Human disturbance, nursing behaviour, and lactational pup growth in a declining southern elephant seal (*Mirounga leonina*) population

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Abstract: We studied lactation behaviour in relation to pup growth in southern elephant seals (*Mirounga leonina*) at Macquarie Island, and compared harems in areas of high and low human presence to determine if there is an effect attributable to human activities, including scientific research. Pup weaning mass, a known correlate of first-year survival, was positively influenced by suckle bout durations during early and middle lactation and by maternal aggression during late lactation; no other behavioural variables were associated with weaning mass. In the area of high human presence, we observed from a distance the behaviour of mother–pup pairs directly before, during, and after visits to harems by other researchers. Alertness was raised threefold in the presence of people but quickly returned to predisturbance levels after their departure; there were no significant short-term effects on other behavioural variables. In the areas of high and low human presence, we observed the undisturbed behaviour of the seals in the absence of other people. No significant differences in any behavioural variables examined were found, indicating no long-term changes in behaviour resulting from human presence. Human disturbance therefore appears not to have significantly contributed to the population decline observed at Macquarie Island, but the conclusion requires caution given the fairly low power of our analyses.

Résumé : Nous avons étudié le comportement d'allaitement en relation avec la croissance des petits chez l'éléphant de mer du sud (*Mirounga leonina*) à l'île Macquarie et comparé les harems des zones fortement utilisées par les humains à ceux des zones de faible densité humaine afin de déterminer si les activités humaines, y compris les recherches scientifiques, ont un effet. La masse des petits au moment du sevrage, que l'on sait être en corrélation avec la survie durant la 1$^{\text{ère}}$ année, est influencée par la durée des tétées au début et au milieu de la période d'allaitement et par l'agressivité maternelle à la fin. Aucune autre variable du comportement n'est associée à la masse des petits au sevrage. Dans la zone de forte densité humaine, nous avons observé à distance le comportement des groupes mère–petit avant, pendant et après la visite de chercheurs. La vigilance est trois fois plus élevée en présence d'humains, mais elle revient au niveau initial après leur départ et la présence humaine ne produit pas d'effet à court terme sur d'autres variables du comportement. Nous avons observé le comportement normal, non perturbé, des phoques en l'absence d'humains, dans les zones de forte densité humaine aussi bien que dans les zones de faible densité. Nous n'avons trouvé aucune différence dans les variables du comportement, ce qui indique que la présence d'humains n'a pas d'effet à long terme sur le comportement des phoques. L'activité humaine n'a donc pas contribué de façon significative au déclin de la population enregistré à l'île Macquarie, mais c'est là une conclusion qu' il faut envisager avec prudence, étant donné la faible puissance de nos analyses.

[Traduit par la Rédaction]

Introduction

The impact of anthropogenic disturbance on free-living marine mammals, a topic of current concern, can be assessed by observations on their behavioural responses. Indeed, several studies documented changes in marine mammal behaviour resulting from human activity (e.g., Salter 1979; Renouf et al. 1981; Allen et al. 1984; Reijnders et al. 1993; Born et al. 1999; Suryan and Harvey 1999). In comparison with data collection on physiological disturbance parameters (e.g.,

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blood values, stress hormones), which often necessitates animal handling or immobilisation (Thomson and Geraci 1985; Gardiner and Hall 1997; Engelhard et al. 2002), behavioural observations incur only minimal disturbance created by the researcher himself. However, in many cases it remains unclear whether behavioural responses to human presence may have any negative consequences for survivorship, reproductive success, and other parameters that have direct implications for population status. Therefore behavioural changes should be considered in a fitness context (Hofer and East 1998).

Southern elephant seal (*Mirounga leonina* (Phocidae)) populations in the southern Atlantic Ocean appear stable (Laws 1994; Boyd et al. 1996), whereas those in the southern Indian and Pacific oceans have been in decline over the past decades, or currently still are (Barrat and Mougin 1978; Hindell and Burton 1987; Guinet et al. 1999; McMahon et al. 1999; Pistorius et al. 1999*a*; Slip and Burton 1999). The causes of population decline remain poorly understood; poor food conditions in the pelagic foraging ranges may be a principal factor, but other local factors that also regulate populations might also be involved (Hindell et al. 1994; Pistorius et al. 1999*b*).

This paper contributes to a project examining to what extent human disturbance (including researcher activity) might be a factor in population decline (cf. Engelhard et al. 2001). Until recently, only one study on disturbance in elephant seals had been carried out; no effect was found based on population census data (Wilkinson and Bester 1988). Little is known on the effect of human activities on (sub-)Antarctic pinnipeds (Wilkinson and Bester 1988; Engelhard et al. 2001). This is remarkable in that research effort on several of these species has been intensive (e.g., Le Boeuf and Laws 1994; Hindell and Kemper 1997), and the southern elephant seal has been described as one of the most widely and exhaustively studied pinnipeds (Ling and Bryden 1992). In addition, presence of people in Antarctica and the sub-Antarctic is increasing and is expected to increase further in the near future (Enzenbacher 1992, 1994; IAATO 2000).

