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Weaning mass and the future survival of juvenile southern elephant seals, *Mirounga leonina*, at Macquarie Island

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Abstract: Seals that survived their first year were on average 2% and 4% heavier at birth and at weaning than the "non-survivors". First year survival rates calculated for weaners over 135 kg weaning masses showed these weaners had higher survival rates than those less than 95 kg at weaning (71.55% and 54.15% respectively). Heavy weaners had greater fat reserves than light weaners and gained relatively more mass during lactation. Size, and therefore condition at weaning, influences first year survival.

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Introduction

The general model for self-regulation of populations in long-lived species suggests that regulation is driven by variations in juvenile mortality, age at first breeding, and reproduction rates of adult females (Eberhardt 1977). The simplest and most direct mechanism leading to such variations is the limitation of an essential resource, for example food (Eberhardt 1977). Thus reduced food availability leads to increased juvenile mortality, lower growth rates of survivors, delayed maturity, increased age at first breeding, and reduced reproductive success (Eberhardt 1977, Fairbanks & McGuire 1995).

Female mammals usually protect offspring and only in a few species do males play any role in the care of offspring (Clutton-Brock *et al.* 1985, Oftedal *et al.* 1987). Parental care in the southern elephant seals is exclusively the responsibility of the female and occurs during the 23 days of lactation when females are ashore during the breeding season (Laws 1953, McCann 1980, McMahon *et al.* 1997). Because female elephant seals fast while ashore, maternal expenditure is limited to the amount of reserves brought ashore prior to parturition (Laws 1953, Fedak & Anderson 1982, Costa *et al.* 1986, Kovacs & Lavigne 1986, Fedak *et al.* 1994, Arnbom 1994, Fedak *et al.* 1996, Trillmich 1996, Arnbom *et al.* 1997, Hindell & Slip 1997). Southern elephant seal females are thus excellent subjects for examining the effect of pre-partum resource acquisition on offspring size and growth (Fedak *et al.* 1996, Carlini *et al.* 1997, Arnbom *et al.* 1997). Numerous studies have considered maternal expenditure through measurements of offspring size (e.g. Trillmich 1996), but few have examined the relationship between maternal expenditure and future survival of progeny (Suttie & Hamilton 1983, Clutton-Brock 1991, Clutton-Brock & Godfray 1991, Le Boeuf *et al.* 1994, Trillmich 1996). In male northern fur seal pups (*Callorhinus ursinus*) heavier seals were more likely to survive the first year than smaller cohort members (Baker & Fowler 1992). There is no evidence, in either northern or southern elephant seals, that condition at weaning affects future survival (Wilkinson & Bester 1990, Arnbom *et al.* 1993, Le Boeuf *et al.* 1994) despite the more than two fold variation in weaning mass.

Elephant seals produce large weaned pups with large blubber stores (mean weaning mass at Macquarie Island is 117 kg (McMahon *et al.* 1997)) accumulated during lactation (Arnbom *et al.* 1993, Fedak *et al.* 1996, Boness & Bowen 1996). These fat reserves act as excellent insulators and crucial fuel reserves once pups are weaned (Bryden 1968, 1969, Hindell *et al.* 1994). Thus, weaned seals with large fat reserves should have some selective advantage (Bryden 1969).

This study aimed to describe the relationships between weaning mass and condition (fat reserves) at weaning to first year survival of southern elephant seals at Macquarie Island.

Methods

The study was conducted at Macquarie Island (54°37'S, 158°53'E) between 1993 and 1996 as part of a long-term demographic study of the southern elephant seal. Throughout the breeding season (September–November) of each year, beach and tussock areas along the isthmus study area (ISA) (Carrick *et al.* 1962) were searched daily for new born and weaned seals. Newborn pups and weaners were temporally marked with paint so as not to confuse them with animals that had already been born or weaned. One thousand pups were weighed within 24 hours of being born, marked with two plastic flipper tags (Jumbo® Rototags, Dalton Supplies Ltd, Henley-on-Thames, UK) and returned to their mothers. These newborn pups were weighed in a canvas bag attached to a 200 kg Salter® spring balance suspended from an aluminium pole. Weaned pups that had been weighed at birth (weaning occurred when pups had left their natal harems regardless of whether their mothers were present or not) were captured on the day of weaning, weighed and paint marked. Weaned pups were weighed in a net sling using a rope pulley system attached to an aluminium tripod and a 300 kg Salter® spring balance. Weaners were permanently marked three weeks after weaning by hot iron brands on both flanks (McMahon *et al.* 1997).

