S}) was finally estimated after correcting for tag loss, assuming that the probability of loss was equal for all tags (see Pistorius *et al.* 2000), and using Arnason & Mills' (1981) equation:

$$\hat{S} = \frac{\text{estimated survival}}{1 - \text{proba. of losing both tags}} = \frac{S}{1 - T^2} \quad \text{eqn 1}$$

In order to test the hypothesis that juvenile survival or temporary emigration were phenotype-specific (i.e. M_w and GR_G) or influenced by oceanographic features, we developed models in which survival or transition probability was a function of a covariate. The effect of the covariate was modelled as a linear-logistic function:

$$\text{logit}(S) = \log\left(\frac{S}{1-S}\right) = \lambda + \theta \text{covariate},$$

where λ and θ are the intercept and slope parameters, respectively.

Post-weaning survival rate (PWS) was defined for each cohort as the proportion of weaned pups that were resighted during their first return at Amsterdam Island. This cohort-adjusted return rate was calculated using the following modified equation of Lander (1975), assuming that all individuals of a given cohort have returned to their native island between α and β years of age:

$$\text{PWS} = \sum_{i=\alpha}^{\beta} \frac{N_i \cdot S^{\alpha-i}}{N_1} \quad \text{eqn 2}$$

where N_i is the number of new individuals seen for the first time at age i on Amsterdam Island, N_1 is the number of weaned pups of a given cohort, and S is the constant yearly juvenile survival rate estimated through the model averaging method.

OCEANOGRAPHIC CONDITIONS

In the Southern Ocean, the sea surface temperature anomalies (SSTa) represent an indicator of trophic conditions: the lower the SSTa, the higher the intensity of biological activity in the given area (Mann & Lazier 1991). Accordingly, interannual changes in the intensity of the SSTa were used as a proxy to assess interannual variation in the marine productivity. The SSTa index was calculated for each year as the mean SSTa recorded in the Amsterdam Island area (from 30 to 50° S and 60–95° E) from September to February (i.e. 6 first months of the weaning period). To filter them out, anomalies relative to the SST mean (i.e. the mean over the 1981–94 period) were extracted monthly with a 1° scale. Measurements were obtained from the Integrated Global Ocean Service System (IGOSS) database, available on the National Ocean and Atmosphere Administration (NOAA) internet website: <http://ingrid.ldeo.columbia.edu> (Reynolds & Smith 1994).

STATISTICAL ANALYSES

Factors influencing the probability for a weaned pup to be resighted were examined by fitting generalized linear models with a binomial error distribution for the response variable and a logistic link function (GENMOD procedure of SAS). The response variable for each weaned pup was the event of being resighted on the rookery after the weaning process, given that animals never resighted after the first departure from the native island were considered as dead. Explanatory variables included pup cohort, sex, growth rate, weaning mass and interactions. Model selection was performed using AIC_C estimated directly from numerical output of the GENMOD procedure, and the best logistic regression model was selected for each cohort following the parsimony principle, as described above.

With the exception of survival, all statistical analyses followed the methods of Sokal & Rohlf (1981), and were performed with the SYSTAT 9.0 statistical software (SYSTAT, 9.0 statistics, SPSS Inc., USA). The Kolmogorov–Smirnov test was used to determine whether the data

were normally distributed. We used a Multinomial Logit regression to test the effects of pup sex, growth rate and weaning mass on the age of the pup at first return. Moreover, a Spearman's rank correlation analysis was used to test the relationship between the SSTa index and survival from 1994 to 1998 ($n = 5$). Unless stated otherwise, values are reported as means \pm SE and statistical significance was considered to be $P < 0.05$.

Results

RESIGHTING OF TAGGED ANIMALS

Among the 1000 pups tagged at birth, a total of 960 resightings from 416 tagged animals were made during the study period. The range of age at first return in the study colony was wide, but over 96% occurred from 3 to 6 years of age (Fig. 2a). Further analyses therefore included only cohorts whose return was fully completed by the 2003 breeding season (i.e. the 1994–98 cohorts). The chronology of the first resighting was tested on animals that had all their individual covariates recorded: the age at first return did not differ between the sexes (Wald statistic = 1.75, d.f. = 3, $n = 255$, $P = 0.62$), and was not influenced by either pup growth rate (Wald statistic = 0.72, d.f. = 3, $n = 255$, $P = 0.87$) or weaning mass (Wald statistic = 0.68, d.f. = 3, $n = 255$, $P = 0.44$).

Age-distribution frequency of first resighting did not differ significantly between year of weaning (two-sample KS test, $n = 352$, $P > 0.1$ in all years). Consequently, the timing of individual first return in the study colony was similar from one year to another, but reached a different plateau depending on the cohort (Fig. 2b). Indeed, 1994 and 1996 cohorts return rates seemed to climax at about 60%, whereas 1995 and 1997 cohorts represented 74 and 45% of the total initial number of weaned pups, respectively.

ESTIMATION OF JUVENILE TAG LOSS RATE

Of the 416 resighted animals, 131 individuals had their number of remaining tags recorded during each season they were observed. They were thus included in a multi-state fully time-dependent model in order to assess the tag loss rate of the juveniles when returning to the study colony. The overall GOF test showed that the global model $[S_t, p_{t+tag}, \psi]$ satisfactorily fitted the data ($\chi^2 = 20.169$, d.f. = 16, $P = 0.21$).

Starting with the general model, we detected a significant effect of time and number of tags on recapture probability (Table 1, model 5 vs. 6 and 7). However, a model with an additive effect (model 3) was preferred over model 5, indicating that recapture probability of one- and two-tagged animals followed the same

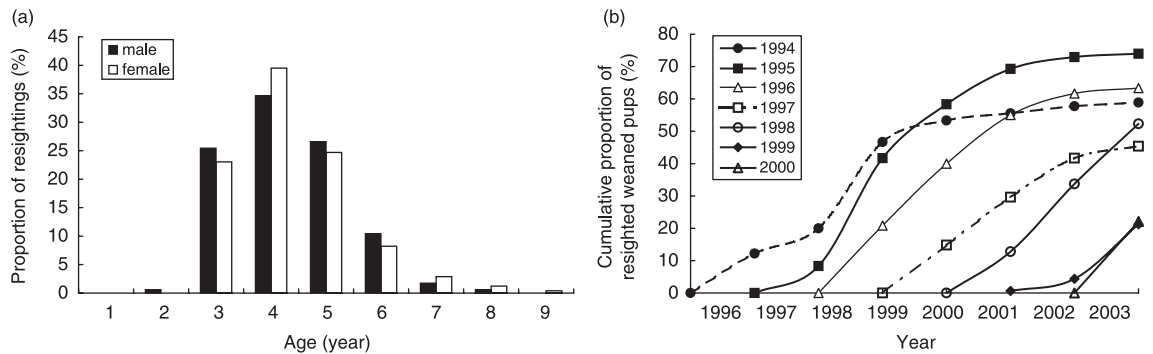


Fig. 2. (a) Age distribution frequency of first-resighted subantarctic fur seal pups ($n = 416$) on their native island during the 1997–2003 breeding seasons. Male and female pups are represented by black and white histograms, respectively. (b) Cumulative proportion (%) of weaned subantarctic fur seal pups resighted as juveniles in their native island during the 1997–2003 breeding seasons. Diverse symbols and lines represent the different cohorts weaned during the 1994–2000 breeding seasons.