Lactation is a period of maximum energetic drain for female mammals and intake by their offspring. This might be a time when animals are most vulnerable to disturbance, where either extra energy has to be spent or where intake is hampered. In both ways, reproductive success is likely to be affected. Lactating female elephant seals spend about 3–4 weeks on land without feeding, fuelled exclusively by energy from stored reserves (Fedak et al. 1996). On the breeding beaches, they cluster into harems that are competed for by males (Carrick et al. 1962). Soon after arrival the females give birth to a single pup and nurse it for 23 or 24 days, on average (Arnbom et al. 1997; McMahon et al. 1997). Pups are then weaned abruptly and left by their mothers to be nutritionally independent (Carrick et al. 1962). Mothers lose, on average, about one-third of their initial mass during lactation; their pups may double to quadruple their mass over that time (Arnbom et al. 1997). There is considerable variation in the mass of the pups at weaning, largely because of variation in the mass of their mothers at the start of lactation (Arnbom et al. 1993, 1997; Fedak et al. 1996). Because females usually nurse a single young per season, pup weaning mass can be interpreted as an index of maternal expenditure (Costa 1991; Trillmich 1996). Heavier weaned southern elephant seal pups have higher chances of first-year survival than light weaned pups (McMahon et al. 2000); thus weaning mass may also be considered a proxy for fitness.

We address two questions related to human disturbance and mother–pup behaviour during lactation. First, which types of behaviour during lactation might (in addition to maternal postpartum mass) affect the mass of the pup at weaning, a parameter associated with survivorship? Second, which aspects of lactation behaviour are affected by human activity, either directly when people are present at elephant seal harems and (or) indirectly over a longer time span when people are absent again from harems?

Materials and methods

Study population

Field investigations were carried out during September to November 1998 on Macquarie Island (54°30′S, 158°57′E), located in the Pacific sector of the Southern Ocean. The island houses the world's third-largest southern elephant seal population (Laws 1994), which is one of those in decline (Hindell and Burton 1987; McMahon et al. 1999). Since 1948, the Australian Antarctic Division has run a research station on the island, permanently occupied by the Australian National Antarctic Research Expeditions (ANARE).

Human activity

We studied elephant seals in two study areas similar in natural features but widely different in the levels of human activity: (1) the eastern beaches of the Isthmus on the north of the island, referred to as Isthmus East (cf. Carrick et al. 1962); and (2) a site 2 km south of Isthmus East named Middle Beach. Both study areas were located on the east coast of the island, which is leeward of the prevailing westerly winds. The sites were similar in beach topography; elephant seal harems formed on 20–40 m wide shingle beaches on Isthmus East and on 15–40 m wide shingle beaches on Middle Beach. Wind and surf conditions were also comparable; during the study period we observed similar wind forces (Beaufort scale) in the two areas (median 3 in both sites, n = 127; Mann–Whitney U test, U = –0.869, P = 0.385). Previously, we found that the average length of adult females and mass of weaned pups were significantly higher on Middle Beach than on Isthmus East; however, in proportion to their own size, mothers in both areas produced pups of similar mass (Engelhard et al. 2001). Moreover, the numbers of adult male and female elephant seals present in breeding harems were comparable in both areas; at the peak of the breeding season (counted 15 October 1998), 866 females were distributed over six harems on Isthmus East, and 509 females were distributed over three harems on Middle Beach. Peak numbers of females present per kilometre of coastline were not significantly different between Isthmus East and Middle Beach (722 vs. 727 females/km of coastline, respectively; χ^2 = 0.0173, P = 0.683). Both adult and juvenile sex ratios were comparable in the two sites (Engelhard et al. 2001).

Isthmus East and Middle Beach are here considered areas of high and low levels of human presence, respectively, on the following grounds. First, Macquarie Island's permanent station, which typically accommodates 30–40 persons in summer and 10–15 persons in winter, is situated on the Isthmus. Most human activity (scientific, maintenance, sightseeing, and tourism) has therefore been at or near that site over the past decades. Other areas of the island, including Middle Beach, generally receive far less frequent human visitation.

Second, for continuation of long-term monitoring studies of the elephant seal population, harems on the Isthmus were visited each day of the 1998 pupping season by four to five persons with a small tractor. On Isthmus East, data on birth mass were collected for 459 pups, or about 50% of all pups born in the area (methods as in McMahon et al. 1997). These newborn animals were dragged just outside the harem, captured in a pup bag, lifted for weighing, and given two flipper tags before being brought back into the harem. This handling procedure, carried out routinely, usually implied a brief mother–pup separation for about 1–3 min. On average this means a disturbance of 24 min per harem repeated over all days of the pupping season. By contrast, no newborn pups were weighed, flipper-tagged, or otherwise physically handled on Middle Beach. The only exception to this were 24 pups (about 4% of all pups born in the area) that were marked with a paint dot by touching them briefly with a paint sponge attached to a long pole to allow individual recognition. The moderate disturbance created thus lasted 1–3 min and did not incur any temporary mother–pup separations. There was no vehicle access to Middle Beach, and the area was closed off for all other people except for our own three-person team that visited both areas daily by foot to carry out behavioural observations. Thus there was a reasonably high difference in the degree of human disturbance between Isthmus East and Middle Beach (Engelhard et al. 2001).

