

SEASONAL SURVIVAL AND THE RELATIVE COST OF FIRST REPRODUCTION IN ADULT FEMALE SOUTHERN ELEPHANT SEALS

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The annual cycle of adult female southern elephant seals (*Mirounga leonina*) can be divided into 2 pelagic phases, separated by relatively short terrestrial phases: breeding and molting. We used resighting data collected from tagged female southern elephant seals at Marion Island during 1986–1999 to investigate seasonal survival during the 2 pelagic phases in relation to reproductive experience. Mean postbreeding (pelagic phase between breeding and molting, about 62 days) survival of primiparous females was 0.830 compared to 0.912 for more-experienced females. Postmolting (pelagic phase between molting and breeding, about 255 days) survival was 0.847 (0.960 when rescaled to 62 days for comparative purposes) and was not dependent on reproductive experience. Postbreeding survival of experienced females was higher than postmolting survival, but per unit time the opposite applied. A 2-stage survival model, in which survival was constrained to be constant before 1994 (when the population was declining) and from 1994 onward (during the stable phase), had overwhelming support from the data. Postbreeding survival of primiparous females increased from 0.799 before 1994 to 0.880 from 1994 onward. Postmolting survival of all females also increased from 0.817 to 0.872 over the same period. Postbreeding and postmolting mortality risk varied independently over time, demonstrating the importance of an intra-annual approach in population studies of southern elephant seals.

Key words: environmental change, Marion Island, mark–recapture models, *Mirounga leonina*, population ecology, seasonal survival

Throughout the course of their annual cycle, animals may be subjected to different mortality risks as a result of activities such as breeding and long-distance movement, which will shape the evolution of basic life-history traits (Beauplet et al. 2006; Gauthier et al. 2001; Hadley et al. 2007; Sendor and Simon 2003; Sillett and Holmes 2002; Stearns 1992). This is especially relevant in long-lived species such as southern elephant seals (*Mirounga leonina*), in which population changes are primarily regulated through survival rather than fecundity (Gaillard et al. 1998). Although a growing number of studies have quantified annual survival in wild populations in a mark–recapture context, relatively few such studies have considered how annual survival varies on a seasonal basis (e.g., Gauthier et al. 2001; Madsen et al. 2002; Pistorius et al. 2006; Sillett and Holmes 2002). These studies have mostly been based on wild-fowl and to our knowledge no previous attempt at such a study has been made on a population of marine mammals. In the case of southern elephant seals in particular, this lack of knowledge

on the seasonal components of annual survival and the interaction between seasonal survival and reproductive experience, expenditure, or both limits our understanding of population regulation in this species.

The last half of the 20th century saw a decline in numbers of southern elephant seals at most of their breeding sites in the southern Indian and Pacific Oceans and some of them have stabilized in recent years (reviewed in McMahan et al. 2005a). Despite the lack of empirical support, the decline in numbers was probably related to food limitation (Bester and Wilkinson 1994; Hindell et al. 1994; McMahan et al. 2005a; Pistorius et al. 1999a, 2001). Although breeding sites of southern elephant seals are limited to the antarctic and subantarctic regions, their vast foraging ranges extend throughout the Southern Ocean, where they fill the role of apex predators (Campagna et al. 1995; Field et al. 2005; Jonker and Bester 1998; Malherbe 1998; McConnell and Fedak 1996; Slip 1997). It is therefore not surprising that the declining numbers of southern elephant seals resulted in several intensive monitoring programs being established to identify causal mechanisms associated with these changes (Bester 1988).

The population of southern elephant seals at Marion Island has been subjected to a thorough mark–recapture program since 1983 (see Pistorius et al. [1999a] for details). This population

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declined from some 12,820 individuals in 1951 to about 1,400 in 1994 (Bester and Wilkinson 1994; Pistorius et al. 1999b). Between 1986 and 1994, the population declined linearly at about 5.8% per annum (Pistorius et al. 1999b), and it has subsequently remained stable (Pistorius et al. 2004; Mammal Research Institute, in litt.). Annual demographic estimates emanating from this mark–recapture program suggested that the decline in numbers was primarily due to low survival of adult females (Pistorius and Bester 2002; Pistorius et al. 2004).

