

Georg H. Engelhard · John van den Hoff
Martijn Broekman · Antonie N. J. Baarspul · Iain Field
Harry R. Burton · Peter J. H. Reijnders

Mass of weaned elephant seal pups in areas of low and high human presence

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Abstract On sub-Antarctic Macquarie Island, we examined pup weaning mass of southern elephant seals in relation to human presence. Pup weaning mass was previously found to be positively associated with 1st-year survivorship. Weaned pups were weighed in a remote area, Middle Beach, and in an area of relatively high human presence, Isthmus East. The areas were reasonably similar in beach topography, wind and surf conditions, numbers of seals present per kilometre of coastline, and numbers of males and females present in harems. For a sub-sample of measured pups, data on the respective maternal size were collected using photogrammetry. Both male and female weaned pups on Middle Beach were significantly heavier than those on Isthmus East. Estimated length of mothers was significantly higher on Middle Beach. In proportion to their own size, mothers in both areas produced weaners of similar mass, indicating no direct effect of human disturbance on the efficiency of lactation. It remained unclear whether the area differences in maternal and pup size were due to natural or human-related factors.

Introduction

Several studies report direct behavioural responses of marine mammals to human presence (e.g. Salter 1979;

Brasseur 1993; Reijnders et al. 1993; Born et al. 1999; Suryan and Harvey 1999). However, it is complicated to assess the long-term impact of disturbance on reproduction and survival chances, and hence at the population level. In long-lived species such as marine mammals, examining human impact at the population level necessarily implies collection of data over a (very) long time span. Thus the implementation of the appropriate conservation measures may also take a long time. Therefore it is of special importance to quickly detect those measurable impacts that are likely to affect fitness.

Antarctica and the sub-Antarctic attract growing numbers of visitors. Scientific, commercial and tourist activities are increasing, in particular near pinniped and penguin breeding sites. Thus there is the potential for impact of disturbance on breeding success and survival in populations of these species. Human disturbance was found to affect Antarctic penguins (e.g. Wilson et al. 1991; Culik and Wilson 1995; Giese 1996, 1998; Regel and Pütz 1997; Copley and Shears 1999). However, little is known on effects of disturbance on (sub-)Antarctic pinnipeds (e.g. Wilkinson and Bester 1988). This is remarkable, as several of these species are relatively well studied and currently the subject of considerable scientific investigations. Pinnipeds are major top predators in Southern Ocean ecosystems, and studies on the impact of humans on their breeding biology might contribute to conservation. Moreover, such studies may also support the assessment of impact of human activity on pinniped populations elsewhere in the world (Trites 1991; Reijnders et al. 1993, 1997).

For the southern elephant seal, *Mirounga leonina* (L.), we examine whether human disturbance can be detected through an easily measurable parameter related to both reproduction and survival: mass of juveniles at weaning. Pinniped females usually nurse a single young per season, and pup weaning mass can be interpreted as an index of maternal investment (Costa 1991; Arnbom et al. 1997). Most importantly, mass of juveniles at nutritional independence is likely to influence their survival (northern fur seals, *Callorhinus ursinus* (L.): Baker and

G. H. Engelhard (✉) · M. Broekman · A. N. J. Baarspul
Centre for Ecological and Evolutionary Studies,
Zoological Laboratory, Groningen University,
P.O. Box 14, 9750 AA Haren, The Netherlands
e-mail: G.H.Engelhard@biol.rug.nl
Tel.: +31-50-3637727; Fax: +31-50-3635205

J. van den Hoff · I. Field · H. R. Burton
Australian Antarctic Division, Channel Highway,
Kingston 7050, Tasmania, Australia

G. H. Engelhard · P. J. H. Reijnders
Alterra Institute, Marine and Coastal Zone Research Team,
P.O. Box 167, 1790 AD Den Burg, The Netherlands