Searches for branded seals were conducted each day on the isthmus; every ten days around the top third of the island and once a month around the whole island (McMahon *et al.* 1999).

Birth and weaning masses from the 1993 cohort of seals known to be alive at age one were compared to those recorded that did not survive their first year. Seals were taken to have survived their first year if resighted up until April 1998 while seals were assumed dead if never seen before April 1998. Survival estimates were based on two independently validated methods, MARK (White & Burnham 1999) and a specifically designed survival model for southern elephant seals (McMahon *et al.* 1999).

To investigate further the effect of post-partum maternal expenditure on first year survival, we calculated the survival rates of heavy and light weaners from the 1993 cohort. Heavy weaners were defined as seals with wean masses greater than 135 kg and light weaners as seals weighing less than 95 kg (after Hindell *et al.* 1999). Seals were grouped into these classes to represent a heavy and a light quartile.

The energetic advantage conferred by an additional 5 kg mass at weaning was calculated from:

$$M_{\text{depature}} = M_{\text{wean}} * 0.68 \text{ (kg) (Arnbom } et\ al. \text{ 1993)}$$

so that $M_{\text{ddeparture}} = M_{\text{dwean}} * 0.68$ (kg)

where M_{dwean} = The difference in weaned mass between the survivors and "non-survivors".

therefore $E_{\text{ddeparture}} = M_{\text{ddeparture}} * (\text{Proportion fat} * E_{\text{fat}} + \text{Proportion lean} * E_{\text{lean}} * H)$

where $E_{\text{ddeparture}}$ is energy difference at departure, E_{fat} is energy density of fat, E_{lean} is energy density of protein and H is hydration constant.

The proportion of body mass represented by fat in weaned southern elephant seal pups at Macquarie Island prior to departure was 42% (Bryden 1970). The hydration constant of lean body mass in seal pups is higher than in adults and has been measured at 74.7% in Antarctic fur seal pups (Arnould *et al.* 1996), 73.8% in harp seals (Worthy & Lavigne 1983, Iverson *et al.* 1993) and 73.6% in ringed seals (Lydersen *et al.* 1992). Since there are no data available for southern elephant seals we assumed a hydration value of lean body mass to be 74%. Standard values for the energy density of fat and protein were taken as 39.5 MJ kg^{-1} and 23.5 MJ kg^{-1} respectively (Schmidt-Nielsen 1983).

Table I. The mean birth masses of all, male and female southern elephant seal pups at Macquarie Island in 1993.

	Mass of survivors (kg)	Mass of non-survivors (kg)	Sample size
All pups	41.12 ± 6.03	40.12 ± 6.03	1362
Male pups	43.52 ± 5.68	42.08 ± 6.08	700
Female pups	38.81 ± 5.26	37.97 ± 5.20	662

Data were compared statistically using χ^2 tests and *t*-tests. Significance was set at $P < 0.05$, and mean values are presented with one standard deviation (± s d) (Sokal & Rohlf 1981, Zar 1984).

Results

Pre-partum maternal investment and first year survival

The mean birth mass of all pups (Table I) that did not survive their first year was significantly less than that of the animals that did survive their first year (t = 366.34, df = 1360, $P < 0.005$). The mean birth masses of female and male elephant seals surviving to age one were different from the mean of the seals assumed not to have survived (t_{female} = 306.33, df = 660, $P < 0.05$, t_{male} = 253.71, df = 699, $P < 0.05$).