The annual cycle of southern elephant seals comprises 2 pelagic phases, partitioned by obligatory terrestrial phases for breeding and molting, the timing of which is highly synchronous between years (Carrick et al. 1962; Kirkman et al. 2003). Multiparous female southern elephant seals at Marion Island haul out and give birth annually (Bester and Wilkinson 1994; Wilkinson 1992) and the same may be true for primiparous females, although skipping a breeding season after 1st reproduction has been noted for northern elephant seals (Reiter and Le Boeuf 1991). Each of the terrestrial phases involves fasting, as there is complete separation from food sources, for up to 3 or 4 weeks in the case of breeding and molting adult females (Condy 1979; Kirkman et al. 2003). Because virtually no deaths of adult females have been reported during the molting or the breeding season (at least at Marion Island), their annual survival schedule encapsulates mortality experienced during the 2 pelagic phases. The duration of the postbreeding pelagic phase (breeding to molting) has been estimated at $62 \text{ days} \pm 8.2 \text{ SD days}$ and the postmolting pelagic phase (molting to breeding) at $255 \pm 15.2 \text{ days}$ (Jonker and Bester 1998; Wilkinson 1992). It is reasonable to suspect that seasonal survival may vary independently over time because of differences in foraging behavior and location as well as duration between the 2 pelagic phases (Jonker and Bester 1998).

Annual mortality rate in northern elephant seals has been reported to be highest immediately after 1st reproduction irrespective of age (Reiter and Le Boeuf 1991). Other studies based on pinnipeds also have demonstrated costs of reproduction to both survival and future breeding (Beauplet et al. 2006; Hadley et al. 2007; Lunn et al. 1994). Such survival costs associated with reproduction are likely to be more apparent in a seasonal context.

Here we use seasonal mark–recapture data based on adult female southern elephant seals at Marion Island to meet the following objectives: to estimate the relative contribution of postbreeding and postmolting mortality in shaping the annual demographic schedule, to test whether reproductive experience affects future seasonal survival and breeding probability in southern elephant seals at Marion Island, to determine the temporal pattern (1986–1999) in postbreeding and postmolting seasonal survival, and to test whether postbreeding survival and postmolting survival of female southern elephant seals are correlated within an annual cycle.

MATERIALS AND METHODS

Study site.—Marion Island ($46^{\circ}54'S$, $37^{\circ}45'E$), 1 of 2 islands in the Prince Edward Islands archipelago, is located in

the subantarctic zone of the southern Indian Ocean, approximately 2,180 km southeast of Cape Town, South Africa. It is 290 km² in area with a coastline of approximately 72 km formed predominantly by cliff faces. Seals mainly haul out on easterly boulder and pebble beaches (Condy 1978). The closest land mass to the Prince Edward group is Ile aux Cochons of Iles Crozet, about 950 km to the east.

Data collection.—We tagged 3,270 (average: 252 annually, range: 198–343) recently weaned female southern elephant seal pups in each of their hind flippers between 1983 and 1995 on Marion Island, using uniquely numbered, color-coded Dal 008 Jumbotags (Dalton Supplies Ltd., Henley-on-Thames, United Kingdom; see Pistorius et al. [2000] for details). We searched for tagged seals on all the beaches that the seals use (40 beaches along a 51.9-km coastline) on the island every 7 days during the breeding season and every 10 days during the molting period each year from 1986 through 1999. We recorded the tag number and color combination of each tagged female observed during these surveys. The mark–recapture procedures were executed in a humane way and had ethics clearance from the Animal Use and Care Committee (AUCC) of the Faculty of Natural and Agricultural Sciences, University of Pretoria, under AUCC 040827-024, and followed guidelines approved by the American Society of Mammalogists (Gannon et al. 2007).

Data analyses.—Encounter-history matrices, which are required for capture–mark–recapture analyses, were constructed from the resighting data of parous females, treating the 1st sighting of a female during the breeding season as the initial release. Future survival of primiparous female southern elephant seals of different ages does not show significant variation (Pistorius et al. 2004), supporting the application of a state-dependent (rather than age-dependent) approach (Boyd 2000) to southern elephant seal demographics. We consequently did not consider age variation in our analyses. Multiple sightings during any given breeding or molting season were treated as a single sighting. The peak haul-out dates for adult females during the breeding and molting seasons are 15 October and 18 January, with mean duration of the haul-out being about 3.5 and 3 weeks, respectively (Bester and Wilkinson 1994; Condy 1978; Kirkman et al. 2003; Wilkinson 1992). Resighting data up to the year 1999 were used, which yielded 27 resighting occasions (13 breeding and 14 molting) for females breeding in 1986, effectively our 1st release. The software program MARK (G. White, Colorado State University, Fort Collins, Colorado; White and Burnham 1999), which is an application for the analysis of encounter-history matrices of marked individuals, was used to obtain maximum-likelihood estimates of seasonal survival and resighting probabilities of adult females. The software program provides parameter estimates under the Cormack–Jolly–Seber model (Cormack 1964; Jolly 1965; Seber 1965), but also under several models that appear as special cases of this model (Lebreton et al. 1992). The 2 fundamental parameters in these models are ϕ , the survival probability for all animals between the i th and $(i + 1)$ th encounter occasion ($i = 1, \dots, k - 1$); and p , the resighting probability for all animals in the i th encounter occasion ($i = 1, \dots, k$).