Fowler 1992; Hawaiian monk seals, *Monachus schauinslandi* Matschie: Craig and Ragen 1999), although in an increasing northern elephant seal [*Mirounga angustirostris* (Gill)] population, no evidence was found that pup weaning mass was related to 1st and 2nd year survivorship (Le Boeuf et al. 1994). However, for the species and population examined in the present paper, previous work has shown that heavier weaned southern elephant seal pups were indeed more likely to survive their 1st year than their light counterparts; 1st year survival of heavy and light quartile weaners was estimated around 71% and 54%, respectively (McMahon et al. 2000). In addition, juvenile size is likely to affect adult size, and larger male and female seals appear to have higher reproductive success (females: Reiter et al. 1981; Arnborn et al. 1994; Pomeroy et al. 1999; males: McCann 1981; Anderson and Fedak 1985; Bartsh et al. 1992; Haley et al. 1994). Because of these long-term implications, we believe that pup weaning mass is an interesting parameter to study in relation to human activity.

Southern elephant seals forage widely in the Southern Ocean and reproduce on traditional breeding locations; most of these are on sub-Antarctic islands, and one is in temperate Patagonia (Laws 1994). During the breeding season (September/November), female elephant seals aggregate on beaches, forming harems that are competed for by males (Laws 1956). Pregnant females give birth to a single pup about 4 days after arrival at the beach and nurse it for about 23 days, whereafter it is weaned abruptly (McCann et al. 1989; Arnborn et al. 1997; McMahon et al. 1997). Throughout the nursing period, mothers neither feed nor drink, while their pups rapidly accumulate fat reserves through milk intake. At weaning, pups are left by their mothers and are nutritionally independent. Male pups have, on average, higher birth and weaning masses than female pups, and in both sexes there is much variation in weaning mass; most of this is related to variation in the mass of mothers at parturition (Arnborn et al. 1993, 1997; Fedak et al. 1996; Carlini et al. 1997; McMahon et al. 1997).

Most populations of southern elephant seals have been harvested commercially in the past, but all have been protected for several decades. In spite of this, populations in the Southern Pacific and Southern Indian Oceans either have since been, or currently are, in decline (Hindell and Burton 1987; Hindell et al. 1994; Guinet et al. 1999; McMahon et al. 1999; Pistorius et al. 1999). The causes of this are not fully understood, but are most likely related to unfavourable conditions in the ocean environment, probably in combination with equilibration processes after the cessation of sealing, and potentially other local factors that also regulate populations (Hindell 1991; Hindell et al. 1994). Is disturbance by humans among these additional factors? To our knowledge, in the past only a single study on disturbance in elephant seals has been carried out. Within the declining breeding population of Marion Island, Wilkinson and Bester (1988) found similar rates of decrease

in the numbers of seals over a 10-year period, regardless of local differences in onshore human activity. In addition, the authors reported that the rates of decline in elephant seal numbers were not different among islands in the Southern Ocean where there had either been permanent research stations or far less frequent human visitation over the past decades. However, disturbance in the earlier stages may not directly affect the total numbers of animals, but rather their condition. Indirect impacts on reproduction and survival as a result of lowered condition may ultimately be detectable by counts, but may not necessarily be identified as a result of disturbance per se.

We hypothesized that during the breeding season of southern elephant seals, human disturbance could have negative impacts on the efficiency of energy transfer from lactating females to pups, thereby affecting mass of pups at weaning. This would have consequences for their survivorship and/or future reproductive success (McMahon et al. 2000). This was examined by comparing a sample of elephant seal pups nursed in two study areas that were similar in geography but different in the levels of human presence. We tested if pup weaning mass was lower in the area of higher human activity. As elephant seal weaning mass is highly dependent upon maternal mass at onset of lactation (Arnborn et al. 1997), we collected data on maternal size for a sub-sample of mother-pup pairs using photogrammetry, and examined the relative effects of maternal size and study area.