Post-partum maternal investment and first year survival

Southern elephant seal pups (sexes combined) which had survived the first year weighed 5 kg more (t = -27.48, df = 1365, $P < 0.05$) at weaning than "non-survivors" (123.53 kg ± 24.58 kg, n = 314 and 118.10 kg ± 25.96 kg, n = 1052, respectively). Similar differences were found when the sexes were examined separately (for males: t = -21.70, df = 701, $P < 0.05$ and for females: t = 306.33, df = 660, $P < 0.05$ respectively). Females that survived their first year had a mean weaning mass of 120.33 kg (± 24.81, n = 160), 5 kg heavier than the mean mass for the females calculated not to have survived (115.46 kg ± 24.63, n = 504). Males surviving the first year weighed almost 6 kg more at weaning than the "non-survivors" did at weaning (126.86 kg ± 23.96, n = 154, and 120.53 kg ± 26.93, n = 548 respectively).

Survival rates

Survival estimates calculated using two independent methods are presented in Table II, showing no differences in the estimates of survival. For heavy weaners (≥135 kg, n = 148) a first year survival rate of 71.55 % was calculated while the rate for light (≤ 95 kg, n = 112) was only 54.15%. To

Table II. A comparison of first year survival estimates of southern elephant seals at Macquarie Island using two independent methods (McMahon *et al.* 1999 and White & Burnham 1999).

	Heavy quartile (≥ 135 kg)	Light quartile (≤ 95 kg)
First year survival after McMahon *et al.* (1999)	71.55%	54.15%
First year survival after White & Burnham (1999)	71.20%	53.95%

compensate for a sex bias in survival, deviance from unity was calculated. The number of males and females in each of the treatments was the same (χ^2= 1.55, df = 1, P = 0.2136).

Energy expenditure

$E_{ddeparture}$ = 5kg * 0.68*((0.42*39.5) + (0.58*23.5*0.74)) = 90.7 MJ

SMR (Kleiber) = 0.293 W0.75 MJ day^{-1} (Lavigne *et al.* 1986)

DMR = SMR * 0.8 (Thorson & Le Boeuf 1994)

So for a 123 kg seal DMR = 8.66 MJ day^{-1}, and for a 118 kg seal DMR = 8.39 MJ day^{-1}.

Thus on average the 90.7 MJ advantage translates to an extra ten days at sea or an extra 6 days ashore (SMR * 1.5 = haulout cost).

The relative mass gain was for light (≤ 95 kg) and heavy (≥ 135 kg) weaners was calculated. Light weaners gained 0.056 kg day^{-1} kg seal^{-1} while heavy weaners gained 0.098 kg day^{-1} kg seal^{-1} (t = -23.244, df = 475, P < 0.01). Furthermore, wean mass alone accounted for 48% of the variation observed in relative mass gain between birth and weaning (Fig. 1).

Discussion

Most phocids give birth to a single pup that is exclusively reared by the mother (Spotte 1982). The energy requirements of the foetus are minimal when compared to the requirements needed to raise a pup to weaning (Oftedal *et al.* 1987, Anderson & Fedak 1987). The nursing period in phocid seals is characterized by its short duration, its efficiency of energy transfer and its abrupt termination (Oftedal *et al.* 1987, Trillmich 1996, Arnbom *et al.* 1997). Female elephant seals derive all the energy required to support lactation from stored energy deposits. Resource allocation to the pup therefore depends on the availability of food to the mother in the remote feeding grounds, the success with which she has procured and stored resources and the transfer of these reserves to the pup (Boyd & McCann 1989). It then follows that those reproductive stages that place the highest demands on female reserves will be most affected by stochastic variations in food supplies (Boyd & McCann 1989), in this case lactation. Variations in wean mass observed in elephant seals and the associated differences in survivorship therefore represent measures of female foraging success and resource availability.