Table 1. Description of constraints, AIC_c , $dAIC_c$, Akaike weights (AIC_w) and number of estimated parameters (No par.) for various models of post-weaning survival of 131 known-tag number juvenile subantarctic fur seals born in Amsterdam Island between 1994 and 1996 and resighted during the 1999–2003 breeding seasons. Models are ranked according to their Akaike weights

Model ¹	Description of constraint	AIC_c	$dAIC_c$	No par.	AIC_w
1 S(t) p(t + tag) $\psi(\cdot)$	Absence of time effect on tag loss rate	794.610	0	9	0.28426
2 S(.) p(t + tag) $\psi(\cdot)$	Absence of time effect on tag loss rate	794.687	0.08	7	0.27353
3 S(t) p(t + tag) $\psi(t)$	Additive effect of time and tag number on recapture	795.897	1.29	12	0.14935
4 S(.) p(t + tag) $\psi(t)$	Absence of time effect on survival	796.071	1.46	10	0.13687
5 S(t) p(t*tag) $\psi(t)$	Starting model	796.771	2.16	16	0.09648
6 S(t) p(t) $\psi(t)$	Absence of tag number effect on recapture	798.831	4.22	11	0.03444
7 S(t) p(tag) $\psi(t)$	Absence of time effect on recapture	799.466	4.86	10	0.02508

¹See Methods section for model nomenclature.

Table 2. Description of constraints, AIC_c, dAIC_c, Akaike weights (AIC_w) and number of estimated parameters (No par.) for various models of post-weaning survival of 365 juvenile subantarctic fur seals born in Amsterdam Island between 1994 and 1998 and resighted during the 1997–2003 breeding seasons. Models are ranked according to their Akaike weights

Model ¹	Description of constraint	AIC _c	dAIC _c	No par.	AIC _w
1 S(.) p(.) Ω _{OU} (sex + coh) Ω _{UO} (.)	Absence of sex effect on immigration	1153.798	0	9	0.61279
2 S(.) p(.) Ω _{OU} (sex + coh) Ω _{UO} (sex)	Absence of cohort effect on immigration	1155.749	1.95	10	0.23104
3 S(.) p(.) Ω(sex + coh)	Absence of cohort effect on survival	1157.438	3.64	14	0.09926
4 S(coh) p(.) Ω(sex + coh)	Absence of sex effect on survival	1158.614	4.82	18	0.05514
5 S(sex × coh) p(.) Ω(sex + coh)	Absence of time effect on survival	1165.486	11.69	23	0.00178
6 S(t × sex × coh) p(.) Ω(sex + coh)	Additive effect of sex and cohort on em/immigration	1214.775	60.98	73	0
7 S(t × sex × coh) p(.) Ω(sex × coh)	Absence of sex effect on recapture	1224.311	70.51	81	0
8 S(t × sex × coh) p(sex) Ω(sex × coh)	Absence of cohort effect on recapture	1226.102	72.30	82	0
9 S(t × sex × coh) p(.) Ω(coh)	Em/immigration function of sex	1230.024	76.23	71	0
10 S(t × sex × coh) p(.) Ω(sex)	Em/immigration function of cohort	1231.394	77.60	63	0
11 S(t × sex × coh) p(sex × coh) Ω(sex × coh)	Absence of time effect on recapture	1252.058	98.26	90	0
12 S(t × sex × coh) p(t × sex × coh) Ω(sex × coh)	Starting model	1350.561	196.76	140	0

¹See Methods section for model nomenclature.

pattern over time. However, animals with two tags had a 7–10% higher probability of being resighted. Although there was no significant difference in model fit between models 1–4 ($\Delta AIC_c < 2$), the AIC_c weight of models 1 and 2 was twice as important as of models 3 and 4, suggesting that tag loss rate was constant throughout the years. Model averaging of models 1–4 led to the estimate of annual juvenile tag loss rate: $T = 0.217$ (SE = 0.027, i.e. a juvenile had 21.7% chance of losing one tag from one year to the next).

ESTIMATION OF JUVENILE SURVIVAL RATE

Of the 416 resighted animals, 365 individuals born during the (1994–98) breeding seasons were studied between 1997 and 2003, as those cohorts had a complete return pattern at that period (Fig. 2b). The overall GOF test revealed no significant bias ($\chi^2 = 49.85$, d.f. = 59, $P = 0.80$), indicating that the model $[S_{t*sex*coh}, P_{t*sex*coh}]$ fitted the data well. We can therefore reasonably suppose that this was so for our starting model (Table 2, model 12), as it was more complex than the tested one, and thus probably captured more heterogeneity in the capture–recapture data set.

Starting with the general model (Table 2, model 12), we showed that there was no significant effect of time on recapture probability (models 11 vs. 12), and that a model with recapture probability constant over cohort and sex was preferred (models 7 vs. 8 and 11). Removing the effects of sex (model 9) or cohort (model 10) on state transition probabilities did not improve the fit of model 7. Thus, temporary em/immigration differed between sexes and cohorts. Moreover, a model with an additive effect of cohort and sex on state transition probabilities (model 6) was preferred over model 7, suggesting that temporary em/immigration of males and females followed the same pattern. Interestingly, a model with survival probability equal over time (models 5 vs. 6) and sex (models 4 vs. 5) was preferred. Although no significant difference in model fit ($\Delta AIC_c < 2$) was

Table 3. Estimation of temporary emigration rate in subantarctic fur seal juveniles born in Amsterdam Island during the 1994–1998 breeding seasons and resighted during the 1999–2003 period

Cohort	Sex	Emigration rate	Standard error
1994	F	0.194	0.056
	M	0.509	0.083
1995	F	0.145	0.034
	M	0.423	0.055
1996	F	0.048	0.016
	M	0.167	0.042
1997	F	0.370	0.086
	M	0.716	0.070
1998	F	0.093	0.060
	M	0.301	0.158
Mean	F	0.170	0.012
	M	0.423	0.035

observed between model 3 and model 4, the higher AIC_c weights of models 1–3 suggested that survival rate was constant over cohorts. Finally, the probability of returning from the unobservable state was found to be equal over cohort (model 2 vs. model 3) and sex (model 1 vs. model 2), and the model-averaging procedure estimated this value at 0.290 (SE = 0.065). Model averaging of models 1–4 also allowed the assessment of state transition values for each cohort and sex, confirming that temporary emigration was higher for males than for females (Table 3). Using the same method, we estimated the constant recapture (0.904, SE = 0.024) and survival ($S = 0.921$, SE = 0.021) rates. Correcting for tag loss using equation 1, the estimated yearly survival probability of juveniles was: $\hat{S} = 0.964$ (SE = 0.022).