Materials and methods

Location

During September/November 1998, fieldwork was carried out on sub-Antarctic Macquarie Island (54°30'S, 158°57'E), which has the third-largest breeding population of southern elephant seals in the world (Laws 1994). Since 1948, the Australian Antarctic Division has run a permanent research station on the island, situated at the Isthmus; for most of this period the elephant seal population has been monitored (Carrick and Ingham 1962; Carrick et al. 1962a; Hindell and Burton 1987; Hindell et al. 1994; McMahon et al. 1999). Traditionally, most human activities (scientific, maintenance, sight-seeing, other) have been on the Isthmus near the station, which continuously accommodates around 10–15 persons in winter and around 30–40 persons in summer; other areas of the island receive relatively infrequent human visitation.

Area of high human presence

The Isthmus was chosen as representing an area with a relatively high level of human presence. Here, elephant seal harems are formed on beaches adjacent to the research station, which are within the official "Station Limits" directly accessible to expedition members and vehicles at the base. Harems on the east and west coasts of the Isthmus were visited each day of the 1998 pupping season by four to five persons in order to continue long-term monitoring studies of the population. Elephant seal pups were weighed and marked with plastic flipper tags within 24 h of birth, a procedure that implied some physical handling and a brief separation from the mother (approximately 1–3 min if carried out routinely). Tagged pups were re-weighed at weaning. Methods of weighing and tagging were similar to those described by McMahon

et al. (1997). Weather and surf conditions, as well as characteristics of beach topography, were rather different between the wind-swept west coast and the more sheltered east coast of the island (Streten 1988; Selkirk et al. 1990). Furthermore, harem size tended to be far more variable on the west side (Australian Antarctic Division, unpublished data; Carrick et al. 1962b). For these reasons, only data for the east coast of the Isthmus were used in the present study; hereafter this area is referred to as Isthmus East. Its shingle beaches were 20–40 m wide at locations where elephant seal harems formed. Locally, there were sites of regular strong winds within the area. In total, 459 day-old pups were weighed on Isthmus East (50% of all pups in the area) during 28 days; on average, 16 animals were weighed each day (median 17.5, range 0–32). Of these animals, 429 were re-weighed at weaning.

Area of low human presence

Middle Beach was chosen as the control area with low level of human presence. The site is also on the east coast, 2 km south of the station but separated from that area by a 1-km zone of steep rocky shore at the foot of a scree slope. Middle Beach is reasonably similar to Isthmus East in beach topography, with shingle beaches 15–40 m wide at sites where elephant seal harems formed. Wind and surf conditions were also comparable; during the study period, we observed similar wind forces (Beaufort scale) in the two areas [for both sites, median 3; Mann-Whitney ($N = 127$), $U = -0.869$, $P = 0.385$]. Three harems in the control area were, as in Isthmus East, visited each day of the pupping season; however, this was by only up to three persons on foot. All other human presence was excluded during the observation period. No day-old pups were weighed or tagged at Middle Beach. For individual recognition during behavioural studies (G.H. Engelhard, unpublished data), 24 study pups (4% of all pups in the area) were marked with a paint dot within 24 h of birth, by touching them briefly with a paint sponge attached to a long pole; they were not otherwise physically handled or separated temporarily from the mother. Pups observed outside harems and considered to be weaners were weighed using similar methods as on the Isthmus, and marked with plastic flipper tags for future recognition. Data on weaning mass were collected for 168 elephant seal pups on Middle Beach.