Indirect effects of human activity

We examined whether human disturbance may indirectly affect normal elephant seal lactation behaviour by comparing the behaviour between mother–pup pairs in the areas of low and high human presence, during intervals when no people were present near harems. Throughout lactation, 24 female elephant seals with previously handled pups distributed over three harems on Isthmus East and 24 females with previously unhandled pups distributed over two harems on Middle Beach were monitored. All animals were marked with a paint dot to allow the recognition of individuals. Three observers recorded behaviour of study animals from remote viewpoints overlooking the harems. Behavioural protocols were made from 11 September through 19 October 1998. Observation sessions lasted about 2 h and were distributed throughout the day between 8:45 and 18:00 local time. There was no significant difference in the onset of observation sessions carried out on Middle Beach or Isthmus East (Mann–Whitney U test: $U = 1085$, $n_{\mathrm{MB}} = 58$, $n_{\mathrm{IE}} = 42$, NS). Because general activity levels in harems were quite low, we were able to follow several mother–pup pairs in a harem simultaneously (each session, 1–5 pairs, median 5). Pairs were observed repeatedly on different days distributed throughout the lactation period; for week 1, week 2, and weeks 3–4 of lactation, the total observation time was 264, 225, and 292 h, respectively.

Direct effects of human activity

On Isthmus East we examined whether human presence may directly affect lactation behaviour by remotely observing the behaviour of the focal elephant seal mother–pup pairs over the time immediately before, during, and after research visits to the harem by other investigators. Typically, four or five persons were present for the weighing and flipper-tagging of 1-day-old pups born to non-focal females within the same harem where focal individuals were situated (as described above). Duration (mean ± SD) of visits to these harems was 24 ± 19 min (median 20 min, range 2–68 min, n = 17). In observation sessions lasting about 2 h, three observers located on viewpoints overlooking harems monitored the behaviour of focal mother–pup pairs (each session, 2–5 pairs, median 5). In total, pairs were observed for 71, 30, and 45 h before, during, and after human visits, respectively.

Behavioural variables

We made continuous visual recordings of the behaviour of mother–pup pairs as focal individuals (Altmann 1974). The duration of behavioural states and timing of events were monitored with the aid of small handheld computers (Psion Organiser LZ-64, Psion PLC, London, U.K.), programmed as event recorders using the software package The Observer 3.0 (Noldus Information Technology b.v., 1994, Wageningen, the Netherlands).

The following behavioural variables were recorded (modified from Fogden 1971; McCann 1982, 1983; Anderson and Harwood 1985; Haller et al. 1996):

(1) Presenting time—percentage of observation time during which the adult female is lying on the side with the venter directed towards her pup, presenting the nipples; the pup may or may not be in oral contact with the nipple (definition similar to suckling session in Oftedal et al. 1987).

(2) Suckling time—percentage of observation time during which the pup is in oral contact with its mother's nipple (on-teat time). Any interruptions of mouth–nipple contact, or any instances where it was impossible to see whether the pup was really in oral contact with the nipple or not, were excluded.

(3) Suckle bout duration (s)—the mean duration of suckling (on-teat) periods per observation session.

(4) Frequency of suckling (h^{-1})—the number of suckling (on-teat) periods per hour of observation.

(5) Frequency of maternal calls (h^{-1})—the number of maternal vocalisations produced by the female per hour of observation, usually in response to the pup's call; often a long, drawn-out falsetto sound, almost a whine (Matthews 1929).

(6) Frequency of alertness (h^{-1})—the number of times per hour that the female's head is raised with the eyes open and gaze directed.

(7) Frequency of flippering (sand flipping; h^{-1})—the number of times per hour that the female uses the foreflippers to scoop sand or shingle backwards and upwards, usually onto the back (Laws 1956).

(8) Frequency of moves (h^{-1})—the number of changes of the female's location per hour of observation.

(9) Frequency of aggressive interactions with other females (h^{-1})—the number of agonistic encounters per hour di-

rected towards or received from other adult females including threat vocalisations, lunges, high rears, bites, and submissions (McCann 1982).

Mass variables

In both study areas and for the same mother–pup pairs that were also focal individuals in behavioural studies, we collected data on the mass of mothers at the start of lactation (maternal postpartum mass) and the mass of pups at the end of lactation (pup weaning mass).

For measuring maternal postpartum mass in a noninvasive way, we applied photogrammetric techniques modified from Haley et al. (1991) and Bell et al. (1997). In this way, disturbance resulting from physical handling necessary for taking direct weight measurements was avoided. Methods were described in detail in a previous paper (Engelhard et al. 2001) and therefore are only briefly outlined here. We made several calibrated, lateral photographs of females, preferably at earlier stages of lactation, under conditions when animals were seen lying quiet and well visible from the side. From the digitized images, body side area (m^2) was measured using image analysis software. From these measurements of body side area taken from multiple images available per female, we derived a single estimate of postpartum mass (kg) for each of 44 study females by applying the previously described conversion calculations (Engelhard et al. 2001). Postpartum mass could not be estimated for the other four study females, because insufficient photographic material was available for these individuals.