INFLUENCE OF INDIVIDUAL AND OCEANOGRAPHIC COVARIATES ON JUVENILE VITAL RATES

Of the 365 studied animals, 226 individuals born during the (1994–98) breeding seasons were investigated, as all

Table 4. Description of constraints, AIC_c, dAIC_c, Akaike weights (AIC_w) and number of estimated parameters (No par.) for various models of post-weaning survival of 226 juvenile subantarctic fur seals born in Amsterdam Island between 1994 and 1998 and resighted during the 1997–2003 breeding seasons. Models are ranked according to their Akaike weights

Model ¹	Description of constraint	AIC _c	dAIC _c	No par.	AIC _w
1 S(.) p(.) Ω _{OU} (sex + coh) Ω _{UO} (.)	Immigration equal over sex and cohort	631.936	0	8	0.25692
2 S(.) p(.) Ω _{OU} (GR _G × (sex + coh)) Ω _{UO} (.)	Growth rate effect on emigration	632.885	0.95	9	0.15983
3 S(M _w) p(.) Ω _{OU} (sex + coh) Ω _{UO} (.)	Weaning mass effect on survival	633.164	1.23	9	0.13908
4 S(.) p(.) Ω _{OU} (M _w × (sex + coh)) Ω _{UO} (.)	Weaning mass effect on emigration	633.602	1.67	9	0.11171
5 S(GR _G) p(.) Ω _{OU} (sex + coh) Ω _{UO} (.)	Growth rate effect on survival	633.702	1.77	9	0.10626
6 S(I ₀) p(.) Ω _{OU} (sex + coh) Ω _{UO} (.)	SSTa index effect on survival	633.895	1.96	9	0.09651
7 S(.) p(.) Ω _{OU} (I ₀ × (sex + coh)) Ω _{UO} (.)	SSTa index effect on emigration	634.019	2.08	9	0.09069
8 S(I ₀ I ₁) p(.) Ω _{OU} (sex + coh) Ω _{UO} (.)	2-years SSTa index effect on survival	635.706	3.77	10	0.03901
9 S(t × sex × coh) p(t × sex × coh) Ω(sex × coh)	Starting model	780.155	148.22	96	0

¹See Methods and Result sections for model nomenclature.

their individual covariates were recorded. The overall GOF test revealed no bias ($\chi^2 = 14.74$, d.f. = 36, $P = 0.95$), indicating that the model [S_{t*sex*coh}, P_{t*sex*coh}] fitted this data set well. As this model is nested within our more parameterized starting model (Table 4, model 9), we can thus reasonably suppose the latter to fit the data satisfactorily.

The best model, after modelling for the effects of time, sex and cohort on S, p and Ω (not shown in Table 4), was the same found with the complete data set (Table 4, model 1). Models testing the effects on juvenile survival of either weaning mass (model 3), pup growth rate (model 5) or SSTa index during the year (I₀, model 6) or the two first years (I₀I₁, model 8) following the weaning process were not preferred to model 1. Moreover, the confidence interval of the slope θ of each tested model included the 0-value, indicating no major influence of any of these parameters on juvenile survival. Similarly, temporary emigration was found to be not affected by individual characteristics or SSTa at weaning (Table 4, model 1 vs. models 2, 4 and 7).

ESTIMATION OF POST-WEANING SURVIVAL RATE

Post-weaning survival rate was calculated using equation 2, and assuming all individuals of a given cohort have completed the return in their native island from 3 to 6 years of age (Fig. 2a):

$$PWS = (N_3 + N_4 \cdot S^{-1} + N_5 \cdot S^{-2} + N_6 \cdot S^{-3}) / N_1$$

Values of PWS are presented together with preweaning and resulting global survival rates of the pups (Table 5). Mean PWS appeared to represent 66% (range = 49–84%) of the weaned pups, resulting in a proportion of pups surviving from birth to first return in their native island of 48% (range = 27–75%). When analysing the data by cohort (Table 6), the probability for a weaned pup of being resighted in the colony as a juvenile was related positively to its growth rate during the rearing period. Except in 1994 where growth could not be

Table 5. Preweaning and post-weaning survival rates in subantarctic fur seal pups born in Amsterdam Island during the 1994–1998 breeding seasons and resighted during the 1999–2003 period. Global survival estimates represent the proportion of pups surviving from birth to their first return in their native island

Cohort	Sex	Preweaning survival ¹ (%)	Postweaning survival (%)	Global survival (%)
1994 ²	F	–	71.5	–
	M	–	59.7	–
1995	F	88.5	84.3	74.6
	M	92.0	82.3	75.7
1996	F	78.7	79.4	62.4
	M	81.9	55.7	45.6
1997	F	54.4	50.2	27.3
	M	57.3	49.4	28.3
1998	F	55.7	75.3	42.0
	M	47.5	58.0	27.5
Mean	F	69.3	72.1	50.0
	M	69.7	61.0	42.5

¹Values revised from Chambellant *et al.* (2003); ²fieldwork in 1994 did not allow to assess pup preweaning survival.

measured, pup weaning mass was found to improve the fit of the model but this effect was not significant (Table 6). Moreover, the probability for a weaned individual of being resighted depended also on its sex, with significantly lower values for males. Interestingly, sex did not significantly influence the probability to be resighted for the 1995 and 1997 cohorts (see Table 6, models 1). These results allowed us to obtain consecutively a logistic regression for each cohort, representing the survival probability of a weaned pup as a function of its sex and growth rate during the lactation period (Fig. 3). Interestingly, for a given low growth rate value, females (Fig. 3b) exhibited higher probability of survival than males (Fig. 3a), but this trend was not effective for higher growth rate values.