The survival probability incorporates both death and permanent emigration of individuals and is therefore usually referred to as apparent survival. Southern elephant seals in general, but particularly breeding females, show a strong site fidelity to their natal grounds (Hofmeyr 2001) and we consequently expect permanent emigration from our study site to be minimal.

We tested the fit of our global model to the data with the program RELEASE goodness-of-fit procedure (Burnham et al. 1987) implemented in program MARK to check whether the assumptions pertaining to the model were met (see Lebreton et al. 1992). When results of the test were significant, we corrected for extra-binomial variation in the data by a variance inflation factor, \hat{c} , which is the ratio of the chi-square goodness-of-fit test divided by the degrees of freedom (Lebreton et al. 1992). This variance inflation factor was used to adjust the deviance in the calculation of the Akaike's information criterion corrected for small sample size, and to adjust the standard errors of the estimates (Lebreton et al. 1992).

We considered a candidate set of 11 models with varying constraints on survival and resighting probability. Because we wanted to know whether primiparous females had lower seasonal survival (during the year after primiparity) than more-experienced females, we included models that separated their postbreeding and postmolting survival from that of more-experienced females. Models constraining survival probabilities to be equal for primiparous and multiparous females also were included for comparison. Likewise, to assess whether the future breeding probabilities of females were affected by reproductive experience we included models with distinct resighting probabilities for primiparous and experienced females and with these grouped together. A cost of primiparity to survival would be indicated by lowered postbreeding survival, postmolting survival, or both relative to more-experienced females. A cost to future reproduction would be indicated through a relatively low resighting probability the year after primiparity. Given the circumstantial evidence that the Marion Island population stabilized around 1994 (Pistorius et al. 2004), we also included models with both postbreeding and postmolting survival constrained to be constant before 1994 and from 1994 onward.

Akaike's information criterion was used for model selection according to the principle of parsimony (Anderson et al. 1994; Lebreton et al. 1993). Models with a $\Delta AIC_c \leq 2$ were considered to have substantial support from the data (Anderson and Burnham 1999).

Estimates of survival are largely dependent on the intervals between resighting events. In order to compare mortality risk per unit time between the 2 pelagic phases we standardized the duration for which survival was estimated, assuming constant survival during each phase. Postmolting survival (duration of 255 days) was estimated for a 62-day period (similar to the postbreeding interval) using the following formula:

$$\text{postmolting survival (62 days)} = (\text{postmolting survival})^{62/255}.$$

We corrected our survival estimates to compensate for tag loss in this study despite the very low loss rates reported for the population (see Pistorius et al. 2000).

TABLE 1.—The number of female southern elephant seals (*Mirounga leonina*) recorded breeding for the 1st time on Marion Island between 1986 and 1999.

Year	Age			Total
	3 years	4 years	5 years and older	
1986	11	0	0	11
1987	4	15	0	19
1988	11	17	9	37
1989	25	29	14	68
1990	17	44	27	88
1991	19	48	12	79
1992	29	41	31	101
1993	43	19	13	75
1994	29	24	6	59
1995	37	37	4	78
1996	30	27	11	68
1997	24	33	9	66
1998	0	4	3	7
1999	34	36	35	105
Total	313	374	174	861

RESULTS

Of the 3,270 female pups that were tagged on Marion Island, three hundred thirteen 3-year-old females, three hundred seventy-four 4-year-old females, and 174 older females were seen breeding at least once on Marion Island during the study period, numbering 861 individuals in total (Table 1).

The goodness-of-fit test of the resighting data gathered from these females indicated that our data showed some deviations from the Cormack–Jolly–Seber model assumptions ($\chi^2 = 72.653$, $d.f. = 52$, $P = 0.031$). For the rest of the analyses we consequently used a \hat{c} of 1.397 to compensate for the limited extra-binomial variation in the data.