Data on pup weaning mass were collected by weighing weaned pups, which were observed outside harems and therefore were considered to have completed the full lactation period. A net, an aluminum tripod, and 300-kg Salter® spring balance (Satter Weigh-Tronix Ltd., West Bromwich, Birmingham, U.K.) were used (McMahon et al. 1997). On Isthmus East, a total of 429 weaned pups previously weighed and tagged at birth were reweighed; on Middle Beach, 168 weaners (previously unhandled) were weighed. These included 45 out of 48 pups observed in detail throughout lactation; three focal pups on Middle Beach could not be relocated after weaning, because they had lost their individual paint marks during the first moult shortly before their mother's departure. As weaned pups were weighed on sites away from the harems, these handling procedures may have caused only minimal degrees of disturbance to mothers inside harems still nursing their young.

Statistics

Statistical analyses were carried out following Zar (1996), using the SPSS 10.0.7 Windows package (SPSS Inc. 1989–1999). For testing if behavioural variables changed in the course of lactation, the mean values of behavioural variables averaged for week 1, week 2, and weeks 3–4 of the lactation period were calculated for individual mother–pup pairs: 7-day intervals were considered necessary to obtain sufficiently large sample sizes for statistical analysis while including the majority of study animals. We grouped observations for the 3rd and 4th weeks of lactation, because there is variability in the total duration of lactation (cf. Arnbom et al. 1997; McMahon et al. 1997). In addition, the first, second, and later weeks of lactation are characterized by different rates of growth of the pup (McCann et al. 1989). In parametric statistical analysis, behavioural data were transformed to improve homogeneity of variance if these were the dependent variables. For percent data, we used arcsine transformation; for bout durations and frequencies, we used log transformation. When testing the hypothesis that human presence has an effect (direct or indirect) on elephant seal behaviour, we performed power analyses to examine the possibility of accepting the null hypothesis when in fact it was false. Power tests were based on values of α set to 0.05.

Results

Study females gave birth between 9 and 30 September 1998 (median 26 September; $n = 48$). The duration of lactation ranged from 20 to 32 days (24.2 ± 2.5 days, $n = 46$; two females were not monitored until the final stage of lactation, because their paint marks faded and became unrecognizable). The dates of weaning ranged from 4 to 29 October 1998 (median 19 October; $n = 46$).

Each female raised her own offspring during the study period, as no adoptions were observed. However, the incidence of adoptions cannot be fully excluded if it occurred in the brief interval (<1 day) between birth and marking of study animals. Allo-suckling was recorded rarely. Throughout all 781 undisturbed observation hours, none of the 48 focal females was observed with certainty to have suckled another pup but their own. Among focal pups, only a single allo-suckle bout (duration 483 s) was observed out of a total of 1390 suckle bouts recorded during undisturbed observation hours.

Behavioural changes over the course of lactation

Changes in behavioural variables from the early (week 1) to the middle (week 2) and late stages of lactation (weeks 3–4) are shown in Table 1. The proportion of time females spent presenting increased significantly from early to middle lactation; thereafter this proportion remained constant. Over the course of lactation, pups spent an increasing proportion of time sucking. This resulted from an increase in the durations of suckle bouts throughout lactation, as well as from an increase in the frequency of suckling during the first 2 weeks of lactation (Table 1). The frequency of alertness and maternal calls was highest during the first week postpartum. Over the course of lactation, there was no significant change in the frequencies of flippering, moves, and aggressive encounters among females (Table 1).

Relationship between behaviour during lactation and the mass of the pup at weaning

We examined to what extent different types of behaviour during lactation, in addition to maternal postpartum mass, were associated with the mass of the pup at weaning. In our data set, as expected, there was a strong relationship between maternal postpartum mass (estimated from photographs) and pup weaning mass (linear regression, $t = 9.47$, $P < 0.0001$); the variable maternal postpartum mass alone explained 67.6% of the variation in pup weaning mass.

A linear regression analysis with backward selection procedure (Table 2) showed that pup weaning mass was also

Table 1. Effect of lactation stage on behavioural variables (mean ± SE), quantified during undisturbed observation sessions carried out on Middle Beach and Isthmus East in the absence of other people.

Behavioural variable[a]	Week 1 (n = 46)	Week 2 (n = 46)	Weeks 3–4 (n = 47)	Test statistic	P	Post-hoc test (Wilcoxon)
Time lying on side (%)	38.7±3.6	49.4±3.2	52.5±2.5	$F_{[2,84]} = 5.302$	**0.007**	e < m ~ l
Time suckling (%)[b]	3.3±0.6	12.6±1.3	17.3±1.7	$F_{[2,84]} = 47.41$	**<0.0001**	e < m < l
Suckle bout duration (s)[b]	151±24[c]	276±22	362±27	$F_{[2,66]} = 30.55$	**<0.0001**	e < m < l
Frequency of suckling (h^{-1})[b]	1.2±0.2	2.1±0.3	2.1±0.2	$\chi^2_2 = 15.12$	**0.0005**	e < m ~ l
Frequency of maternal calls (h^{-1})	2.4±0.3	1.1±0.2	0.7±0.1	$\chi^2_2 = 14.00$	**0.0009**	e > m ~ l
Frequency of alertness (h^{-1})	2.4±0.2	1.4±0.2	1.1±0.1	$\chi^2_2 = 18.00$	**0.0001**	e > m ~ l
Frequency of flippering (h^{-1})	0.8±0.2	0.3±0.1	0.4±0.1	$\chi^2_2 = 4.044$	0.132	
Frequency of moves (h^{-1})	1.4±0.2	1.2±0.1	1.1±0.1	$\chi^2_2 = 0.671$	0.715	
Frequency of aggressive interactions with other females (h^{-1})	1.2±0.2	1.2±0.2	0.9±0.1	$\chi^2_2 = 0.228$	0.892	