Photogrammetry

For a randomly selected sub-sample of pups in both study areas, data were collected on the size of their respective mothers. Rather than sedating and physically weighing females, we used photogrammetric techniques modified from Bell et al. (1997), in order to minimize handling disturbance. Females were photographed repeatedly on different days of lactation, preferably at earlier stages. Standardized lateral photographs were made, under conditions when the subject was lying on a flat surface, well visible from the side, at right angles to the body axis. A black and white 100-mm scale was held above the animal's midline and images taken at distances of 5–20 m, depending on circumstances. We used a Canon Eos 100QD body fitted with a lens of 50 mm (Canon EF, 1:1.8 II) or 200 mm (Canon EF, 1:2.8). Prints were digitized and analysed using Optimas 5.0 (1988–1994 Optimas, Seattle, Wash.). From the images, body length L (metres, from snout tip to base of hind flipper; Haley et al. 1991; Bell et al. 1997) and body side area SA (square metres) were measured (Bell et al. 1997).

Maternal length

For 46 females (22 Middle Beach, 24 Isthmus East), maternal snout-to-tail length was estimated from the photographic variable L measured on all images available per female ($N = 151$), as follows:

$$ML = \Sigma(1.074 \cdot L)/N [r^2 = 0.998; N = 36] \quad (1)$$

The multiplication factor was based on a set of calibration images of females taken during an earlier field season (1996) for the

same project on Macquarie Island. In that year, direct data on snout-to-tail length and mass were collected on 32 females at different stages of the lactation period.

Maternal postpartum mass

For estimating mass M of a female from an image taken n days after parturition, model [18] in Bell et al. (1997) was modified based on data collected during our earlier (1996) field season, as follows:

$$M = 506.99 \cdot SA^{1.193} [r^2 = 0.707; N = 39] \quad (2)$$

Reasons for modification were: (1) for mass estimation of lactating females, only images of postlactation females were available in Bell et al.'s (1997) study; the present study, however, examines females at all stages of lactation; (2) it was found that models [18], [19], and [20] (Bell et al. 1997) underestimated female mass when applied to our 1996 set of known-mass females.

As lactating females lose on average 35% of mass from parturition to departure (Arnbom et al. 1997), maternal mass is highly variable throughout lactation. For each of our 1998 study females, we established one estimate of maternal postpartum mass (MPPM) from multiple images per individual taken over the first 12 days of lactation (most of these within a week of parturition). This was done by adding the number of days n that the image was taken after parturition, multiplied by the average mass loss per day for lactating females, as measured during our 1996 study season (7.615 kg day⁻¹; cf. McCann et al. 1989):

$$MPPM = \Sigma(M + 7.615 \cdot n)/N \quad (3)$$

Postpartum mass was estimated for 44 females (21 Middle Beach, 23 Isthmus East), based on a total of 91 photographs.

Maternal condition

An index of the condition of females at onset of lactation was obtained using the postpartum mass:length ratio derived from photographic variables (unit: kg m⁻¹).

Parameters examined

Parameters examined were: (1) maternal length, (2) maternal postpartum mass, and (3) maternal condition index, derived from photographic measures, and (4) pup weaning mass directly measured. Statistics were carried out following Zar (1984), using the SPSS 9.0.1 Windows software package (SPSS 1999).

Results

At the peak of the breeding season (counted 15 October 1998), 509 females were distributed over 3 harems on Middle Beach, and 866 females distributed over 6 harems on Isthmus East. Peak numbers of females present per kilometre of coastline were similar for the two study areas (respectively, 727 vs 722 females km⁻¹ of coastline; $\chi^2 = 0.0173$, $P = 0.683$). Harem size, defined as the number of females present in a harem on 15 October, was comparable for the study areas (Middle Beach, from south to north 172, 319 and 18 females; Isthmus East, from south to north 29, 104, 113, 303, 310 and 7 females; Mann-Whitney, $U = 7.00$, exact $P = 0.714$).

For two harems on Middle Beach and three harems on Isthmus East, where the numbers of adult males were monitored regularly over the breeding season, there

was no evidence for differences in male presence between the study areas. The number of males situated in a harem, expressed as average per week, was not significantly different between the two areas (repeated measures ANOVA, $F_{1,2} = 0.078$, $P = 0.806$); neither was the number of males in or within 30 m of a harem, averaged per week (repeated measures ANOVA, $F_{1,2} = 0.040$, $P = 0.861$). Adult sex ratio, defined as the proportion of adult males to the total of both sexes in or within 30 m of a harem, was similar for the two areas (repeated measures ANOVA, $F_{1,2} = 0.536$, $P = 0.540$).

