

Adult female survival, population trend, and the implications of early primiparity in a capital breeder, the southern elephant seal (*Mirounga leonina*)

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Abstract

Adult female survival as a potential proximate factor responsible for observed changes in southern elephant seal *Mirounga leonina* populations was investigated. We compared the survival rate estimates from mark–recapture data for female elephant seals from the Marion Island population (using program MARK) for two periods (pre- and post-decline) during the past 15 years and with estimates from another population in southern Argentina, which had increased steadily during the same period. Survival of prime-age adult females increased significantly by 6.2% during the latter part of the decline at Marion Island, and the survival of adult females at the colony in southern Argentina was 3.2% greater than at Marion Island after the stabilization. We thereby demonstrated the importance of adult female survival in population regulation and emphasized the importance of monitoring adult females in order to understand population changes in southern elephant seals. In addition, we investigated whether reproductive expenditure early on in life reduces future reproductive potential in the population at Marion Island. We did this by estimating and comparing future survival and breeding probabilities of females primiparous at different ages. The future annual survival and breeding probabilities of females breeding at a young age, was similar to those from females primiparous at an older age. There was also no reduced survival in the year following first breeding in young or older first time breeders. Reproductive expenditure in young primiparous females therefore did not entail future fitness costs relative to older primiparous females, and we found no evidence supporting the existence of various life-history strategies in terms of age of primiparity within a population of southern elephant seals.

Key words: *Mirounga leonina*, elephant seals, mark–recapture, survival, primiparity, life-history strategies

INTRODUCTION

The significance of the various demographic variables and their respective potential contributions to population change forms an important issue in population ecology (Eberhardt & Siniff, 1977; Eberhardt, 1981; Promislow & Harvey, 1990; Gaillard, Festa-Bianchet & Yoccoz, 1998). The fitness implications of one of these demographic variables, the age of primiparity, also has a bearing on life-history theory as natural selection is expected to favour a reproductive strategy that takes into account the average chances of successful reproduction at any age and the consequences of breeding for subsequent survival and reproduction (Gadgil & Bossert, 1970; Jorgenson *et al.*, 1993).

Population size responds directly to changes in age-specific survival and fecundity (Jorgenson *et al.*, 1997), and is mediated by environmental conditions (Saether &

Heim, 1993). Accurate measures of these parameters are, however, difficult to acquire since they necessitate long-term monitoring of known aged individuals. Demographic parameters are expected to vary according to age in populations that are age-structured (as is the case in most vertebrates), and these demographic parameters have different consequences for population dynamics (Krebs, 1985). Deferred reproduction, for example, is seen as the result of a trade-off between current reproductive effort and subsequent reproduction, growth and/or survival (Reiter, Panken & Le Boeuf, 1981; Reiter & Le Boeuf, 1991; Boyd *et al.*, 1995). In northern elephant seals and Antarctic fur seals, females that give birth early in life evidently have lower future reproductive success and poorer survival than those that give birth for the first time later in life (e.g. Huber, 1987; Reiter & Le Boeuf, 1991; Lunn, Boyd & Croxall, 1994; Sydeman & Nur, 1994). Similar reductions in these vital rates associated with early breeding have been reported for several ungulate species (Clutton-Brock, Guinness & Albon, 1983; Miura, Kita & Sigmura, 1987). On the other hand, if mass or

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body size is the fundamental criterion affecting age of first breeding (Laws, 1956a; Reimers, 1983; Jorgenson *et al.*, 1993; Boyd, 2000), then the future reproductive success of females breeding for the first time at the various ages is expected to be similar, with early breeders gaining a competitive advantage in terms of gene investment. This could be the case in bighorn ewes *Ovis canadensis* and bison *Bison bison* where females that breed at an early age of primiparity have been shown to have the same or better survival and reproductive success than females that breed at an older age (Festa-Bianchet, 1989; Green & Rothstein, 1991).

Although several studies have quantified survival and fecundity rates for specific populations, few have compared these rates among populations growing at different rates to assess their effects on population trends. Studies on adult survival and fecundity in large mammals are particularly sparse due to the requirement for long-term monitoring of many marked individuals to obtain accurate estimates. Many recent demographic studies of southern elephant seals *Mirounga leonina* concentrated on population trends (e.g. Hindell & Burton, 1987; Guinet, Jouventin & Weimerskirch, 1992; Bester & Wilkinson, 1994; Pistorius, Bester & Kirkman, 1999a) and on identifying proximate and ultimate causes of variation in population size (Hindell, 1991; Bester & Wilkinson, 1994; Pistorius, Bester & Kirkman, 1999b). A key concern has been the long-term decline of southern elephant seals throughout the southern Indian and southern Pacific oceans (van Aarde, 1980; Burton, 1986; Hindell & Burton, 1987; Guinet *et al.*, 1992; Bester & Wilkinson, 1994). Several of these populations have apparently stabilized subsequently, or are thought to be in the process of stabilizing (Guinet, Jouventin & Weimerskirch, 1999; Pistorius *et al.*, 1999a).

The southern elephant seal population at Marion Island declined from 12 817 individuals in 1951 to about 1400 in 1999 (Bester & Wilkinson, 1994; Laws, 1994; Pistorius *et al.*, 1999a). It declined from 2120 seals in 1986 to 1330 seals in 1994 (a 37% decline at an annual rate of 5.8%; Pistorius *et al.*, 1999a). Results of long-term mark-recapture studies have suggested that this decline was due to low survival of adult females (Pistorius *et al.*, 1999b). A decline in prey availability is thought to be the ultimate cause as deduced from low survival estimates of seals with high energetic demands and low reproductive rates which increased with the slowing down of the rate of population decline (Pistorius *et al.*, 1999b; Pistorius *et al.*, 2001a). By contrast, the southern elephant seal population at Patagonia (Peninsula Valdés, Argentina) numbers around 43 300 (Lewis *et al.*, 1998) and has increased at a rate of 5.1% annually between 1975 and 1982 (Campagna & Lewis, 1992; Laws, 1994). More recently the increase has been 3.6% annually (Lewis *et al.*, 1998).