Note: Stages include early, middle, and late lactation (respectively, week 1, week 2, and weeks 3–4 postpartum). Effect of lactation stage on percentages and bout durations was tested using repeated measures ANOVA, after arcsine transformation of percentages and log transformation of bout durations. Effect of lactation stage on frequency variables was tested using the Friedman test. If a significant effect was found, Wilcoxon's signed-rank test was applied for post-hoc comparisons: e, early lactation (week 1); m, middle lactation (week 2); l, late lactation (weeks 3–4); symbols "<" and ">" indicate significant increase or decrease ($P < 0.05$); symbol "~" indicates increase or decrease not distinguishable from coincidence. Values of $P < 0.05$ are shown in boldface type.

[a] Mother–pup pairs were, on average, observed for 5 h 44 min during week 1, for 4 h 53 min during week 2, and for 6 h 13 min during weeks 3–4. Not all pairs were observed during each stage of the lactation period.

[b] Because of unequal sample sizes and positively skewed distributions in these variables, multiplication of the mean suckle bout duration with the mean suckling frequency does not result in the mean proportion of time spent suckling.

[c] In some mother–pup pairs, suckling was not recorded in week 1 of lactation if observations were few; hence, n = 37 for suckle bout duration during week 1.

significantly and positively influenced by the mean durations of suckle bouts during the first ($P = 0.002$) and second ($P = 0.019$) weeks of lactation and by the frequency of aggressive encounters by the respective mothers during the last week of lactation ($P = 0.042$). A regression model including these three behavioural variables in addition to maternal postpartum mass explained 83.1% of the variation in pup weaning mass.

All other behavioural variables were rejected, indicating that these variables were not linked to lactational pup growth (Table 2). It should be noted, however, that a linear regression model including all behavioural variables except for mean suckle bout durations would reveal effects approaching significance of the proportion of time spent suckling during the first ($P = 0.063$) and second ($P = 0.082$) week of lactation on pup weaning mass. Mean suckle bout durations and proportion suckling time were correlated during the first ($r_S = 0.853$, $P < 0.0001$) and second week of lactation ($r_S = 0.297$, $P = 0.045$). By contrast, there was no effect of the frequency of suckling (i.e., the spread of suckling) during any of the weeks of lactation on pup weaning mass.

Direct behavioural responses to human visits

The behaviour of elephant seal mother–pup pairs immediately before, during, and after visits to seal harems by field investigators was compared (Table 3). Most noticeably, presence of people resulted in a significant change ($P < 0.0001$) in the alertness of elephant seal mothers; frequency of alertness was, on average, raised to a threefold level during human visits when compared with the periods directly before or after human visits. Alertness after visitation was similar to alertness before human visits (Table 3). Moreover, there was a decrease in the frequency of maternal calls directly after people departed the harems compared with the time immediately before human visits.

There was no immediate effect of human presence on the proportion of time females spent presenting, the proportion of time pups spent sucking, the duration and frequency of suckle bouts, or the frequencies of flippering, moves, or agonistic encounters among females. It should be noted that between periods before, during, and after human presence there was much variability within individuals in these behavioural variables. This resulted in only low or moderate power to detect significant effects ($P < 0.05$) on these variables with the current sample sizes (power ranging from 0.061 to 0.403 for rejected behavioural variables; see Table 3).

Behaviour in areas of low and high human presence

Behavioural variables, quantified in the absence of people near elephant seal harems, were compared between mother–pup pairs in the areas of low human presence (Middle Beach) and high human presence (Isthmus East) for three stages of the lactation period (Table 4). Of nine variables examined, none was significantly different between seals on Middle Beach and Isthmus East. In addition, there was no significant interaction of week of lactation with area for any of the behavioural variables examined. This indicated that changes in behavioural variables over the course of lactation were similar in the areas of low and high human presence.

However, power analysis indicated only low power to detect significant differences ($P < 0.05$) in single behavioural variables between elephant seals in the two areas (power ranging from 0.055 to 0.248). Therefore, we further examined if mother–pup pairs in the two areas showed differences in overall behaviour using a multivariate repeated-measures ANOVA on the effect of area (remote or visited) on all be-

Table 2. Linear regression model examining the effects of maternal postpartum mass and different aspects of lactation behaviour on pup weaning mass.