Mean SSTa index was lowest in 1995 and highest in 1997 (–0.156 vs. 0.181, respectively). Mean pup post-weaning (Spearman’s rank correlation, $r_s = -1.0$, $n = 5$, $P < 0.01$) and global ($r_s = -1.0$, $n = 4$, $P < 0.01$) survival

Table 6. Logistic analyses for the effects of sex, growth rate (GR_G), weaning mass (Mw) and interactions on the probability for a subantarctic fur seal pup weaned between 1994 and 1998 to be resighted in Amsterdam Island during the 1999–2003 breeding seasons. Deviance, AIC_c , $dAIC_c$, sample size (n) and number of estimated parameters (No par.) are presented for each plausible model, and ranked according to its AIC_c

Model	n	No par.	Deviance	AIC_c	$dAIC_c$
1994 ¹					
1 Sex, Mw	60	3	22.016	28.44	0.00
2 Sex, Mw \times sex	60	4	21.790	30.52	2.07
3 Mw	60	1	28.536	30.60	2.16
4 Sex	60	2	27.228	31.44	2.99
1995					
1 GR_G	98	1	108.094	110.14	0.00
2 Sex, GR_G	98	3	107.166	113.42	3.29
3 Sex, Mw, $GR_G \times$ sex	98	5	102.806	113.46	3.32
4 Mw	98	1	111.918	113.96	3.82
5 Sex, Mw, GR_G	98	4	105.884	114.31	4.18
6 Sex, Mw \times sex, $GR_G \times$ sex	98	6	102.430	115.35	5.22
7 Sex, Mw	98	3	110.608	116.86	6.73
8 Sex	98	2	114.516	118.64	8.51
1996					
1 Sex, GR_G	121	3	142.062	148.27	0.00
2 Sex, Mw	121	3	144.448	150.65	2.39
3 Sex, Mw, GR_G	121	4	142.732	151.08	2.81
4 Sex, Mw, $GR_G \times$ sex	121	5	141.334	151.86	3.59
5 Sex, Mw \times sex, $GR_G \times$ sex	121	6	140.118	152.85	4.59
6 Mw	121	1	152.162	154.20	5.93
7 GR_G	121	1	152.616	154.65	6.38
8 Sex	121	2	153.316	157.42	9.15
1997					
1 GR_G	99	1	133.030	135.07	0.00
2 Mw	99	1	135.912	137.95	2.88
3 Sex, Mw	99	3	133.002	139.25	4.18
4 Sex, GR_G	99	3	133.558	139.81	4.74
5 Sex	99	2	136.412	140.54	5.47
6 Sex, Mw, GR_G	99	4	132.896	141.32	6.25
7 Sex, Mw, $GR_G \times$ sex	99	5	132.190	142.84	7.77
8 Sex, Mw \times sex, $GR_G \times$ sex	99	6	132.190	145.10	10.03
1998					
1 Sex, GR_G	83	3	99.010	105.31	0.00
2 Sex, Mw, GR_G	83	4	99.008	107.52	2.21
3 Sex, Mw	83	3	101.394	107.70	2.38
4 Sex, Mw \times sex, $GR_G \times$ sex	83	6	94.728	107.83	2.52
5 Sex, Mw, $GR_G \times$ sex	83	5	97.068	107.85	2.53
6 GR_G	83	1	106.138	108.19	2.88
7 Sex	83	2	106.582	110.73	5.42
8 Mw	83	1	110.106	112.16	6.84

¹Field work in 1994 did not allow to assess pup growth rate.

rate changes were significantly negatively correlated with changes of mean SSTa index throughout the years (Fig. 4).

Discussion

RESIGHTING OF TAGGED ANIMALS

Our results indicate that the pattern of pups' first return in Amsterdam Island is similar over sex, preweaning growth rate and weaning mass, as found previously in Northern fur seals (Baker & Fowler 1992). Nearly all individuals returned to their native island between 3

and 6 years of age (Fig. 2a), which implies a minimum at-sea post-weaning period of 2 years. This extended post-weaning period is consistent with the later entry to reproduction observed in this population and may be related to the high population density (Dabin *et al.* 2004), as demonstrated in other species (Weimerskirch & Jouventin 1987; Gaillard *et al.* 1998a). Notably, although males fur seals start reproduction later than females (Wickens & York 1997), they did not exhibit a later return in this study, suggesting a more difficult access to reproduction than that of females, due probably to competition with older established males for access to territories. Alternatively, young males may

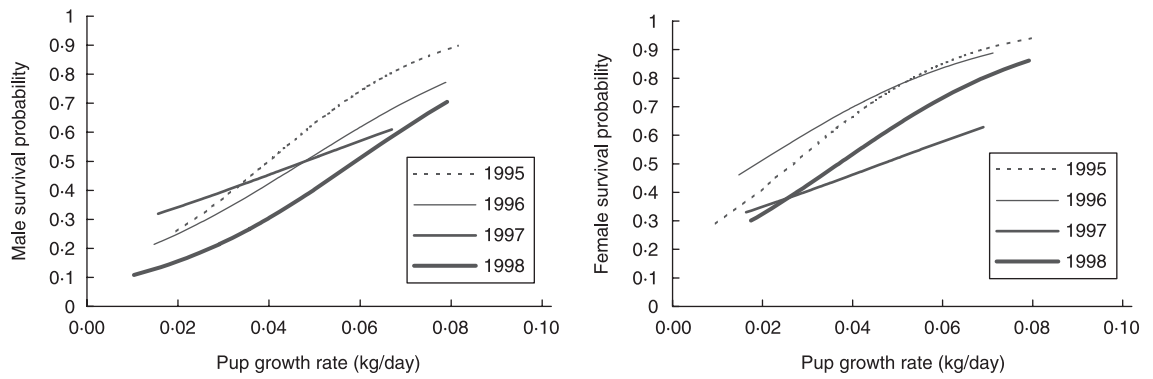


Fig. 3. The relationship between growth rate during the lactation period and post-weaning survival probability in (a) male and (b) female weaned subantarctic fur seal pups during the 1995–98 breeding seasons. Successive cohorts are represented by increasing line thickness.

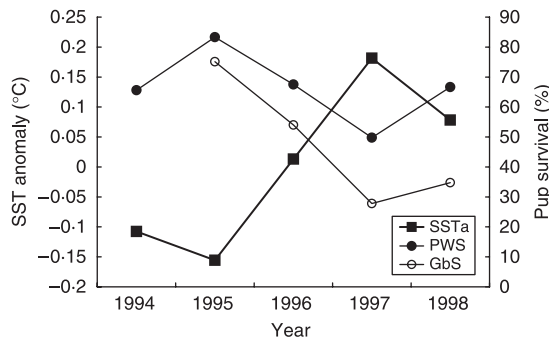


Fig. 4. Changes in the mean sea surface temperature anomaly (SSTa) in the Amsterdam Island area and in the mean post-weaning (PWS) and global (GbS) survival of subantarctic fur seal pups.

exhibit a similar return pattern than that of females because they prospect the colony to identify and select future breeding areas (Boulinier *et al.* 1996), and consequently enhance their future breeding success (Boulinier & Danchin 1997; Schjoerring, Gregersen & Bregnballe 1999). Interestingly, the patterns of the first return of males and females to their birth site were unrelated to oceanographic conditions during the weaning period, and were also similar over years (Fig. 2b).