Maternal size

Estimated snout-to-tail length of all study females averaged 2.42 ± 0.24 m (mean \pm SD; $N = 46$, range 2.00–2.99 m). Estimated maternal postpartum mass averaged 516 ± 112 kg ($N = 44$, range 355–769 kg). Maternal condition index or mass:length ratio averaged 211 ± 27 kg m⁻¹ ($N = 46$, range 164–269 kg m⁻¹). Fig. 1a–c shows length, postpartum mass and condition index for mothers of male and female pups on Middle Beach and Isthmus East.

Length estimates were similar for mothers of male or female pups [respectively, 2.43 ± 0.24 m ($N = 15$) vs 2.42 ± 0.24 m ($N = 29$), independent samples t -test, $t = 0.120$, $P = 0.905$]. Mothers of male or female pups were not significantly different in either estimated post-

partum mass [500 ± 129 kg ($N = 15$) vs 528 ± 104 kg ($N = 27$), $t = -0.786$, $P = 0.436$] or condition index [203 ± 33 kg m⁻¹ ($N = 15$) vs 216 ± 24 kg m⁻¹ ($N = 27$), $t = -1.448$, $P = 0.155$].

Size differences were detected when females were compared between areas. Study females on Middle Beach were significantly longer than on Isthmus East [2.53 ± 0.25 m ($N = 22$) vs 2.33 ± 0.20 m ($N = 24$), $t = 2.798$, $P = 0.008$]. There appeared to be a similar tendency in estimates of maternal postpartum mass for the two areas [respectively, 543 ± 113 kg ($N = 21$) vs 492 ± 107 kg ($N = 23$)], but the difference was not statistically significant ($t = 1.535$, $P = 0.132$). Condition index was similar for females on Middle Beach and Isthmus East [213 ± 26 kg m⁻¹ ($N = 21$) vs 209 ± 29 kg m⁻¹ ($N = 23$), $t = 0.528$, $P = 0.600$].

For the sample of photographed females, there was a tendency of somewhat earlier parturition date on Middle Beach (median 25 September 1998, range 9–30 September, $N = 22$) when compared to Isthmus East (median 26 September 1998, range 16–30 September, $N = 24$; Mann-Whitney, $U = 175.5$, $P = 0.0503$).

Pup size

Mass at weaning of male and female elephant seal pups in both study areas is shown in Fig. 1d. Over the whole sample, weaning mass averaged 119.7 ± 29.6 kg (mean \pm SD; $N = 597$, range 38–208 kg).

On Middle Beach, average weaning mass was 128.3 ± 29.9 kg ($N = 87$) and 121.7 ± 30.2 kg ($N = 81$) for male and female pups, respectively; on Isthmus East; mass of males and females averaged 120.5 ± 29.3 kg ($N = 205$) and 114.9 ± 29.3 kg ($N = 224$). Weaning mass was significantly different between the two sexes, and between pups on Middle Beach and Isthmus East. This was shown with a 2-way ANOVA of weaning mass with the factors sex and area. Both factors enhanced the explained variance significantly (sex: $F_{1,593} = 5.146$, $P = 0.024$; area: $F_{1,593} = 7.371$, $P = 0.007$), while no significant interaction term was found (sex \times area: $F_{1,593} = 0.035$, $P = 0.851$). On average, male and female weaners, respectively, were 7.8 kg (6.4% of overall mean for males) and 6.8 kg (5.8% of overall mean for females) heavier on Middle Beach than on Isthmus East.

There was no significant difference in the sex ratio of weighed weaners between both areas (males:females, Middle Beach 87:81, Isthmus East 205:224; Pearson's $\chi^2 = 0.77$, $P = 0.379$).