Behavioural variables	Coefficient	SE	*t*	*P*
Final model				
Constant	–65.3	15.5	–4.20	**0.0002**
Maternal postpartum mass (kg)	0.307	0.028	11.13	**<0.0001**
Suckle bout duration, week 1 (s)	0.074	0.022	3.4	**0.002**
Suckle bout duration, week 2 (s)	0.045	0.018	2.85	**0.019**
Frequency of aggressive interactions with other females, week 3 (h^{-1})	7.37	3.47	2.12	**0.042**
Rejected terms				
Time lying on side, week 1 (%)			–0.576	0.569
Time lying on side, week 2 (%)			0.862	0.396
Time lying on side, week 3 (%)			1.049	0.303
Time suckling, week 1 (%)			–0.086	0.932
Time suckling, week 2 (%)			0.137	0.892
Time suckling, week 3 (%)			–0.599	0.554
Suckle bout duration, week 3 (s)			0.292	0.773
Frequency of suckling, week 1 (h^{-1})			0.305	0.762
Frequency of suckling, week 2 (h^{-1})			0.220	0.828
Frequency of suckling, week 3 (h^{-1})			–0.885	0.383
Frequency of maternal calls, week 1 (h^{-1})			0.738	0.466
Frequency of maternal calls, week 2 (h^{-1})			–0.808	0.425
Frequency of maternal calls, week 3 (h^{-1})			0.172	0.864
Frequency of alertness, week 1 (h^{-1})			–0.016	0.987
Frequency of alertness, week 2 (h^{-1})			0.027	0.979
Frequency of alertness, week 3 (h^{-1})			–0.291	0.773
Frequency of flippering, week 1 (h^{-1})			0.934	0.358
Frequency of flippering, week 2 (h^{-1})			–0.061	0.951
Frequency of flippering, week 3 (h^{-1})			–0.180	0.859
Frequency of moves, week 1 (h^{-1})			0.084	0.933
Frequency of moves, week 2 (h^{-1})			–0.235	0.816
Frequency of moves, week 3 (h^{-1})			0.414	0.682
Frequency of aggressive interactions with other females, week 1 (h^{-1})			–0.489	0.628
Frequency of aggressive interactions with other females, week 2 (h^{-1})			0.425	0.674

Note: Weekly averages of behavioural variables are included as covariates. A model including only maternal postpartum mass as explanatory variable explained 67.6% of the variation in pup weaning mass; the final model including, in addition, all significant behavioural variables explained 83.1% of the variation in pup weaning mass. Initially, a backward selection procedure was used; the significance of rejected terms was then reexamined by adding these to the final model one at a time. Values of $P < 0.05$ are shown in boldface type.

havioural variables combined. The inclusion of all behavioural variables into a single analysis still yielded, with increased power of 0.477, no significant difference in overall behaviour between seals in areas of low and high human presence ($F_{[9,25]} = 1.281$, $P = 0.297$).

Discussion

Significance of different types of behaviour

In the context of human disturbance, (*i*) natural variation in behavioural parameters should be taken into account as a possible confounding factor in assessing which changes are due to human presence; and (*ii*) it should be considered which possible behavioural impacts are of highest biological significance, i.e., may have consequences for survival or reproductive success (Hofer and East 1998; Gill et al. 2001). There was a significant effect of the stage of lactation on six out of nine variables examined in this study (Table 1). Increases in suckling frequency and suckle bout duration over the lactation period, resulting in an increase in the percentage suckling time, have been recorded previously for southern elephant seals (Bryden 1968) and northern elephant seals (*Mirounga angustirostris*; Le Boeuf et al. 1972). Suckling time also varied or tended to vary over the course of lactation in Weddell seals (*Leptonychotes weddellii*; Tedman and Bryden 1979), grey seals (*Halichoerus grypus*; Kovacs 1987*b*), harbour seals (*Phoca vitulina*; Arts and Rijniers 1986; Hedd et al. 1995), and harp seals (*Phoca groenlandica*; Kovacs 1987*a*). In addition, we report that presenting time increased from the first to the second week of lactation in southern elephant seals, whereas alertness and frequency of maternal calls decreased over this time. Because of these natural changes in behavioural parameters over the weeks of lactation (see also Tedman and Bryden 1979; Kovacs 1987*a*, 1987*b*), the stage of lactation should be considered as an additional factor in assessing the effect of human presence on behaviour.

Because the mass of pups at nutritional independence from their mothers is associated with their chances of survival (McMahon et al. 2000), we used this measure as a proxy for fitness in assessing the biological significance of

Table 3. Comparison of elephant seal behaviour directly before, during, and after human visits to seal harems, monitored in 24 mother–pup pairs on Isthmus East (area of high human presence).