None of the models without the “primiparity effect” in postbreeding survival received noticeable support (the best without the effect was model 5: $\Delta AIC_c = 30.63$, model weight $[w] = 0$; Table 2). However, postmolting survival did not differ according to breeding experience (model 6 versus 8). There was no support for a difference in resighting probability (in surviving females) as an index of breeding probability based on experience (model 8 versus 10). When comparing full time-dependent with constant-survival models we found strong support for a year effect in postbreeding survival of primiparous females (model 2 versus 3) but not postbreeding survival of experienced females and postmolting survival (model 3 versus 6). The most-parsimonious model had postbreeding and postmolting survival constrained before and after 1994, and was far superior to any of the other candidate models. The ΔAIC_c between this model and the next best model was 8.75 (Table 2). The model incorporated resighting probability as time-dependent during both the terrestrial phases (Table 2).

Over the study period postbreeding survival for primiparous females was 0.830 (95% confidence interval [95% CI] 0.798–0.858) and for more-experienced females was 0.912 (95% CI 0.890–0.934; model 3). Therefore, there was an 8.2% lower postbreeding survival in primiparous females as a survival cost

TABLE 2.—Akaike information criterion (AIC_c), difference in AIC_c in relation to most parsimonious model (ΔAIC_c), Akaike weight (*w*), number of parameters (np), and deviance (Dev) for the full set of candidate survival (ϕ) and resighting (p) models.

Model ^a	AIC _c	ΔAIC _c	<i>w</i>	np	Dev
(1) ϕ _{PB1&2-94} : PM(1=2)-94, P _T	6,454.49	0.00	0.984	33	1,979.38
(2) ϕ _{PB1T} : PB2C: PM(1=2)C, P _T	6,463.24	8.75	0.012	43	1,967.69
(3) ϕ _{PB1&2C} : PM(1=2)C, P _T	6,465.56	11.08	0.004	30	1,996.56
(4) ϕ _{PB1T} : PB2C: PM(1=2)T, P _T	6,476.77	22.29	0.000	55	1,956.56
(5) ϕ _{PB(1=2)C} : PM(1=2)C, P _T	6,485.11	30.63	0.000	29	2,018.15
(6) ϕ _{PB1&2T} : PM(1=2)T, P _T	6,489.87	35.39	0.000	67	1,944.83
(7) ϕ _{PB1C} : PB2T: PM(1=2)T, P _T	6,490.30	35.82	0.000	54	1,972.15
(8) ϕ _{PB1&2T} : PM1&2T, P _T (B1=B2)	6,495.88	41.40	0.000	79	1,925.83
(9) ϕ _{PB(1=2)T} : PM(1=2)T, P _T	6,502.19	47.71	0.000	53	1,986.10
(10) ϕ _{PB1&2T} : PM1&2T, PB1≠B2T	6,507.68	53.20	0.000	92	1,910.36
(11) ϕ _{PB(1=2)T} : PM(1=2)T, PMC:BT	6,521.16	66.68	0.000	41	2,029.71

^a PB = postbreeding; PM = postmolting; 1 refers to survival the year following primiparity and 2 refers to subsequent survival; T = time-dependent; C = constant, 94 is used for 2-stage models where survival was constrained to be constant before 1994 and from 1994 onward; B1 = breeding resight probability 1 year following primiparity; B2 = breeding resight probability 2 years and more following primiparity; MC = molting resight probability constant; BT = breeding resight probability time-dependent.

associated with primiparity. Postmolting survival over the study period was 0.847 (95% CI 0.825–0.866; model 2). Over the study period, the resighting probability for females during the breeding season after primiparity was 0.715 (95% CI 0.673–0.753) compared to 0.706 (95% CI 0.675–0.737) for more-experienced females.

According to the 2-stage model, postbreeding survival of primiparous females and postmolting survival increased by 8.1% and 5.5%, respectively, whereas postbreeding survival of experienced females declined slightly by 1.7% (Table 3). The fitness cost associated with primiparity (in terms of low postbreeding survival relative to more-experienced females) declined from 14.1% over the 1st part of the study to 4.3% over the 2nd part, demonstrating the dynamic state of this cost.