Pup size relative to maternal size

For all studied mother-pup pairs, the factor maternal length alone explained 69.4% of the variation in pup weaning mass (linear regression, $F_{1,41} = 92.813$, $P < 0.001$). Fig. 2 shows pup weaning mass as a func-

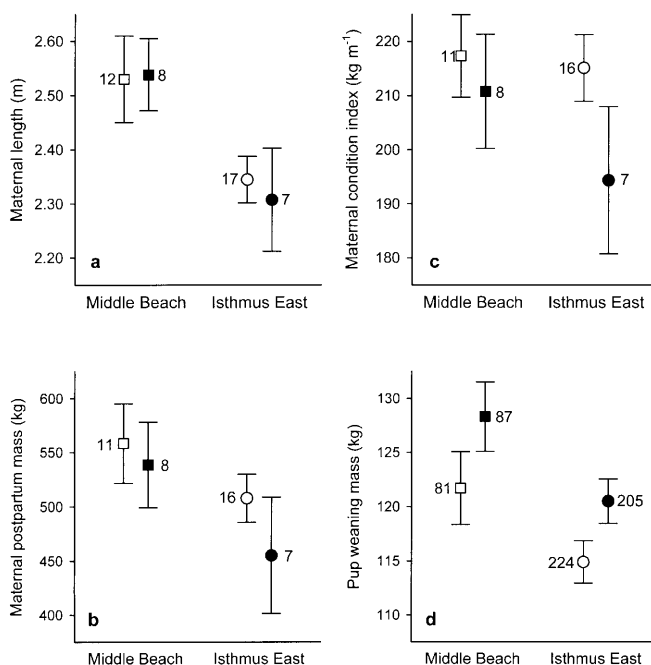


Fig. 1a–d Maternal and pup size parameters (mean \pm SE) for Middle Beach and Isthmus East, Macquarie Island. **a** Maternal length. **b** Maternal postpartum mass. **c** Maternal condition index. **d** Pup weaning mass. Unfilled symbols (mothers of) female pups; filled symbols (mothers of) male pups. Numbers indicate sample sizes

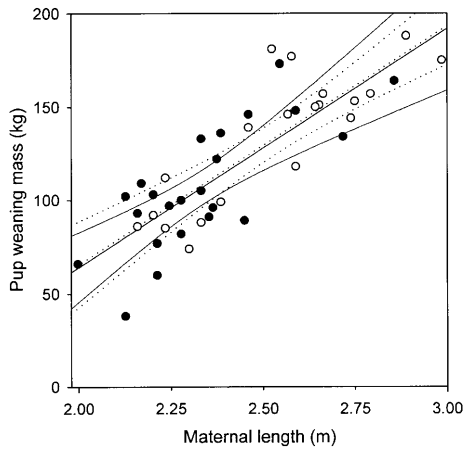


Fig. 2 The relation between maternal length and pup weaning mass for elephant seals on Middle Beach (unfilled symbols, dotted lines) and Isthmus East (filled symbols, solid lines). Regression lines with 95% confidence intervals are shown

tion of estimated maternal length for Middle Beach and Isthmus East. The factor estimated maternal postpartum mass accounted for 67.6% of the variation in pup weaning mass (linear regression, $F_{1,39} = 81.517$, $P < 0.001$).