Primiparous southern elephant seal females are known to range in age from 3 to 6 years, a time when active growth is still taking place (Laws, 1953), and adult females start hauling out onto land to breed in early September and peak in numbers in mid-October (Wilkinson, 1992; Bester & Wilkinson, 1994). Females rely entirely upon

stored energy reserves to feed their offspring to weaning and are extreme examples of capital breeders (Jonsson, 1997; Boyd, 2000). They give birth to a single pup about a week after hauling out, wean the pup in 3 weeks during which a massive transfer of energy takes place involving a 35% loss in the mother's weight (Fedak, Arnborn & Boyd, 1996), and then depart to sea again (Condy, 1979; Wilkinson, 1992).

The aims of the present study were to: (1) determine trends in the elephant seal population at Marion Island since 1994; (2) estimate survival of adult females at Marion Island and Peninsula Valdés in Patagonia; (3) compare survival estimates between the two sites (stable and increasing population) as well as with survival data for adult females at Marion Island prior to 1994 (declining population); (4) document the fitness correlates of variation in age of first reproduction in southern elephant seal females at Marion Island in terms of the patterns of later survival and breeding success using recapture data collected during the period 1986 to 1999 from marked females.

METHODS

Study sites

Marion Island (46°54'S, 37°45'E), 1 of 2 islands in the Prince Edward Island group, is located in the sub-Antarctic region of the southern Indian Ocean, approximately 2180 km south south-east of Cape Town, South Africa (Fig. 1; Wilkinson, Pascoe & Bester, 1987). Peninsula Valdés (42°30'S, 64°W) is on the east coast of Patagonia, Argentina, and along the temperate waters of the south Atlantic Ocean (Fig. 1). Elephant seals haul out and breed there along 200 km of pebble and sandy beaches (Campagna & Lewis, 1992).

Data collection

The survival estimates for the 2 populations were derived from 2 different types of data sets. At Marion Island the elephant seals were marked as pups allowing estimation of age-specific probabilities, whereas females at Peninsula Valdés were tagged as adult females of unknown age. We therefore made use of average adult survival rather than age-specific survival.

Marion Island

We tagged 3070 (average: 256 annually, range: 198–343) weaned female elephant seal pups in each of their hind flippers between 1983 and 1994 on Marion Island, using uniquely numbered, colour-coded Dal 008 Jumbotags® (Dalton Supplies Ltd., Henley-on-Thames, U.K.) (for details see Pistorius *et al.*, 2000). We searched for tagged seals at all the beaches (32 along a 51.9-km coastline) on

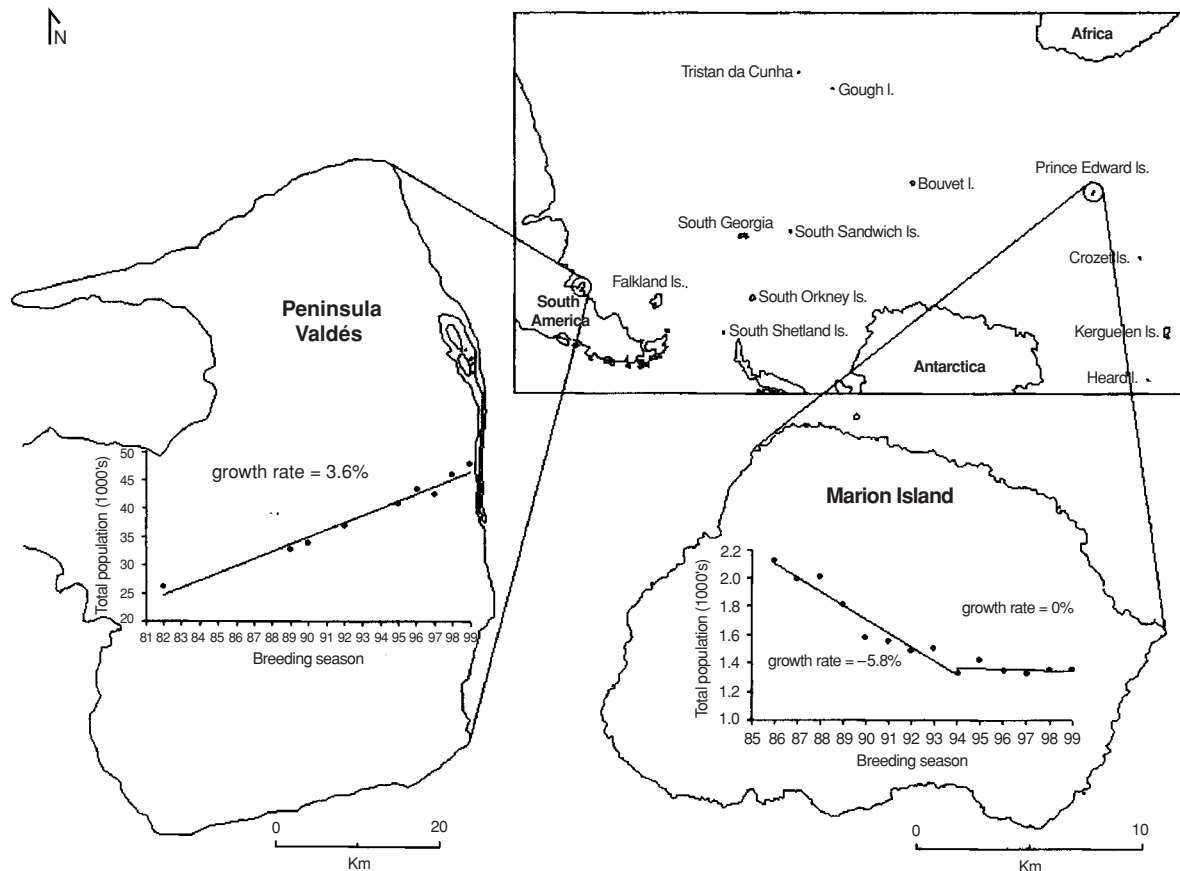


Fig. 1. Position and growth of the southern elephant seal *Mirounga leonina* populations at Marion Island and Peninsula Valdés. Population estimates exclude pups.

the island every 7 days during the breeding season (mid-August to mid-November) and every 10 days during the moulting period (mid-November to mid-April) each year from 1983 to 1999 and every 10 days during the winter (June, July and August) since 1990. We recorded the tag number and colour combination of each tagged seal during these surveys.