JUVENILE TAG LOSS AND SURVIVAL RATES

The best-fitting model indicated that recapture probability was constant, with single-tagged juveniles exhibiting a lower detection probability. This result indicated no significant difference between fieldworker observation skills, and thus a homogeneous effort accomplished from one year to another. Such a consistency in capture probabilities therefore suggested an absence of bias in our survival estimates (see Prévot-Julliard, Lebreton & Pradel 1998). We strongly suspect the volcanic boulders and large blocks of rocks constituting the coastline beaches in Amsterdam Island (Guinet *et al.* 1994) to be the cause of the relative high juvenile tag loss rate (i.e. 21.7%).

The annual survival rate of juveniles did not vary with cohort, which suggests no long-term influence of pup early condition on their survival after returning to their native island. Interestingly, unlike post-weaning survival, no sexual difference in juvenile survival was detected; yet sex differences in mortality are observed commonly in polygynous and highly sexually dimorphic species (Clutton-Brock, Guinness & Albon 1982; Promislow 1992). The lack of breeding activity (Dabin *et al.* 2004) and of sexual dimorphism (Beauplet, personal observation) observed in 3–6-year-old animals may explain this result, which are similar to those found in monomorphic species (Sarno & Franklin 1999). It would thus be of major interest to explore sexual heterogeneity in survival of reproductively mature animals when sexual dimorphism is evident. Overall, our annual survival probability estimate ($\hat{S} = 0.964 \pm 0.022$) confirms a common pattern in mammals: yearly survival after returning to the native island is higher than the first-year post-weaning survival (Clutton-Brock *et al.* 1982; Ballachey *et al.* 2003). In this population the estimated value was found to be somewhat higher than the range exhibited in other mammal species (Gaillard *et al.* 2000), and constant over time, indicating a minor impact of environmental conditions once the juvenile state is reached. Consistent with the within-cohort selection process detected in red deer (Rose, Clutton-Brock & Guinness 1998), the lack of relationship between juvenile survival and pup preweaning performances suggests that individuals exhibiting lower preweaning growth rate tend to die earlier during the months following the weaning process. In such a context, the first return to the native island appeared to represent the end of a within-cohort selection process that started at weaning, and consequently illustrated some significant changes in the animals' status.

POST-WEANING SURVIVAL RATES

Although the maximum values found in this study were somewhat higher, the mean post-weaning survival (i.e. 66%) was similar to that observed in other pinniped species (Trites 1989; McMahon, Burton & Bester 1999).

Moreover, except in 1998, when the tropical storm Anacelle struck the island leading to a high proportion of drowned pups, the preweaning survival rate was always higher than the post-weaning ones, as observed in Northern fur seals (Trites 1989). We detected a significant positive relationship between pup preweaning growth rate and individual post-weaning survival and interestingly, this effect was greater for males than for females (see Fig. 3). This result is consistent with that found during the rearing period (Chambellant *et al.* 2003), and confirms that the growth and survival of males are affected more strongly by environmental conditions than that of females in polygynous and sexually dimorphic mammals (Clutton-Brock, Albon & Guinness 1985; Rose *et al.* 1998; Kruuk *et al.* 1999; Festa-Bianchet *et al.* 2000; Coulson *et al.* 2003). Many mammal studies showed that weaning mass affects post-weaning survival (Baker & Fowler 1992; Festa-Bianchet *et al.* 1997; McMahon *et al.* 2000). However, in this study pup growth rate was found to take precedence over pup weaning mass in its positive effect on post-weaning survival (Table 6). We therefore suggest consideration of the pup preweaning growth rate as a better indicator of postnatal investment in long-lactating species, because the effective weaning time is difficult to assess precisely (Georges *et al.* 1999).

As stated in previous pinniped studies, heavier weaners have greater diving capabilities (Kooyman 1989; Hindell *et al.* 1999), and they suffer a reduced heat loss owing to their higher blubber content (Bryden 1964) and larger size (Peters 1983). They are therefore expected to have an advantage over lighter pups by being able to spend more time searching for food during the first months of nutritional independence. Nevertheless, when sexual differences occur within a mammal species, juvenile males commonly exhibit a lower survival (Clutton-Brock *et al.* 1982; Hall *et al.* 2001), although males are usually heavier than females (Doidge, Croxall & Ricketts 1984). Such sex difference in post-weaning survival was also found in our study, and we suggest two possible non-exclusive explanations for this apparent inconsistency. First, the post-weaning dispersion pattern of male pups may be wider than that of females (Boyd *et al.* 1998), which would consequently entail greater risks for their survival (Greenberg 1980) and/or lower site fidelity to their natal beaches. This hypothesis is supported by the opportunistic observations reported in other southern islands, where the 11 tagged individuals observed either in Gough ($n = 1$), Macquarie ($n = 7$), Kerguelen ($n = 2$) or Crozet ($n = 1$) islands were all males. However, although we observed some returns of those transient individuals (i.e. 6 of 11), lower site fidelity in males would need further investigations to be confirmed. Secondly, previous studies of sexually dimorphic species have suggested that the faster growing sex (i.e. usually the male) may suffer additional mortality because of nutritional stress (Clutton-Brock, Albon & Guinness 1994; Stewart 1997). We suggest that this phenomenon may be due to the lower body lipid

proportion exhibited by male pups coupled with a lower propensity to rely on protein reserves than do females (Beauplet, Guinet & Arnould 2003). Although this protein-conserving pathway leads to a higher muscular mass (i.e. better diving capabilities), it may also entail a lower global body reserves in male pups, and consequently less time available to search for food after nutritional independence. This hypothesis is supported by the lack of sexual differences in post-weaning survival during years of extreme environmental conditions (see Tables 5 and 6 and Fig. 4). Indeed, during years of high SSTa (i.e. 1997) both sexes, including females, may not dispose of enough reserves to compensate for the low food availability during the first months after weaning. In such a case, the probability of resighting a weaned pup was not significantly related to its growth rate. Conversely, during years of low SSTa (i.e. 1995) both sexes, including males, seem to dispose of sufficient reserves to become energetically independent in an environment of higher food availability.