Using backward general linear model analysis, we tested for the relative effects of maternal size, pup sex and study area (Middle Beach or Isthmus East) on pup weaning mass. Maternal size was included as the terms maternal length, postpartum mass and squared postpartum mass (Table 1; see note for explanation). The final model consisted of the constant and each of the maternal size terms, and explained 76.1% of the variation in pup weaning mass. The factor area was rejected

Table 1 Analysis of pup weaning mass with maternal length (*ML*), maternal postpartum mass (*MPPM*) and squared maternal postpartum mass (*MPPM*²) by pup sex and study area. $N = 41$ (8 males and 11 females on Middle Beach, 7 males and 16 females on Isthmus East). The final model explained 76.1% of the variation in pup weaning mass. Areas are Middle Beach (remote) and Isthmus East (accessible to people). *ML* and *MPPM* were derived from different photographic variables. Squared *MPPM* is included in the model

	(Change in SS (type III))	(Change in <i>df</i>)	<i>F</i>	<i>P</i>	Coefficients
Null model	55177.1	40			
Final model	13214.2	37			
Constant	4791.0	+1	13.415	0.001	-296.3
<i>ML</i>	+2631.6	+1	7.369	0.010	76.94
<i>MPPM</i>	+2980.0	+1	8.344	0.006	0.744
<i>MPPM</i> ²	+2172.1	+1	6.082	0.018	-0.000555
Rejected terms					
Area	+225.0	-1	0.624	0.435	
Sex	+250.1	-1	0.694	0.410	
Area × Sex	+76.0	-1	0.203	0.655	
Area × <i>ML</i>	+12.9	-1	0.035	0.853	
Area × <i>MPPM</i>	+190.5	-1	0.521	0.475	
Sex × <i>ML</i>	+264.9	-1	0.730	0.399	
Sex × <i>MPPM</i>	+758.8	-1	2.176	0.149	

($P = 0.435$, $\eta^2 = 1.7\%$); inclusion of this factor into the model enhanced the explained total variation only slightly (76.5%). There were no significant effects of the factor pup sex or of any of the interactions of area and sex with terms of maternal size.

Discussion

Our working hypothesis was that in southern elephant seals, human disturbance may reduce energy transfer from mothers to pups during lactation, resulting in lower masses of pups at weaning. At first sight, the results of this study seem to support the hypothesis: weaning mass was indeed, both for male and female pups, higher in the remote area of Middle Beach when compared to the human-accessible area of Isthmus East; an average difference of 7.5 kg (6.3% of mean weaning mass) was recorded.

However, pup weaning mass is largely determined by maternal postpartum mass (Arnbom et al. 1993, 1997; Fedak et al. 1996; McMahon et al. 1997). The photographic data set on the size of adult females showed evidence of maternal size differences between the two areas consistent with pup weaning mass differences. Length estimates of adult females were significantly higher on Middle Beach than on Isthmus East (mean 2.53 m vs 2.33 m). A similar tendency was found in estimated maternal postpartum mass, but the effect was not significant even though there was a 51 kg difference in average mass estimates (mean 543 kg vs 492 kg). That discrepancy could be explained as follows. Maternal length remains constant over lactation; the parameter could be estimated using all images available per female

since pup weaning mass relative to maternal postpartum mass decreases with maternal postpartum mass (Arnbom et al. 1997). Null model includes the constant only. Final model includes all significant parameters. Changes in *SS* and *df* indicate the changes when parameters are dropped from the final model one at a time (or added to the final model in case of rejected terms). When testing the significance of higher order interaction terms, the lower order terms were included in the model, regardless of their significance

($N=151$). However, as females show considerable mass loss over lactation (McCann et al. 1989), estimates of postpartum mass could be derived only from images taken during the initial stage of lactation ($N=91$). In cases where females were photographed on later days than the parturition date, postpartum mass had to be extrapolated using the average mass loss rate for females as measured previously. Thus, length estimates were probably of higher accuracy than postpartum mass estimates, which could explain the finding of a significant difference in length but only a trend in postpartum mass. There was no significant difference in maternal postpartum condition index between areas. In the sample of study females, there was a trend of slightly earlier parturition date on Middle Beach when compared to Isthmus East (median 25 vs 26 September 1998), but this date tendency of 1 day only cannot explain the difference in female size between areas; moreover, younger (and therefore smaller) pregnant females (Laws 1953; Carrick et al. 1962a) are expected to arrive earlier on breeding beaches (Kirkman 1999).