Peninsula Valdés

At Peninsula Valdés most tagging of seals took place along 11 km of beaches in the area of Punta Delgada. Resighting efforts were also focused there, although a larger area of about 31 km was searched less often. The mark-recapture study site is located within the most concentrated section of the population's distribution on the peninsula. A total of 804 adult females was marked during the breeding season from 1990 to 1994 at Punta Delgada (1990: $n=243$; 1991: $n=36$; 1992: $n=19$; 1993: $n=60$; 1994: $n=446$). Only females with pups or females that were visibly pregnant were tagged. We did not know the exact ages of any of these sexually mature females. Colour coded and uniquely numbered Dal 008 Jumbotags® (Dalton Supplies Ltd., Henley-on-Thames, U.K.) were applied to the interdigital webbing of either 1 or 2 hind flippers of the seals. For each year of tagging the proportion of single- and

double-tagged seals were recorded. Since 1990 the Punta Delgada area was traversed on foot on a weekly basis during the breeding seasons and tag numbers and colours of re-sighted seals were recorded, yielding 8 years of recapture data for animals tagged in 1990 and 4 years for those tagged in 1994.

Data analyses

Population trend

After estimates of population size at Marion Island were log-transformed, we performed a regression analysis using a 2-stage linear model for the periods 1986–1994 and 1994–1999 (with 1994 visually appearing to be the most parsimonious division between pre- and post-decline). In addition, we applied a single linear regression over the entire period. A runs test (used to test for a random distribution of data points above and below the regression curves) was used to select the most appropriate model. The model with the best fit was used to describe trends in abundance and exponential growth rate at Marion Island (Fig. 1). We similarly used 1992, 1993, 1995 and 1996 as the division points and used residual analysis to determine which model gave the best fit to the data in order to test whether any of the above years may have

been a more appropriate division between the 2 time periods. Annual estimates of population size prior to 1998 and methods used to calculate population size for 1998 and 1999 are described by Pistorius *et al.* (1999a). Annual estimates of population size were derived from annual pup production, which in turn was estimated from counts of adult females during their peak haul-out date during the breeding season (see Pistorius *et al.* (1999a) for more detail). Only single counts were performed, thereby not allowing for standard error estimation. Population estimates for Peninsula Valdés were taken from Campagna & Lewis (1992) and Lewis *et al.* (1998) and methods used to acquire these estimates are described in these sources.

Female survival

Encounter-history matrices, which are required for capture-mark-recapture (CMR) analysis, were constructed from the resight data, treating multiple sightings in a year as a single sighting. Seals were assumed to age by 1 year on 15 October and 2 October which is the peak haul-out date for adult females at Marion Island and Peninsula Valdés respectively (Condy, 1979; Campagna, Lewis & Baldi, 1993; Bester & Wilkinson, 1994). Females seen during the breeding season were taken to survive up to the parturition date. The software program MARK (G. White, Colorado State University; White & Burnham, 1999), which is an application for the analysis of mark-recapture data, was used to obtain maximum likelihood estimates of survival and capture probability using the above-mentioned matrices. The software program provides parameter estimates under the essential Cormack-Jolly-Seber (CJS) model (Cormack, 1964; Jolly, 1965; Seber, 1965), but also under several models that appear as special cases of this model (Lebreton *et al.*, 1992). As it was impossible to distinguish mortality from permanent emigration in our study, we refer to apparent rather than absolute survival.

The two fundamental parameters in these models are:

Φ = the survival probability for all animals between the i th and $(i + 1)$ th sample ($i = 1, \dots, k - 1$), and
 p = the capture probability for all animals in the i th sample ($i = 1, \dots, k$).

The first step in the mark-recapture analyses involved Goodness of Fit (GOF) tests of the CJS model (full time-dependent model) using the program RELEASE (Burnham *et al.*, 1987) to validate the model assumptions (see Lebreton *et al.*, 1992). We performed the test on the recapture data from both the populations.

The Akaike Information Criterion (AIC) was used to select the most parsimonious models for the respective data sets. AIC is a standard procedure for model selection in a CMR context, and it weighs the quality of fit (deviance) and the precision (via the number of parameters), so as to select the model that best describes

the data (Lebreton *et al.*, 1992). It was similarly used to test hypotheses regarding survival and capture probabilities of southern elephant seal females. Age-specific female survival (fourth year, fifth year, sixth year) and survival of females older than this was, for example, maintained constant over the entire period and then maintained constant during the declining and stable population phase. If the latter model gave a lower AIC value, it suggested a significant difference in these estimates between the 2 periods. We maintained survival of all the females constant during and after the population decline at Marion Island to get single (rather than age-specific) estimates of adult female survival. We also compared models with different years (1992–1996) as the division between the 2 periods to assess the most parsimonious division between the 2 periods (declining and stable) in terms of survival of adult southern elephant seal females at Marion Island. Juvenile survival (first 3 years of life) at Marion Island is age-dependent but has not been influenced by time over the duration of the study (Pistorius *et al.*, 2001b; Pistorius & Bester, 2002a). In all the models we therefore maintained juvenile female survival as age but not time dependent.

The relatively high cumulative age-specific tag retention rates (age-specific tag loss increased with age), which have been estimated from double-tagged individuals and detailed by Pistorius *et al.* (2000), were used to adjust the survival estimates from females at Marion Island to compensate for tag loss. Due to insufficient tag loss data from the Peninsula Valdés population and the inability to differentiate between various age classes, the survival estimates for this population were corrected using the average annual tag loss rate for adult females in their fifth to tenth year at Marion Island (3% single tag loss; Pistorius *et al.*, 2000) to estimate cumulative tag retention. It is important to note that tag loss is predominantly a result of the enlargement of the cavity in the flipper rather than structural failure of the tag (personal observation). We therefore anticipate that the ageing of the tags themselves would have had a negligible effect on the tag loss estimates, thereby allowing for the use of annual tag loss rates for adult females at Marion Island (where the tags are older since females were marked as pups) on the females at Peninsula Valdés.