				Repeated measures ANOVA			
Behavioural variable[a]	Before (n = 24)	During (n = 24)	After (n = 21)[b]	F	P	Power	Post-hoc test (Wilcoxon)
Time lying on side (%)	53.2±5.7	49.2±6.3	44.9±7.2	1.903	0.162	0.372	
Time suckling (%)	7.8±1.4	6.3±1.6	6.3±1.3	0.146	0.865	0.071	
Suckle bout duration (s)	227±40[c]	183±23[c]	242±51[c]	0.114	0.893	0.065	
Frequency of suckling (h^{-1})	1.6±0.4	1.3±0.3	1.5±0.4	0.224	0.800	0.083	
Frequency of maternal calls (h^{-1})	1.8±0.4	3.0±0.9	1.0±0.3	3.765	**0.032**	0.654	b ~ d ~ a, b > a
Frequency of alertness (h^{-1})	1.7±0.2	5.0±0.9	1.5±0.3	12.422	**<0.0001**	0.994	b < d > a, b ~ a
Frequency of flippering (h^{-1})	0.2±0.1	0.2±0.1	0.2±0.1	0.08	0.923	0.061	
Frequency of moves (h^{-1})	1.2±0.2	1.4±0.3	0.6±0.2	2.081	0.138	0.403	
Frequency of aggressive interactions with other females (h^{-1})	1.8±0.9	1.6±0.4	0.9±0.2	1.044	0.361	0.220	

Note: During visits, four or five investigators weighed newborn pups born to other females than those observed (see text). Means (± SE) represent individually monitored mother–pup pairs. Behavioural variables were analyzed using repeated measures ANOVA, after arcsine transformation of percentages and log transformation of durations and frequencies. If a significant difference was found, Wilcoxon's signed-rank test was applied for post-hoc comparisons: symbols b, d, and a refer to periods immediately before, during, and after human visits, respectively; symbols "<" and ">" refer to directions of significant differences ($P < 0.05$); symbol "~" refers to absence of a significant difference. Values of $P < 0.05$ are shown in boldface type.

[a] Mean duration of investigator visits, 24 min; mean observation duration before and after visits, 61 and 35 min, respectively.

[b] For three mother–pup pairs, no observations directly following human visits were available.

[c] Suckling was not recorded for all individuals during each observation session. Sample sizes for suckle bout durations before, during, and after visits were n = 15, 14, and 17, respectively. Sample size in the test, n = 12.

different types of mother–pup behaviour during lactation (Table 2). Although weaning mass of pups is primarily determined by the mass of their mothers at parturition (Arnbom et al. 1993, 1997; Fedak et al. 1996), the present study shows that it is also linked with some aspects of nursing behaviour during lactation. Mean suckle bout durations during the first and second week of lactation were significantly and positively associated with pup weaning mass, and similar but weaker tendencies were found for the proportion of time spent suckling in the same weeks; there was no evidence of such an association during later weeks (Table 2). Thus we provide correlational evidence that during the initial stages of lactation, suckle bouts are a factor limiting the growth rate of the pup. This implies that if disturbance leads to a reduction in average durations of suckle bouts, a negative effect on weaning mass and, hence, probability of survival is also to be expected.

At first hand, suckling time may appear a straightforward behavioural measure of milk intake and, as a result, growth rate of the pup. However, Cameron (1998), who reviewed this relation, concluded that suckling time is not a useful predictor of milk intake in many mammalian species. She discussed a number of possible confounding factors, including variation in the suckle ability of offspring (e.g., Higgins et al. 1988), the motivation for suckling (hunger) of juveniles (Hall et al. 1978; Mendl and Paul 1989), the mother's experience and ability to release milk (Green 1990), and the energy content of the milk (Oftedal et al. 1987). Some factors of influence in other species do not apply in elephant seals, because mothers fast throughout lactation and pup growth over this period is entirely dependent on milk intake (Ortiz et al. 1984; Fedak et al. 1996). Thus, there is no effect of variation in maternal diet during the lactation period itself (e.g., bighorn sheep (*Ovis canadensis*; Berger 1979)), and there is no possibility of additional feeding of solid food by juveniles during lactation (e.g., cat (*Felis catus*; Martin 1986)).

Our analysis suggests that after we account for maternal mass and suckling behaviour, the aggression of elephant seal mothers during the late stage of lactation is also positively associated with the weaning mass of their pups. Although earlier studies on elephant seal mothers and related species indicated that maternal aggression serves to protect and successfully wean the pup (Boness et al. 1982; Christenson and Le Boeuf 1978; McCann 1982), these did not report a possible effect on pup growth. We found no evidence that other types of behaviour during lactation either positively or negatively influenced the pup's weaning mass. We conclude that suckle bouts during early and middle lactation and, to a lesser extent, maternal aggression during late lactation (perhaps in addition to the proportion of time spent suckling) are the most robust measures of lactation behaviour to study in the context of maternal reproductive performance in elephant seals.

Direct and indirect effects of human presence

On Isthmus East, visits by research investigators to elephant seal harems resulted in directly observable behavioural responses by lactating adult females, as revealed by the significantly increased frequency of alert behaviour ($P < 0.0001$; see Table 3). In the presence of people, seal alertness was elevated to threefold levels in comparison with periods immediately before human presence. Directly after departure of researchers from harems, alertness returned to predisturbance levels; we found no difference in alertness between periods before or after human presence. The frequency of maternal calls was apparently lower after human visits than before them (Table 3). Nevertheless, it is unlikely that a negative indirect impact on pup growth occurred because of temporary

Table 4. Comparison of behaviour between 24 elephant seal mother–pup pairs on Middle Beach (remote study area) and 24 pairs on Isthmus East (area of high human presence) during three stages of the lactation period.