Previous studies have shown that environmental factors before and/or immediately after weaning can obscure the influence of maternal investment in entire cohorts (Rose *et al.* 1998; Coulson *et al.* 2003), which may have long-term reproductive-fitness consequences (Gaillard *et al.* 1998b). Consistently, our results showed that environmental conditions during the 6 first months of pup nutritional independence represent a decisive factor that significantly affects pup post-weaning survival, especially during years of extreme SSTa values (Table 5 and Fig. 4). Moreover, a negative relationship between SSTa and pup survival was demonstrated over a 5-year period, and interestingly during years of intermediate SSTa [i.e. $(-0.1; +0.1)$ °C], post-weaning survival rates showed similar values and constant sexual bias. Such a bias may have a direct impact on the population dynamics of this species in the case of a long-term and large-scale climatic change by modifying the juvenile's sex-ratio bias toward females to a 1 : 1 sex-ratio. This change would reduce the proportion of reproductive females and lead consequently to a reduction in pup production, which may ultimately entail destabilizing effects on population dynamics (Clutton-Brock 1988; Clutton-Brock *et al.* 2002).

Variability in survival is known to shape the evolution of basic life-history traits (Stearns 1992). This is especially true in long-lived species in which population growth is much more sensitive to survival than to fecundity (Lebreton & Clobert 1991). To our knowledge, this study is the first empirical evidence in a fur seal species indicating that post-weaning survival depends on pup growth rate, which represents a proxy of maternal investment. The importance of early condition in future survival and fitness has been demonstrated previously in two phocid seal studies (McMahon *et al.* 2000; Hall *et al.* 2001) but not yet on otariids, which alternate long foraging trips at sea with short periods ashore to feed their pup (Beauplet *et al.* 2004). In addition, we were able to demonstrate that the

influence of early development on survival was greatest during the months following weaning and negligible after the first return on the native island. This finding is also in line with those found in some passerine birds (Naef-Daenzer, Widmer & Nuber 2001) and a few long-lived seabirds (Olsson 1997; Sagar & Horning 1998; Keedwell 2003) studies. Higher pup growth rate during lactation leads to greater energetic body reserves stored before weaning and would thus enhance the future reproductive success of the weaner by increasing its post-weaning survival probability. Variation in growth rate and weaning mass and the associated differences in post-weaning survival thus represent an objective measure of reproductive success, and ultimately maternal performance under a given environmental condition. A comprehensive longitudinal study of known-aged tagged females' performances should therefore be conducted to help interpret individual differences in maternal lifetime reproductive success.

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References

Anderson, D.R. & Burnham, K.P. (1999) General strategies for the analysis of ringing data. *Bird Study*, **46**, 261–270.

Arnason, A.N. (1973) The estimation of population size, migration rates and survival in a stratified population. *Researches on Population Ecology*, **15**, 1–8.

Arnason, A.N. & Mills, K.H. (1981) Bias and loss of precision due to tag loss in Jolly–Seber estimates for mark–recapture experiments. *Canadian Journal of Fisheries and Aquatic Sciences*, **38**, 1077–1095.

Baker, J.D. & Fowler, C.W. (1992) Pup weight and survival of Northern fur seals *Callorhinus ursinus*. *Journal of Zoology, London*, **227**, 231–238.

Ballachey, B.E., Bodkin, J.L., Howlin, S., Doroff, A.M. & Rebar, A.H. (2003) Correlates to survival of juvenile sea otters in Prince William Sound, Alaska, 1992–93. *Canadian Journal of Zoology*, **81**, 1494–1510.

Beauplet, G., Dubroca, L., Guinet, C., Cherel, Y., Dabin, W., Gagne, C. & Hindell, M.A. (2004) Foraging ecology of subantarctic fur seals (*Arctocephalus tropicalis*) breeding on Amsterdam Island: seasonal changes in relation to maternal characteristics and pup growth. *Marine Ecology Progress Series*, **273**, 211–225.

Beauplet, G., Guinet, C. & Arnould, J.P.Y. (2003) Body composition changes, metabolic fuel use and energy expenditure during extended fasting in subantarctic fur seal (*Arctocephalus tropicalis*) pups at Amsterdam Island. *Physiological and Biochemical Zoology*, **76**, 262–270.

Blix, A.S., Grav, H.J. & Ronald, K. (1979) Some aspects of temperature regulation in newborn harp seal pups. *American Journal of Physiology*, **236**, 188–197.

Boltnev, A.I., York, A.E. & Antonelis, G.A. (1998) Northern fur seal young: interrelationships among birth size, growth and survival. *Canadian Journal of Zoology*, **76**, 843–854.

Boulinier, T. & Danchin, E. (1997) The use of conspecifics reproductive success for breeding patch selection in terrestrial migratory species. *Evolutionary Ecology*, **11**, 505–517.

Boulinier, T., Danchin, E., Monnat, J.-Y., Doutrelant, C. & Cadiou, B. (1996) Timing of prospecting and the value of information in a colonial breeding bird. *Journal of Avian Biology*, **27**, 252–256.

Bowen, W.D. (1991) Behavioural ecology of pinniped neonates. *Behaviour of Pinnipeds* (ed. D. Renouf), pp. 66–127. Chapman & Hall, Cambridge.

Boyd, I.L., McCafferty, D.J., Reid, K., Taylor, R. & Walker, T.R. (1998) Dispersal of male and female Antarctic fur seals (*Arctocephalus gazella*). *Canadian Journal of Fisheries and Aquatic Sciences*, **55**, 845–852.

Bradshaw, C.J.A., Barker, R.J., Harcourt, R.G. & Davis, L.S. (2003) Estimating survival and capture probability of fur seal pup using multistate mark–recapture models. *Journal of Mammalogy*, **84**, 65–80.

Bryden, M.M. (1964) Insulating capacity of the subcutaneous fat of the southern elephant seal. *Nature*, **203**, 1299–1300.

Bryden, M.M. (1968) Growth and function of the subcutaneous fat of the elephant seal. *Nature*, **220**, 597–599.

Burnham, K.P. & Anderson, D.R. (1998) *Model Selection and Inference: a Practical–Theoretic Approach*. Springer-Verlag, New York.

Chambellant, M., Beauplet, G., Guinet, C. & Georges, J.-Y. (2003) Long-term evaluation of pup growth and pre-weaning survival rates in subantarctic fur seals (*Arctocephalus tropicalis*) on Amsterdam Island. *Canadian Journal of Zoology*, **81**, 1222–1232.