Fitness implications of age of primiparity

To obtain future survival and capture probability estimates from females primiparous at the different ages, we constructed encounter-history matrices from breeding season re-sightings of marked females seen to give birth for the first time when 3-, 4-, 5- and 6-years old. We combined 5- and 6-year-olds because of small sample sizes. The first sighting of a female breeding was treated as the first release, effectively yielding a sample size of 147, 229, and 117 females for the 3 groups respectively. The analysis of the recapture data proceeded similarly to that stated in the above section.

Table 1. Goodness-of-fit tests of the Cormack–Jolly–Seber model for southern elephant seal *Mirounga leonina* females from Marion Island and Peninsula Valdés as well as for females breeding for the first time at different ages at Marion Island

	χ^2	d.f.	P
Marion Island			
	1590.45	66	< 0.001
<i>Age at primiparity</i>			
3	10.98	8	0.203
4	9.57	7	0.215
5+	4.43	5	0.489
Peninsula Valdés			
	4.04	4	0.401

The capture probability estimates that we obtained were used to investigate potential costs of early breeding in terms of reduced future breeding rates. Southern elephant seals mate for the first time while at sea (Le Boeuf & Laws, 1994) and virtually all females that haul out during the breeding season give birth (Huber, 1987; Wilkinson, 1992). Due to the constant, high re-sighting effort, we have assumed that any female that hauls out on land during the breeding season is seen, and thus we interpret re-sighting probabilities (obtained through MARK) as breeding probabilities (see Pistorius *et al.*, 2001a).

RESULTS

Population trend

The two-stage linear model fitted the population data better than the single linear model and 1994 was the most parsimonious division between pre- and post-decline (runs test $p = 0.643$ and $p = 0.700$ vs. $p = 0.004$, showing the data points for the entire period to be significantly non-linear). Using the two-stage linear model we found no change in population size at Marion Island from 1994 through 1999 ($y = -0.0018x + 7.3848$, $r^2 = 0.0183$, $P = 0.7984$) suggesting that the population was stable during this period (Fig. 1; note that data points are limited but the population has remained within the range recorded for the stable period during 2000 and 2001, unpublished data). The population declined from 1986 to 1994 ($y = -0.0575x + 12.609$, $r^2 = 0.9418$, $P < 0.0001$) at an annual rate of 5.8%.

Female survival

The GOF test for the female recapture data from Marion Island demonstrated significant departures from the CJS assumptions (Table 1). The data from the Peninsula Valdés females showed a satisfactory fit according to Test 3.Sm (Table 1).

The capture probability of all the females from Marion Island was time, and age dependent (Table 2). In most individual cohorts, capture probability was, however, not

time/age dependent and we therefore applied constraints within the individual cohorts. The most parsimonious model in terms of capture probability was one in which this parameter was constant over the 1983, 1986 and 1991 cohorts, the 1984, 1990, 1992, 1993 and 1994 cohorts, and time and age dependent in the rest of the cohorts (Table 2). For the Peninsula Valdés females the most parsimonious model was fully time dependent (Table 2). The most parsimonious model in terms of survival of the Marion Island females was one in which survival was constrained over the fourth to sixth year and the seventh year onwards for the two time periods (declining and stable) (Table 2). No significant age-specific survival effects were therefore apparent between ages four and six years, and females older than this. Survival estimates and a comparison between the age-specific survival estimates from Marion Island during and after the population decline are presented in Table 3.

Survival of females at Marion Island was significantly higher during the latter part of this study (Tables 2 & 3). An increase in survival probabilities of 6.7% in prime-age females (years 4, 5 and 6 which contribute more than 50% to the reproductive schedule; Pistorius *et al.*, 1999b), and 6.1% in older females was evident with the stabilization of the Marion Island population (combined increase of 6.2%; model C, Table 3).

Adult females from Peninsula Valdés had an average survival rate of 84.2%. This was approximately 3.2% higher compared to that for females 5 years and older in the stable Marion Island population.

Fitness implications of age of primiparity

The CJS model fitted the recapture data for all three groups (females primiparous at the respective ages) according to Test 2 and Test 3 (Table 1), suggesting that no model assumptions were violated.

We selected the constant survival and constant capture probability model as the most parsimonious one for females who gave birth first when 3, and 5 and 6 years old (Table 2). The constant survival and time-dependent capture probability model was the most suitable for females breeding for the first time when 4 years old (Table 2).

We found no significant age-effect on female survival after the first breeding event in females primiparous at ages 3, 4 or older (Table 2). Future survival did not differ significantly between females who gave birth when 3 vs. 4 years old (AIC 1861.74 vs. 1863.76) neither between females giving birth when 3 vs. 5 and 6 years old (AIC 1277.88 vs. 1279.22).

There was no significant change in age-specific breeding probability after first breeding at age 3 years and ages 5 and 6 years, although such an age-effect appeared to occur in 4-year-old primiparous females (Table 2).

We found no significant difference between future breeding probabilities of females primiparous at ages 3 and 4 years (AIC 1868.17 vs. 1870.62), nor between

Table 2. Elimination of nonsignificant effects from the full Cormack–Jolly–Seber model in modelling survival and capture probability in southern elephant seals *Mirounga leonina* from Marion Island and Peninsula Valdés: for each model the number of estimable parameters (np), the deviance (DEV), and the Akaike Information Criterion (AIC) are given. Survival probabilities are referred to as ϕ and capture probabilities as p . The figures in the model descriptions refer to the year of life. t, time-dependent; a, age-dependent; c, constant; d, a single parameter for the declining period and another for the stable period. ¹ Capture probabilities for cohorts 1983, 1984, 1986, 1990, 1991, 1992, 1993, 1994 constant and rest time-dependent according to AIC from single cohort models (see Pistorius *et al.*, 1999b). ² Cohorts with similar constant capture probabilities grouped together. Selected models are presented in bold