Among pinnipeds, small offspring often suffer greater mortality (Coulson & Hickling 1964, Baker & Fowler 1992), suggesting that larger (heavier) offspring should be over-represented in a sample of surviving animals. Baker & Fowler (1992) have shown that pre-partum expenditure by northern fur seals mothers is positively related to first year survival but do not comment on the effect of post-partum expenditure. There is evidence that mass at weaning (post-partum maternal expenditure) reflects the extent to which offspring are able to cope and survive within the adult niche (Millar 1977). Furthermore, the cumulative amount of energy parents expend on their offspring during the breeding episode has been shown to determine the future survival of young (Lack 1968, Ricklefs 1968, Case 1978). In mountain baboons increased maternal expenditure increased infant survival (Lycett *et al.* 1998).

However, Le Boeuf *et al.* (1994) in a study of 734 northern elephant seal weaners showed that mass at weaning was not related to survival in the first and second year. Our study of 970 weaners from 1993 differs from that of Le Boeuf *et al.* (1994) and showed that heavier weaned southern elephant seal pups were indeed more likely to survive their first year. The heavy quartile seals gained relatively more mass than their light quartile counterparts. Because mass gain during lactation is largely a gain in fat (Bryden 1969), heavy weaners must have more fat than light weaners (Hindell *et al.* 1999, this study). Clearly, post-partum maternal expenditure as measured by the size of weaners and first year survival are associated. Since mass gain during lactation is primarily gain in fat

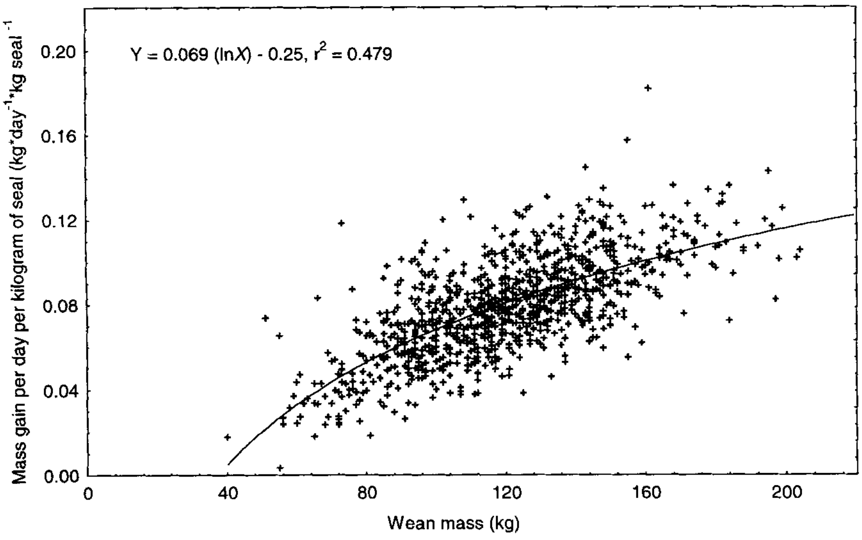

Fig. 1. The asymptotic relationship between relative mass gain of heavy and light weaners at Macquarie Island, showing greater mass gain per unit seal mass for heavy weaners.

(Bryden 1968, Hindell *et al.* 1994) representing 3% of body mass at birth and 41% at weaning (Hindell *et al.* 1994), it follows that heavy weaners were fatter than light weaners and therefore fat weaners had higher survival prospects than light weaners. By virtue of their superior fat reserves heavier elephant seal weaners may have an advantage over lighter conspecifics by being able to spend more time (10 days on average) searching for food when they left on their first foraging trip.

Survival of heavy and light weaners were calculated using two independently validated methods (McMahon *et al.* 1999, White & Burnham 1999) from resight data collected at Macquarie Island up until April 1998. Animals were assumed to have survived if seen during this period and to have died if not. It can be argued that these assumptions were flawed. However, the estimates of survival were conservative, because as more resights were made survival for both groups would increase but at the same rate; thus the differences in survival would become pronounced over time as more animals were resighted and found to have survived.

Differences in resource availability and the success with which these accumulated resources are transferred to offspring, independent of genetically programmed variability in size (Slade *et al.* 1998), are crucial determinants of population growth in elephant seal colonies. Because mean weaning mass is an indicator of resource availability population growth seems to be at least partially restricted by the availability of resources to seals because pup size and survival probabilities are related.

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