Choquet, R., Reboulet, A.M., Pradel, R. & Lebreton, J.-D. (2002) *U-Care (Utilities–Capture–Recapture) User's Guide*. Available at: <http://www.cefe.cnrs-mop.fr/wwwbiom/default.htm>.

Clutton-Brock, T.H. (1988) *Reproductive Success: Studies of Individual Variation in Contrasting Breeding Systems*. University of Chicago Press, Chicago.

Clutton-Brock, T.H., Albon, S.D. & Guinness, F.E. (1994) Maternal dominance, breeding success and birth sex ratios in red deer. *Nature*, **308**, 358–360.

Clutton-Brock, T.H., Albon, S.D. & Guinness, F.E. (1985) Parental investment and sex differences in juvenile mortality in birds and mammals. *Nature*, **313**, 131–133.

Clutton-Brock, T.H., Coulson, T.N., Milner-Gulland, E.J., Thomson, D. & Armstrong, H.M. (2002) Sex differences in emigration and mortality affect optimal management of deer populations. *Nature*, **415**, 633–637.

Clutton-Brock, T.H., Guinness, F.E. & Albon, S.D. (1982) *Red Deer: Behavior and Ecology of Two Sexes*. University of Chicago Press, Chicago.

Clutton-Brock, T.H., Major, M., Albon, S.D. & Guinness, F.E. (1987) Early development and population dynamics in red deer. I. Density-dependent effects on juvenile survival. *Journal of Animal Ecology*, **56**, 53–64.

- Clutton-Brock, T.H., Price, O.F. & Albon, S.D. (1991) Persistent instability and population regulation in Soay sheep. *Journal of Animal Ecology*, **60**, 593–608.
- Coulson, T., Albon, S.D., Guinness, F.E., Pemberton, J. & Clutton-Brock, T.H. (1997) Population substructure, local density and calf winter survival in red deer (*Cervus elaphus*). *Ecology*, **78**, 852–863.
- Coulson, T., Kruuk, L.E.B., Tavecchia, G., Pemberton, J.M. & Clutton-Brock, T.H. (2003) Estimating selection on neonatal traits in red deer using elasticity path analysis. *Evolution*, **57**, 2879–2892.
- Dabin, W., Beauplet, G., Crespo, E.A. & Guinet, C. (2004) Age structure, growth and demographic parameters in breeding-age female subantarctic fur seals, *Arctocephalus tropicalis*. *Canadian Journal of Zoology*, **82**, 1043–1050.
- Doidge, D.W., Croxall, J.P. & Ricketts, C. (1984) Growth rates of Antarctic fur seal *Arctocephalus gazella* pups at South Georgia. *Journal of Zoology, London*, **203**, 87–93.
- Eberhardt, L.L. (1981) Population dynamics of the Pribilof fur seals. *Dynamics of Large Mammal Populations* (eds C.W. Fowler & T.D. Smith), pp. 197–220. John Wiley & Sons, Inc., New York.
- Festa-Bianchet, M., Jorgensen, J.T., Berube, C.H., Portier, C. & Wishart, W.D. (1997) Body mass and survival of bighorn sheep. *Canadian Journal of Zoology*, **75**, 1372–1379.
- Festa-Bianchet, M., Jorgensen, J.T. & Reale, D. (2000) Early development, adult mass, and reproductive success in bighorn sheep. *Behavioral Ecology*, **11**, 633–639.
- Fujiwara, M. & Caswell, H. (2002) A general approach to temporary emigration in mark-recapture analysis. *Ecology*, **83**, 3266–3275.
- Gaillard, J.-M., Andersen, R., Delorme, D. & Linnell, J.D.C. (1998b) Family effects on growth and survival of juvenile roe deer. *Ecology*, **79**, 2878–2889.
- Gaillard, J.-M., Festa-Bianchet, M. & Yoccoz, N.G. (1998a) Population dynamics of large herbivores: variable recruitment with constant adult survival. *Trends in Ecology and Evolution*, **13**, 58–63.
- Gaillard, J.-M., Festa-Bianchet, M., Yoccoz, N.G., Loison, A. & Toigo, C. (2000) Temporal variation in fitness components and population dynamics of large herbivores. *Annual Review of Ecology and Systematics*, **31**, 367–393.
- Georges, J.-Y. & Guinet, C. (2000) Maternal care in the subantarctic fur seals on Amsterdam island. *Ecology*, **81**, 295–308.
- Georges, J.-Y., Sevot, X. & Guinet, C. (1999) Fostering in a subantarctic fur seal. *Mammalia*, **63**, 384–388.
- Greenberg, R. (1980) Demographic aspects of long-distance migration. *Migrant Birds in the Neotropics: Ecology, Behavior, Distribution, and Conservation* (eds A. Keast & E.S. Morton), pp. 493–504. Smithsonian Institution Press, Washington, DC.
- Guinet, C., Jouventin, P. & Georges, J.-Y. (1994) Long term population changes of fur seals *Arctocephalus gazella* and *Arctocephalus tropicalis* on subantarctic (Crozet) and subtropical (St. Paul and Amsterdam) islands and their possible relationships to El Niño Southern Oscillation. *Antarctic Science*, **6**, 473–478.
- Hall, A.J., McConnell, B.J. & Barker, R.J. (2001) Factors affecting first-year survival in grey seals and their implications for life history strategy. *Journal of Animal Ecology*, **70**, 138–149.
- Hindell, M.A., Bryden, M.M. & Burton, H.R. (1994) Early growth and milk composition in southern elephant seal (*Mirounga leonina*). *Australian Journal of Zoology*, **42**, 723–732.
- Hindell, M.A., McConnell, B.J., Fedak, M.A., Slip, D.J., Burton, H.R., Reijnders, P.J.H. & McMahon, C.R. (1999) Environmental and physiological determinants of successful foraging by naive southern elephant seal pups during their first trip to sea. *Canadian Journal of Zoology*, **77**, 1807–1821.
- Keedwell, R.J. (2003) Does fledging equal success? Post-fledging mortality in the black-fronted tern. *Journal of Field Ornithology*, **74**, 217–221.
- Kendall, W.L. & Nichols, J.D. (2002) Estimating state-transition probabilities for unobservable states using capture-recapture/resighting data. *Ecology*, **83**, 3276–3284.
- Kooymann, G.L. (1989) *Diverse Divers*. Springer-Verlag, Berlin and Heidelberg.
- Kruuk, L.E.B., Clutton-Brock, T.H., Rose, K.E. & Guinness, F.E. (1999) Early determinants of lifetime reproductive success differ between the sexes in red deer. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, **266**, 1655–1661.
- Lander, R.H. (1975) Method of determining natural mortality in the northern fur seal (*Callorhinus ursinus*) from known pups and kill by age and sex. *Journal of Fisheries Research Board Canada*, **32**, 2447–2452.
- Lebreton, J.-D., Burnham, K.P., Clobert, J. & Anderson, D.R. (1992) Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs*, **62**, 67–118.
- Lebreton, J.-D. & Clobert, J. (1991) Bird population dynamics, management, and conservation: the role of mathematical modelling. *Bird Population Studies* (eds C.M. Perrins, J.-D. Lebreton & G.J.M. Hirons), pp. 105–125. Oxford University Press, Oxford.
- Lindström, J. (1999) Early development and fitness in birds and mammals. *Trends in Ecology and Evolution*, **14**, 343–348.
- Mann, K.H. & Lazier, J.R.N. (1991) *Dynamics of Marine Ecosystems, Biology – Physical Interactions in the Ocean*. Blackwell Scientific Publications, London.
- McMahon, C.R., Burton, H.R. & Bester, M.N. (1999) First-year survival of southern elephant seals (*Mirounga leonina*) at sub-Antarctic Macquarie Island. *Polar Biology*, **21**, 279–284.
- McMahon, C.R., Burton, H.R. & Bester, M.N. (2000) Weaning mass and the future survival of juvenile southern elephant seals (*Mirounga leonina*) at Macquarie Island. *Antarctic Science*, **12**, 149–153.
- Merilä, J. & Svensson, E. (1997) Are fat reserves in migratory birds affected by condition in early life? *Journal of Avian Biology*, **28**, 279–286.
- Naef-Daenzer, B., Widmer, F. & Nuber, M. (2001) Differential post-fledging survival of great and coal tits in relation to their condition and fledging date. *Journal of Animal Ecology*, **70**, 730–738.
- Newton, I. (1989) *Lifetime Reproduction in Birds*. Academic Press, London.
- Oftedal, O.T., Boness, D.J. & Tedman, R.A. (1987) The behavior, physiology, and anatomy of lactation in the pinnipedia. *Current Mammalogy*, **1**, 175–245.
- Olsson, O. (1997) Effects of food availability on fledging condition and post-fledging survival in king penguin chicks. *Polar Biology*, **18**, 161–165.
- Peters, R.H. (1983) *The Ecological Implications of Body Size*. Cambridge University Press, Cambridge.
- Pfister, C.A. (1998) Patterns of variance in stage-structured populations: evolutionary predictions and ecological implications. *Proceedings of the National Academy of Sciences*, **95**, 213–218.
- Pistorius, P.A., Bester, M.N., Kirkman, S.P. & Boveng, P.L. (2000) Evaluation of age- and sex-dependent rates of tag loss in southern elephant seals. *Journal of Wildlife Management*, **64**, 373–380.
- Pomeroy, P.P., Fedak, M.A., Rothery, P. & Anderson, S. (1999) Consequences of maternal size for reproductive expenditure and pupping success of grey seals at North Rona, Scotland. *Journal of Animal Ecology*, **68**, 235–253.
- Pradel, R., Wintrebert, C.M.A. & Gimenez, O. (2003) A proposal for a goodness-of-fit test to the Arnason–Schwarz multisite capture–recapture model. *Biometrics*, **59**, 43–53.