Model	np	DEV	AIC
Marion Island			
$(\phi_{a,t}; p_{a,t})$	214	2735.61	19682.22
$(\phi_{a,t}; p_c)$	95	3037.04	19735.77
$(\phi_{a,t}; p_t)$	110	2956.89	19686.54
$(\phi_{a,t}; p_a)$	109	3019.10	19746.68
$(\phi_{a,t}; p_{\text{cohort specific}}^1)$	145	2808.24	19610.37
$(\phi_{a,t}; p_{\text{cohort specific grouped}}^2)$	138	2897.10	19607.70
$(\phi_{4c}, \text{rest } a,t; p_{\text{cohort specific grouped}})$	126	2931.89	19610.07
$(\phi_{4d}, \text{rest } a,t; p_{\text{cohort specific grouped}})$	127	2929.18	19607.37
$(\phi_{4d,5c}, \text{rest } a,t; p_{\text{cohort specific grouped}})$	115	2941.51	19597.14
$(\phi_4 \& 5d, \text{rest } a,t; p_{\text{cohort specific grouped}})$	116	2938.22	19593.85
$(\phi_4 \& 5d, 6c, \text{rest } a,t; p_{\text{cohort specific grouped}})$	105	2955.31	19590.47
$(\phi_4, 5 \& 6d, \text{rest } a,t; p_{\text{cohort specific grouped}})$	106	2953.83	19589.00
$(\phi_4, 5 \& 6d, 7 \text{ and older } c; p_{\text{cohort specific grouped}})$	58	3002.09	19541.66
$(\phi_{4,5 \& 6 \& 7 \text{ and older } d; p_{\text{cohort specific grouped}})$	59	2998.27	19539.85
$(\phi_{4-6(\text{grouped})c} \& 7 \text{ and older } d; p_{\text{cohort specific grouped}})$	54	3017.71	19549.18
$(\phi_{4-6(\text{grouped})d} \& 7 \text{ and older } d; p_{\text{cohort specific grouped}})$	55	3003.81	19537.30
$(\phi_4 \text{ and older } (\text{grouped}) c; p_{\text{cohort specific grouped}})$	52	3027.37	19554.80
$(\phi_4 \text{ and older } (\text{grouped}) d; p_{\text{cohort specific grouped}})$	53	3016.57	19546.01
<i>Primiparous at age 3 years</i>			
$(\phi_t; p_t)$	11	44.09	828.35
$(\phi_c; p_t)$	7	45.23	821.09
$(\phi_c; p_c)$	2	50.86	816.48
<i>Primiparous at age 4 years</i>			
$(\phi_t; p_t)$	9	26.65	1106.60
$(\phi_c; p_t)$	6	30.93	1104.72
$(\phi_c; p_c)$	2	39.87	1105.54
<i>Primiparous at ages 5 and 6 years</i>			
$(\phi_t; p_t)$	7	8.98	414.13
$(\phi_c; p_t)$	5	11.17	412.05
$(\phi_c; p_c)$	2	13.03	407.66
Peninsula Valdés			
$(\phi_t; p_t)$	15	385.62	3783.59
$(\phi_t; p_c)$	9	434.96	3820.75
$(\phi_c; p_t)$	9	483.72	3869.51

females primiparous at age 3 years and ages 5 and 6 years (AIC 1280.87 vs. 1288.43) (Table 4).

DISCUSSION

Factors that influence population growth, and explain variation in growth rate between populations, are of major interest in population ecology for both practical and theoretical reasons (Gaillard *et al.*, 1998). In addition, life histories are thought to be the end result of a variety of functional responses to different state variables that have varying degrees of influence (Boyd, 2000). Therefore, studies that can identify what shifts in vital rates are required to influence changes in population size are of particular interest for life-history theory, wildlife management and conservation biology (Caughley, 1977;

Gaillard *et al.*, 1998). Comparing vital rates between populations with varying growth rates is required in order to quantify changes in these rates that influence population change, and to determine what parameters are density-dependent. It also affords the opportunity to investigate the costs of early reproduction (age of primiparity) and its implications for life history.

The general approach used to obtain the demographic data upon which this study is based was analogous for the Marion Island and Peninsula Valdés populations (mark–recapture rather than cross-sectional data sets). This permits comparison of vital rates between the two populations, subject to limitation imposed by one data set (Peninsula Valdés) having no information about age. To overcome this limitation, we used a model with no age-effects on survival to obtain a single estimate for the two periods from the Marion Island population to

Table 3. Survival probability estimates of southern elephant seal *Mirounga leonina* females from Marion Island and Peninsula Valdés

Year	Survival probability	SE	Confidence intervals (95%)	Survival probability	SE	Confidence intervals (95%)
Marion Island						
<i>Declining population</i>				<i>Stable population</i>		
<i>Model A ($\phi_{4,5 \text{ \& } 6 \text{ \& } 7 \text{ and older d; } P_{\text{cohort specific grouped}}$)</i>						
4	0.799	0.021	0.755	0.837	0.851	0.801
5	0.727	0.025	0.676	0.774	0.810	0.750
6	0.769	0.030	0.704	0.822	0.839	0.772
7–15	0.751	0.023	0.700	0.795	0.810	0.770
<i>Model B ($\phi_{4-6(\text{grouped}) \text{ \& } 7 \text{ and older d; } P_{\text{cohort specific grouped}}$)</i>						
4–6	0.766	0.012	0.741	0.789	0.833	0.806
7–15	0.749	0.023	0.699	0.793	0.810	0.772
<i>Model C ($\phi_{4 \text{ and older (grouped) d; } P_{\text{cohort specific grouped}}$)</i>						
4–15	0.765	0.010	0.745	0.786	0.827	0.805
Peninsula Valdés						
<i>Increasing population</i>						
<i>Adult females tagged in 1990–1994</i>						
1991	0.856	0.044	0.760	0.933		
1992	0.856	0.047	0.734	0.916		
1993	0.947	0.046	0.842	0.983		
1994	0.860	0.043	0.744	0.933		
1995	0.727	0.024	0.665	0.771		
1996	0.751	0.036	0.676	0.821		
1997	0.896	0.058	0.751	0.964		

Table 4. Survival (ϕ) and capture (p) probabilities of southern elephant seal *Mirounga leonina* females giving birth for the first time at the respective ages at Marion Island