For the pups with known maternal data, 76.1% of the variation in weaning mass could be explained by maternal length, postpartum mass and squared postpartum mass (Table 1). Once these parameters were taken into account, there was no effect of area (remote or disturbed) on pup weaning mass. This implies that in proportion to their own size, study females on Middle Beach and Isthmus East produced weaners of similar masses. If this finding based on the smaller set of mother-pup pairs with both maternal and juvenile data ($N=44$) can be extrapolated to the larger pool of measured weaners ($N=597$), then it may be concluded that the area differences in pup size found here were due to differences in maternal size, which were already present at the stage that pregnant females arrived on breeding beaches.

Significant differences in weaning mass of elephant seal pups between populations in the Atlantic, Indian and Pacific sectors of the Southern Ocean are probably partly attributable to variation in food availability between these regions (Burton et al. 1997). All animals in the present study came from breeding sites less than a few kilometres apart, distances negligible to the scale of foraging ranges of elephant seals (Hindell et al. 1991; Slip et al. 1994); for example, adult female elephant seals previously tagged on the Isthmus of Macquarie Island foraged in moderately warm sub-Antarctic as well as cold Antarctic waters between around 50°S and over 70°S (Slip et al. 1994). With these extensive foraging ranges, it seems unlikely that variation in local food availability can explain the differences in maternal and pup size found here between adjacent breeding beaches.

Rather, it seems that upon arrival, there was some degree of site selection by females depending on their size. Several causes might be adduced to explain why larger females apparently chose relatively more often to breed on Middle Beach than on Isthmus East. Female elephant seals continue to grow after reaching sexual

maturity, and length is proportional to age (Laws 1953; Carrick et al. 1962a); size and age are associated with dominance in female elephant seals (Reiter et al. 1981; McCann 1982). Older, more experienced and/or dominant females might be expected to be more selective in breeding site choice. Middle Beach may have been preferred above Isthmus East as a breeding area either because of (subtle) differences in natural characteristics, or because of its remoteness from human activity. Although beach and surf conditions appeared similar, wind force was variable at a local scale especially on Isthmus East. Harem sizes, numbers of adult males present in or near harems, and adult sex ratios were not significantly different between the areas. However, there could have been differences in harem characteristics not quantified, such as aggressive activities of adult males potentially causing natural disturbance (Le Boeuf and Briggs 1977; Modig 1996). High-quality males may have been unequally distributed, causing differential site selectivity among females (Cox 1981). Aggression is likely to affect reproductive success especially in smaller females, possibly forcing these to move to sites where they can more effectively compete, thus causing size segregation (Le Boeuf and Briggs 1977; McCann 1982). Alternatively, as there has been a research station on the Isthmus for several decades, there could be some degree of avoidance by older females of breeding in that area, caused by human disturbance during a previous breeding season (cf. Thiel et al. 1992). Breeding site fidelity of female southern elephant seals is high (Nicholls 1970; Hindell and Little 1988), but females may show increased breeding dispersal and reduced site fidelity in the case of low reproductive success in the previous season, as described in several other species (Wauters et al. 1995; Murphy 1996; Haas 1998; Schjørring et al. 2000).

We underline the importance of quickly measurable parameters with known or expected links to survivorship in studies of human impact on wildlife, especially in long-lived animals. The present study examines such a survival parameter, pup weaning mass in southern elephant seals (McMahon et al. 2000), in relation to human presence on Macquarie Island. It shows no significant difference in pup weaning mass between sites other than that due to the size of the mothers, indicating no direct effect of human presence on the efficiency of lactation in southern elephant seals. This is in line with the results of Wilkinson and Bester (1988): onshore human activity appears not to be a significant factor in the drastic decline of the species in the southern Indian and Pacific Oceans. Population declines are most likely attributable to changes in ocean productivity (Hindell et al. 1994; Pistorius et al. 1999).

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