As well as being less variable, postbreeding survival of experienced females was between 5.1% and 12.3% higher than postmolting survival (Table 3). Mortality during the latter pelagic phase is therefore the more important factor in determining annual survival in adult females. Nonetheless, per unit time, and assuming constant survival within each pelagic phase, postbreeding survival was much lower than postmolting survival (mean of 0.912 compared to 0.960 over a 62-day period).

TABLE 3.—Postbreeding (about 62 days in duration) and postmolting (about 255 days in duration) survival of female southern elephant seals (*Mirounga leonina*) at Marion Island derived from a 2-stage model (model 1) constraining survival before and from 1994 onward.

Period ^a	Survival (ϕ)	SE (ϕ)	95% CI	
1986–1993				
Postbreeding R1	0.799	0.021	0.754	0.837
Postbreeding R2	0.940	0.019	0.888	0.969
Postmolting	0.817	0.016	0.783	0.846
1994–1999				
Postbreeding R1	0.880	0.021	0.831	0.916
Postbreeding R2	0.923	0.015	0.885	0.948
Postmolting	0.872	0.013	0.843	0.896

^a R1 refers to survival after 1st breeding and R2 refers to survival after subsequent breeding events.

Over the study period the resighting probability of females during the breeding season was 0.708 (95% CI 0.681–0.734) and ranged between 0.127 (95% CI 0.089–0.179), which was a breeding season with exceptionally low search effort, and 0.902 (95% CI 0.850–0.937). During the molting season it was 0.695 (95% CI 0.666–0.723) and ranged between 0.565 (95% CI 0.494–0.635) and 0.933 (95% CI 0.654–0.990).

Based on the full time-dependent model (without a primiparity effect), we found no correlation between postbreeding and postmolting survival within an annual cycle over our study period (postbreeding with subsequent postmolting survival: Pearson correlation: -0.415 , $df = 13$, $P = 0.158$; postmolting with subsequent postbreeding survival: Pearson correlation: 0.005 , $df = 12$, $P = 0.987$).

DISCUSSION

Results from this study provide strong evidence for a reproductive cost associated with 1st breeding in female southern elephant seals. Postbreeding survival of 1st-time breeders was significantly lower than postbreeding survival of more-experienced females, and the difference varied according to population status. This supports the notion that reproductive costs are dependent on factors such as population density and environmental conditions, both of which could influence food availability (Hadley et al. 2007; Tavecchia et al. 2005). It has been speculated that an increase in per capita prey availability contributed to the stability of the Marion Island population during the 2nd half of this study period after a long-term decline (Pistorius et al. 2004). In general, female southern elephant seals give birth for the 1st time while they are still undergoing somatic growth (Laws 1956a, 1956b). Therefore, it is reasonable to expect these young females to have relatively large energetic requirements, and to be more affected by food availability than older females. The increase in the postbreeding survival rate of 1st-time breeders and corresponding reduction in cost of 1st breeding over the duration of the study period accords with the notion that per capita prey availability has increased in recent years.

Examination of our data showed some departures from the Cormack–Jolly–Seber model assumptions based on the goodness-of-fit test. This suggests some heterogeneity in survival or resighting probability or both within groups of individuals last released on the same sampling occasion. The “primiparity” effect in survival as well as possible heterogeneity in resighting probability during the molting season could have been responsible for the above. Adult females are highly philopatric during the breeding season and resighting probability during this terrestrial phase is likely to have been homogenous among individuals (Hofmeyr 2001).

Primiparous females had the same future breeding probabilities as more-experienced breeders, counter to what has been reported for northern elephant seals (Reiter and Le Boeuf 1991) and Weddel seals (Hadley et al. 2007). Irrespective of age (Pistorius et al. 2004) or experience (this study), adult female southern elephant seals therefore breed consistently after reproductive maturity is attained. This argues against the existence of different life history strategies in southern elephant seals (Stearns 1992).

Although postbreeding survival of experienced females was higher than postmolting survival, when considering the duration of the 2 pelagic phases it is clear that postbreeding survival was much lower per unit time. Southern elephant seals have large energy requirements (Boyd et al. 1994) and their existence depends on the availability and consumption of considerable quantities of fish and squid (Hindell et al. 2003; Laws 1977). The fact that these seals fast twice annually for long periods when they are restricted to land means that this demand is not uniform over time. During a breeding season, a southern elephant seal female may lose >50% of her body energy reserves (Carlini et al. 2004, 2005; Fedak et al. 1996). The limited time to build up body condition during the 2-month postbreeding pelagic phase may render an adult female equally or even more energy-deprived at the close of the molting period (Boyd et al. 1993; Carlini et al. 2005). These animals are consequently expected to be under much pressure to find and sequester the considerable prey biomass needed to ensure survival soon after the fasting periods when their energy reserves are low. We therefore suspect a critical period after each of the terrestrial phases, in which adult females urgently need to locate adequate prey resources to regain body condition. Seasonal survival could therefore largely be a function of survival during these critical periods, with the total duration of the pelagic phases being of lesser importance.