		CI (95%)			CI (95%)			
Age	ϕ	SE (ϕ)	Lower	Upper	p	SE (p)	Lower	Upper
Age at first breeding								
Age 3 years								
3	0.747	0.021	0.703	0.787	0.739	0.029	0.678	0.793
4	0.747	0.021	0.703	0.787	0.739	0.029	0.678	0.793
5	0.747	0.021	0.703	0.787	0.739	0.029	0.678	0.793
6	0.747	0.021	0.703	0.787	0.739	0.029	0.678	0.793
7	0.747	0.021	0.703	0.787	0.739	0.029	0.678	0.793
8	0.747	0.021	0.703	0.787	0.739	0.029	0.678	0.793
Age 4 years								
4	0.746	0.019	0.708	0.782	0.789	0.037	0.708	0.852
5	0.746	0.019	0.708	0.782	0.778	0.042	0.686	0.849
6	0.746	0.019	0.708	0.782	0.913	0.033	0.823	0.959
7	0.746	0.019	0.708	0.782	0.748	0.063	0.606	0.851
8	0.746	0.019	0.708	0.782	0.828	0.095	0.564	0.947
Age 5 and 6 years								
7, 8	0.733	0.028	0.676	0.784	0.733	0.038	0.652	0.802
8, 9	0.733	0.028	0.676	0.784	0.733	0.038	0.652	0.802
9, 10	0.733	0.028	0.676	0.784	0.733	0.038	0.652	0.802
10, 11	0.733	0.028	0.676	0.784	0.733	0.038	0.652	0.802

facilitate comparison of adult female survival between the two populations.

An important assumption made in this study is that marked animals do not permanently emigrate from the study sites, and are therefore not lost for potential recaptures. When using the above-mentioned models for mark–recapture analyses, permanent emigrations are functionally similar to mortalities, and result in negatively biased survival estimates. Adult females have been shown to be highly philopatric with respect to their particular

breeding beaches (Hindell & Little, 1988; Bester, 1989; Hofmeyr, 2001), and we expect that permanent adult female emigration from our study areas was minimal.

A site-specific rate of tag loss could not be calculated for Peninsula Valdés, and if tag loss rates were lower at this site than at Marion Island then using a conversion based on tag loss rates, calculated for Marion Island, would produce an overestimate in adult survival. A major contributing factor to tag loss in southern elephant seals is the enlargement of the cavity through which the shaft of the tag protrudes as a

result of infection (Wilkinson & Bester, 1997). Peninsula Valdés is situated further north relative to Marion Island resulting in a substantially warmer climate, and hence increased likelihood of wound infection. We therefore expect, if anything, that tag loss would be greater at Peninsula Valdés and the survival estimates from this site will be negatively biased.

When evaluating the data in terms of meeting the underlying assumptions of the CJS model, the Valdés adult female data set failed to pass the Test 2 component and the Marion Island year-round data failed both components. This suggests the presence of heterogeneity in survival and/or capture probability within groups of individuals last released on the same sampling occasion. We suspect survival to be homogenous amongst individuals, although size, and therefore condition at weaning, clearly influence first year survival rates at Macquarie Island in the Southern Ocean (McMahon, Burton & Bester, 2000). Heterogeneity in re-sighting probability could also be the reason for the departures. This heterogeneity (in re-sighting or survival probabilities) is often encountered in real data sets and it results in relatively small if any biases on survival rates since the analysis methods used have some robustness to heterogeneity (Carothers, 1979; Nichols *et al.*, 1982; Pollock & Raveling, 1982; Burnham *et al.*, 1987). It may, however, result in actual variances of estimates exceeding estimated theoretical variances (Burnham *et al.*, 1987) and this does form a weakness in the present study. Our sample size of tagged elephant seals was fortunately particularly large and we consequently obtain very low standard errors, that if even doubled would not have been excessively high (i.e. Gaillard *et al.*, 1993; Jorgenson *et al.*, 1997; Hastings, Testa & Rexstad, 1999). As the present mark-recapture program is based on an extremely rigorous re-sighting protocol, we expect that if any estimate bias occurred, that it would have been constant throughout the study period. It would therefore not have weakened the confidence placed on the comparison of estimates and on hypothesis testing (i.e. presence of inter-annual variability in estimates) within the study.

In the present study, shifts in adult female survival were associated with changes in population growth rate as has been demonstrated for a few other mammal populations including Alpine ibex and porcupine caribou (Eberhardt, 1985; Walsh, Griffith & McCabe, 1995; Toigo, Gaillard & Michallet, 1997). A 6.7% increase in prime-age adult female survival was associated with a halt of a 5.8% annual rate of decline at Marion Island, whereas a 3.2% higher adult female survival in the Peninsula Valdés population (compared to the stable Marion Island population) was associated with a 3.6% annual rate of increase. Survival of young adult fur seal females has similarly been noted to be of major importance in determining the rate of population change due to these females having high reproductive values (York & Hartley, 1981).

A few previous studies have found that food availability apparently had a greater influence on adult than on juvenile survival (Sinclair, Dublin & Borner, 1985; Fryxell, 1987). There is considerably more evidence that juvenile survival is more strongly related to food availability

(Clutton-Brock, Guinness & Albon, 1982; Skogland, 1985; Owen-Smith, 1990; Jorgenson *et al.*, 1997). Pistorius *et al.* (1999b) suggested that the decline of the Marion Island elephant seal population has been ultimately related to food limitation. If this is the case, then the results of this study support the notion that food availability has a greater influence on adult female than on juvenile survival, the latter remaining high even in declining elephant seal populations (Bester & Wilkinson, 1994; McMahon, Burton & Bester, 1999; Pistorius *et al.*, 1999b). First, second, and third year southern elephant seal survival at Marion Island was 59.5%, 81.4% and 78.1% during the decline, and 60.7%, 78.1% and 76.3% after the decline, with no significant differences in these age-specific estimates between the two periods (Pistorius & Bester, 2002a), while pup mortality was exceptionally low at about 4.0% throughout the entire period (Pistorius *et al.*, 2001b). Should energetic requirements of pregnant females, which include nourishment of the growing foetus and accumulation of sufficient fat reserves to wean her pup (Condy, 1979; Oftedal, Boness & Tedman, 1987; Carlini *et al.*, 1997), outweigh those of juveniles, as suggested by Hastings, Testa & Rexstad (1999) in a study of Weddell seals *Leptonychotes weddellii*, this would explain why the assumed food limitation had a more pronounced effect on adult female than on juvenile survival. As birth mass and weaning mass can influence first-year survival of elephant seals (McMahon, Burton & Bester, 2000), and weaning mass is considered to be closely linked to female foraging success prior to parturition (Burton *et al.*, 1997), one would expect a food mediated drop in adult female survival to impact on first-year survival. This could not be demonstrated for the Marion Island elephant seal population, first-year survival remaining consistently high over all the years of study (Pistorius *et al.*, 1999b). However, in the period of probable food limitation during the population decline, southern elephant seal males have been shown to have a lower survival rate than females and this was ascribed to the increased energetic requirements of the larger male morph (Pistorius *et al.*, 1999b).