- Prévot-Julliard, A.C., Lebreton, J.-D. & Pradel, R. (1998) Re-evaluation of adult survival of black-headed gulls (*Larus ridibundus*) in presence of recapture heterogeneity. *Auk*, **115**, 85–95.
- Promislow, D.E.L. (1992) Costs of sexual selection in natural populations of mammals. *Proceedings of the Royal Society of London B*, **247**, 203–210.
- Reynolds, R.W. & Smith, T.M. (1994) Improved global sea surface temperature analyses. *Journal of Climate*, **7**, 929–948.
- Rose, K.E., Clutton-Brock, T.H. & Guinness, F.E. (1998) Cohort variation in male survival and lifetime breeding success in red deer. *Journal of Animal Ecology*, **67**, 979–986.
- Sagar, P.M. & Horning, D.S. Jr (1998) Mass-related survival of fledgling sooty shearwaters *Puffinus griseus* at The Snares, New Zealand. *Ibis*, **140**, 329–331.
- Sarno, R.J. & Franklin, W.L. (1999) Maternal expenditure in the polygynous and monomorphic guanaco: suckling behavior, reproductive effort, yearly variation, and influence on juvenile survival. *Behavioral Ecology*, **10**, 41–47.
- Schjoerring, S., Gregersen, J. & Bregnballe, T. (1999) Prospecting enhances breeding success of first-time breeders in the great cormorant, *Phalacrocorax carbo sinensis*. *Animal Behaviour*, **57**, 647–654.
- Schwarz, C.J., Schweigert, J.F. & Arnason, A.N. (1993) Estimating migration rates using tag-recovery data. *Biometrics*, **49**, 177–193.
- Sinclair, A. (1996) Mammal populations: fluctuation, regulation, life history theory and their implications for conservation. *Frontiers of Population Ecology* (eds R.B. Floyd, W. Sheppard & P.J. De Barro), pp. 127–154. CSIRP, Melbourne, Australia.
- Singer, F.J., Harting, A., Symonds, K.K. & Coughenour, M.B. (1997) Density-dependence, compensation, and environmental effect on elk calf mortality in Yellowstone National Park. *Journal of Wildlife Management*, **61**, 12–25.
- Sokal, R.R. & Rohlf, F.J. (1981) *Biometry*. WH Freeman and Sons, New York.
- Stearns, S.C. (1992) *The Evolution of Life Histories*. Oxford University Press, Oxford.
- Stewart, B.S. (1997) Ontogeny of differential migration and sexual segregation in northern elephant seals. *Journal of Mammalogy*, **78**, 1101–1116.
- Trillmich, F. (1996) Parental investment in pinnipeds. *Advances in the Study of Behavior*, **25**, 533–577.
- Trites, A.W. (1989) Estimating the juvenile survival rate of male northern fur seals (*Callorhinus ursinus*). *Canadian Journal of Fisheries and Aquatic Science*, **46**, 1428–1436.
- Weimerskirch, H. & Jouventin, P. (1987) Population dynamics of the wandering albatross, *Diomedea exulans*, of the Crozet Islands: causes and consequences of the population decline. *Oikos*, **49**, 315–322.
- White, G.C. & Burnham, K.P. (1999) Program MARK: survival estimation from populations of marked animals. *Bird Study*, **46** (Suppl.), 120–138.
- Wickens, P. & York, A.E. (1997) Comparative population dynamics of fur seals. *Marine Mammal Science*, **13**, 241–292.

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