Although the foraging ranges of several postmolting and postbreeding adult females from Marion Island have been recorded (Jonker and Bester 1998), sample sizes have not been large enough to detect major differences between the 2 pelagic phases. On average, adult female southern elephant seals at Marion Island forage up to about 1,400 km from the island during the postbreeding phase and over double that distance during the postmolting phase (Bester 1989; Jonker and Bester 1998). During the postbreeding phase at Marion Island, females tend to make directed outbound and inbound journeys to and from well-circumscribed foraging grounds located largely within interfrontal zones. In contrast, adult postmolting

females seem to display more opportunistic, patchy foraging, meandering between different foraging grounds (Jonker and Bester 1998), although females have been reported to be loyal to foraging grounds elsewhere (Bradshaw et al. 2004). These differences in the Marion Island population may be a result of varying time constraints between the 2 pelagic phases (Jonker and Bester 1998), although only a much larger sample of tracking records for adult females may elucidate their spatial foraging patterns.

Pistorius et al. (2004) recently reported a 6.2% increase in annual survival of adult females associated with the stabilization of the population. Survival of adult females was therefore inferred to be the most important life history variable influencing population growth in southern elephant seals at Marion Island, as has been reported in several other demographic studies on mammals (e.g., Eberhardt 1985; Gaillard et al. 2000; Toigo et al. 1997; Walsh et al. 1995), but which may not apply to all populations of southern elephant seals (McMahon et al. 2005b). Our study suggests that observed changes in population growth in southern elephant seals at Marion Island (Pistorius et al. 2004) were primarily due to an increase in postbreeding survival of primiparous females and in postmolting survival. Interestingly, postbreeding survival of experienced females did not show much variation during the study period. This would imply that food limitation, or any other mechanism driving population change in this population, has a greater effect on postmolting than postbreeding survival (of experienced females). Worth noting is that after the molting haul-out, female southern elephant seals at South Georgia have been reported to be more energy-deprived than after the breeding season (Boyd et al. 1993). Females may therefore be more vulnerable to and influenced by food limitation during this phase.

It seems unlikely that predation by killer whales (*Orcinus orca*), which could potentially impact small populations of southern elephant seals (Guinet 1992; McMahon et al. 2003; Pistorius et al. 2002), contributed to the observed changes in survival. If predation had affected survival, we would have expected similar shifts in survival of primiparous and older females. It is worth noting that the mean mass of pups at weaning at Marion Island was significantly higher in the period 1993–1998 relative to previous years (Burton et al. 1997; McMahon et al. 2003). It has been argued that this increase in mass at weaning was either due to an increase in the quality, quantity, or both of prey resources available to adult females (McMahon et al. 2003). Alternatively, it was speculated that survival of adult females might have increased, resulting in a higher proportion of older (larger) females in the age distribution, producing heavier pups (Burton et al. 1997). Our study suggests that survival of primiparous females increased significantly in recent years and this would have resulted in a shift toward an older age distribution. On the other hand, the increased presence of primiparous females in the younger age classes (McMahon et al. 2003; Pistorius et al. 2001) would have had an opposing effect. Nevertheless, the increase in mass of pups at weaning, whatever the mechanism, is a likely response to an increase in availability of food to adult females that allows them to wean heavier pups.

We found no correlation between the 2 constituents of annual survival that we studied and this underscores the importance of an intra-annual evaluation of the demographic schedule in southern elephant seals. This is particularly true when the aim is to understand growth and regulation of a population, because critical periods and causes of mortality can more readily be identified. Different mortality factors could be operative during the 2 phases, which could account for postbreeding and postmolting survival varying independently over time. However, a more likely explanation is because the distribution of biological resources within the Southern Ocean is highly variable, unpredictable, and patchy (Constable et al. 2003; Field et al. 2005). Our results suggest that these characteristics hold true for the prey resources of southern elephant seals.

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