An alternative explanation for food limitation affecting adults rather than juveniles could potentially be separate foraging grounds, or different foraging strategies between the two population components. Such contrasting foraging behaviour, could also potentially mask the above-mentioned impact that food limitation applying to adult females would have on juvenile survival. Although foraging ranges and diving behaviour of adult elephant seals at Marion Island and Valdés Peninsula have been investigated (Campagna *et al.*, 1995; Campagna *et al.*, 1998; Jonker & Bester, 1998; Malherbe, 1998; Campagna, Fedak & McConnell, 1999) juvenile foraging behaviour at these populations remains unknown. Slip (1997) has, however, provided evidence that these two population components use similar foraging ranges and strategies, at least at Heard Island, which points to the differential energy requirement hypothesis as a more likely explanation. On the other hand, juvenile and adult southern elephant seals at Macquarie Island appear to use different foraging areas (McConnell *et al.*, 2002) and the adults and

juveniles might be exploiting different prey as very young elephant seals do not dive as deep (Thorson & Le Boeuf, 1994), although by age 2 years the dive pattern is similar to that of adults (Le Boeuf, 1994).

Several studies have highlighted the difficulties associated with teasing apart the respective contribution of recruitment and adult survival towards population growth (Escos, Alados & Emlen, 1994; Walsh *et al.*, 1995; Wickens & York, 1997; Gaillard *et al.*, 1998). Recruitment can be measured as a combination of juvenile survival and the proportion of females breeding. Juvenile survival has been dismissed as a population component bringing about population change at Marion Island (Pistorius & Bester, 2002a). Fecundity in Marion Island elephant seal females has, however, increased and their age of maturity has decreased during the period 1986 to 1997 (Pistorius *et al.*, 2001a). It follows that the combination of increased adult female survival and fecundity has been instrumental in altering the trend of population growth at Marion Island. Using a stochastic population modelling approach, changes in age-specific fecundity of 3- to 5-year-old southern elephant seal females have, however, been shown to have an impact in the region of an order of magnitude less than similar changes in age-specific survival on population growth rate (Pistorius, 2001). This lesser importance of age-specific fecundity to population growth rate is consistent with the observations of Bester & Wilkinson (1994) and Bradshaw *et al.* (2002). The changes in adult female survival at Marion Island that were recorded in this study have also been shown to be adequate for the observed changes in population growth (see Pistorius, 2001). When considering the above, it is evident that changes in population growth at Marion Island (and possibly other southern elephant seal breeding sites in the Southern Ocean) must primarily have been a result of shifts in adult female survival.

Nevertheless, in terms of fitness, southern elephant seal females breeding at a young age at Marion Island had similar future annual probabilities of survival and breeding relative to older primiparous females. First, this suggests that no fitness costs were incurred through early (relative to later) primiparity, counter to what has been reported for several other species (e.g. Clutton-Brock *et al.*, 1983; Miura *et al.*, 1987; Boyd *et al.*, 1995), including northern elephant seals (Reiter & Le Boeuf, 1991). Second, it suggests that there was no variation in life-history strategies within the population regarding age of primiparity as has been suggested for northern elephant seals (Reiter & Le Boeuf, 1991). Furthermore, after the first breeding event, there were no significant annual changes in female survival, suggesting that in adult southern elephant seal females (this study), survival does indeed reach a plateau after primiparity (Caughley, 1977). It is important to note that the above does not imply that no costs are incurred through reproduction, but that the costs incurred are similar between females primiparous at the respective ages. Estimates of particularly 3-year-old female survival from recapture data collected year-round (breeding and non-breeding females) (Table 3) were higher than the estimates from data restricted to

breeding females (Table 4) and this difference represents a fitness cost of reproduction as the majority of females at Marion Island are not parous at this age (Pistorius *et al.*, 2001a). An increase in mortality of at least 5–10% the year following parity is associated with a breeding event (present study).

The similar survival between females primiparous at the respective ages suggests that they were likely to have been of similar condition or body mass. If this was not the case, and if younger breeding females were of poorer condition than the older ones, this would have been reflected in their future survival and reproduction (i.e. Festa-Bianchet, Gaillard & Jorgenson, 1998; Pomeroy *et al.*, 1999). This is particularly so given the likelihood that food limitation had been instrumental in the population decline at Marion Island, and which purportedly had a direct impact on adult female survival estimates (Pistorius *et al.*, 1999b; Pistorius, 2001). Mass therefore appears to be the most important state variable influencing reproduction in southern elephant seals (Laws, 1956a,b). Breeding in southern elephant seals is therefore likely to be determined by a critical threshold body mass (as is the case for some (Albon, Mitchell & Staines, 1983; Saether & Haagenrud, 1983) but not all (Jorgenson *et al.*, 1993) ungulate species) and once this is reached no further delay in the onset of reproduction, or a trade-off between growth and reproduction, takes place. This study, therefore, lends support to the notion that in capital breeders, mass has a fundamental influence on reproductive potential (Festa-Bianchet *et al.*, 1998; Pomeroy *et al.*, 1999; Boyd, 2000).

Similar studies on Antarctic fur seals and northern elephant seals demonstrated distinct future reductions in survival and fecundity as costs incurred through reproduction (Reiter & Le Boeuf, 1991; Boyd *et al.*, 1995). Antarctic fur seals are income breeders, implying that breeding females rely mainly on energy obtained through foraging during the lactation period to wean their pups, whereas elephant seals are extreme examples of capital breeders, and females therefore rely entirely upon stored energy reserves to wean their pups (Jonsson, 1997; Boyd, 2000). Seals in these two breeding categories are likely to have contrasting life-history determinants (Boyd, 2000). Mass has been shown to be the dominant state variable influencing pregnancy in some phocids that are capital breeders, with it being less important in an income breeder – e.g. the Antarctic fur seal (Boyd, 2000). The difference in fitness costs associated with breeding between the southern elephant seal and Antarctic fur seals could therefore be a reflection of the varying influence of mass on reproduction in capital and income breeding mammals. Conversely, an obscure dichotomy exists between the results from the present study for southern elephant seals and that found for northern elephant seals (both capital breeders).

The absence of fitness costs associated with early (relative to later) breeding in the southern elephant seal population at Marion Island (this study) contrasts with several purported fitness costs associated with early breeding in an increasing population of northern elephant seals (Le Boeuf & Reiter, 1988; Reiter & Le Boeuf, 1991).

One of these presumed fitness costs, reduced chances of pup survival, in northern elephant seals can be explained by resource limitation in the form of restricted space availability at the breeding beaches (Reiter *et al.*, 1981). Fitness costs in terms of reduced future reproductive success and survival of early (relative to later) breeders have, however, also been documented (Huber, 1987; Reiter & Le Boeuf, 1991) and this begs explanation in view of the findings in the present study. Unlike the present study, it was also found that annual mortality rate was highest immediately following first reproduction irrespective of age (Huber, 1987; Reiter & Le Boeuf, 1991). Although reference is widely made to this work, the methods used to obtain the above results have been questioned on statistical and biological grounds and larger sample sizes have been recommended to reach sound conclusions (Sydeman & Nur, 1994).

From the present study we would expect a positive correlation between growth, particularly in the first few years of life, and lifetime reproductive success and hence fitness in southern elephant seals. This concept has been supported for several species by the fact that faster-growing females begin reproducing earlier in life (Ozoga & Verme, 1982; Saether & Haagenrud, 1983). Natural selection is therefore likely to act primarily on early foraging behaviour and on factors influencing weaning mass in order to maximize individual fitness in southern elephant seals.

The reproductive success of a female can be measured as the number of successful offspring she manages to produce throughout her life. It comprises several interdependent aspects, including survival and longevity of the female, the age of primiparity and subsequent breeding probabilities and the survival of the offspring. In this study we have discounted fitness costs incurred through early reproductive expenditure in terms of a relative reduction in future breeding probabilities and survival, at least up to age 9 years. A senescence effect (in terms of declining reproduction and survival with age) does not appear prevalent in the population (Pistorius & Bester, 2002b) and we therefore expect age-specific post-primiparous reproductive participation to be equal among females primiparous at the respective ages.

An aspect of fitness we have not dealt with is the successful weaning of pups from variously aged females and their future survival. In several phocid species, including southern elephant seals, larger females tend to produce pups that are larger both at birth and at weaning (McCann, Fedak & Harwood, 1989; Bowen *et al.*, 2001). Moreover, size, and therefore condition at weaning, has been shown to influence first-year survival in southern elephant seals at both Macquarie Island (McMahon *et al.*, 2000) and Marion Island (McMahon *et al.*, 2003), as well as in grey seals (Hall *et al.*, 2001), although no such relationship was evident for northern elephant seals (Le Boeuf *et al.*, 1994). Delaying the onset of reproduction by a year in order to invest in growth rather than reproduction (Reiter & Le Boeuf, 1991) may therefore increase the probability of survival of the offspring. With the exceptionally low pre-weaning mortality in elephant

seals at Marion Island (3.8%; Pistorius *et al.*, 2001b), a fitness cost in terms of reduced offspring survival associated with early primiparity would presumably entail reductions in post-weaning and first year (McMahon *et al.*, 2000) and juvenile survival (Coulson *et al.*, 1997; Reed & Plante, 1997). Unlike adult females, juveniles (ages 0–2 years) at Marion Island do not appear to be food limited since the survival of these animals has been constant over time irrespective of changes in population growth rate (Pistorius & Bester, 2002a), and adult females wean their pups at a similar mass here (Marion Island) as at other sites (e.g. Macquarie Island) in the southern ocean (McMahon *et al.*, 2003), although formerly this was not the case (Burton *et al.*, 1997). We consequently do not suspect differences in weaning mass of pups from females primiparous at different ages to greatly influence survival in this population component. In the absence of future fitness costs incurred through early primiparity (this study), we argue that even if offspring survival of young primiparous females is lower than that for older primiparous females, the high overall future chances of offspring survival (although possibly slightly lower than in older primiparous females; McMahon *et al.*, 2000; Pistorius & Bester, 2002a) and the experience gained from the first reproductive event, would presumably curtail any potential fitness cost associated with early breeding.

In conclusion, Eberhardt (1977) postulated the widely accepted view that population regulation in large mammals commences with changes in survival of juveniles, followed by changes in the age of first reproduction and reproductive rates of females, and ultimately by shifts in adult survival. By contrast, the Marion Island elephant seal population showed that reproductive rates was the first parameter to respond to environmental change (Pistorius *et al.*, 2001a) followed by changes in survival of prime-age females (present study), while juvenile survival remained high (Pistorius & Bester, 2002a). These differences caution against generalizing when dealing with patterns of population regulation in large mammals. In this study it was not possible to distinguish prime-age female survival from survival of all adult females at Peninsula Valdés. The results from Marion Island suggest that prime-age female survival is an important variable influencing elephant seal population status, and marking females as pups so as to allow estimation of age-specific survival at Peninsula Valdés, should therefore be a prerogative of future research. This step will also permit estimation of age of maturity and other reproductive rates for the population. We found that no future fitness costs were incurred through reproductive expenditure at an early, relative to at a later stage of life in southern elephant seals. We consequently discount the existence of various life-history strategies within a population in terms of age of primiparity. We argue that mass, and hence condition, is likely to be the most important variable influencing the age of primiparity in a capital breeder such as southern elephant seals (Laws, 1956a,b; Boyd, 2000), and that no delay in reproduction takes place once the critical breeding mass has been achieved.

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