		Mean ± SE (*n*)		Effect of area			Interaction week × area		
Behavioural variable	Stage (week(s))	Middle Beach	Isthmus East	$F_{[1,41]}$	P	Power	$F_{[2,82]}$	P	Power
Time lying on side (%)	1	38.9±4.6 (24)	38.4±5.9 (22)	0.05	0.825	0.055	0.367	0.694	0.107
	2	46.8±4.2 (24)	52.2±5.1 (22)						
	3–4	52.3±3.5 (23)	52.7±3.6 (24)						
Time suckling (%)	1	3.8±0.6 (24)	2.8±0.9 (22)	0.631	0.431	0.121	0.76	0.471	0.175
	2	12.2±2.2 (24)	13.1±1.5 (22)						
	3–4	18.1±2.4 (23)	16.6±2.5 (24)						
Suckle bout duration (s)	1	175±35 (21)	119±29 (16)	0.657[a]	0.424	0.123	1.692[b]	0.192	0.341
	2	255±29 (24)	299±33 (22)						
	3–4	355±34 (23)	368±41 (24)						
Frequency of suckling (h^{-1})	1	1.2±0.2 (24)	1.1±0.3 (22)	0.656	0.423	0.124	0.471	0.626	0.125
	2	2.0±0.4 (24)	2.2±0.4 (22)						
	3–4	2.1±0.1 (23)	2.1±0.3 (24)						
Frequency of maternal calls (h^{-1})	1	2.1±0.4 (24)	2.6±0.5 (22)	0.196	0.660	0.072	0.834	0.438	0.188
	2	1.3±0.2 (24)	0.9±0.2 (22)						
	3–4	0.6±0.1 (23)	0.7±0.2 (24)						
Frequency of alertness (h^{-1})	1	2.6±0.4 (24)	2.2±0.3 (22)	0.122	0.729	0.063	0.829	0.440	0.188
	2	1.4±0.2 (24)	1.4±0.3 (22)						
	3–4	1.0±0.2 (23)	1.2±0.1 (24)						
Frequency of flippering (h^{-1})	1	1.0±0.4 (24)	0.6±0.2 (22)	1.707	0.199	0.248	0.509	0.603	0.131
	2	0.4±0.1 (24)	0.2±0.1 (22)						
	3–4	0.4±0.1 (23)	0.4±0.1 (24)						
Frequency of moves (h^{-1})	1	1.3±0.3 (24)	1.4±0.2 (22)	0.439	0.511	0.099	0.409	0.665	0.114
	2	1.1±0.2 (24)	1.2±0.2 (22)						
	3–4	0.9±0.1 (23)	1.2±0.2 (24)						
Frequency of aggressive interactions with other females (h^{-1})	1	1.2±0.3 (24)	1.2±0.3 (22)	1.542	0.221	0.228	2.439	0.094	0.478
	2	1.5±0.2 (24)	0.9±0.3 (22)						
	3–4	0.9±0.1 (23)	0.9±0.2 (24)						

Note: Differences in behavioural variables between areas were tested using repeated measures ANOVA, after arcsine transformation of percentages and log transformation of durations and frequencies.

[a] Error df = 32.

[b] Error df = 64.

changes in these aspects of behaviour: neither the frequency of alertness nor that of maternal calls was significantly associated with pup weaning mass (Table 2). Other behavioural variables were not significantly different directly before, during, and after human visits (Table 3). We detected no effect of human presence on flippering (sand flipping), a behaviour previously described as a displacement activity in response to conditions of stress (Laws 1956; Heath and Schusterman 1975; Lewis and Campagna 1998).

Observations carried out in the absence of people yielded no significant difference in any of the behavioural parameters examined between 24 mother–pup pairs in the frequently visited area of Isthmus East and an equal number of pairs in the remote area of Middle Beach (Table 4). In addition, natural changes in behaviour over the course of lactation were similar for mother–pup pairs in the two areas (Table 4, interaction of week with area). This indicated no indirect changes in mother–pup behaviour over a period of weeks as a result of the more intense levels of human activity on the Isthmus. Caution is required, however, when drawing this conclusion; based on all examined behavioural variables, the power to detect a significant effect was only moderate (power = 0.477). Therefore, possible small-scale changes in behaviour that may nevertheless be relevant may have remained undetected.

Implications at population level

We found that disturbance to elephant seal harems caused by visits by researchers resulted in direct but transient changes in some types of behaviour; we found no long-term changes in behaviour (over a period of weeks) as implied from the comparison made between the areas of high and low human presence. From a conservation perspective, fitness consequences of impacts should be considered (e.g., on the effects of disturbance on breeding success in Antarctic penguins, see Woehler et al. 1994, Giese 1996, and Cobley and Shears 1999). Thus, we examined how different types of behaviour during lactation are related to a proxy for fitness in elephant seals, as indexed by the mass of the pup at weaning. For those aspects of behaviour that were affected by human disturbance, including alertness and maternal call frequencies, no association with pup weaning mass was found. By contrast, for the behavioural variables apparently of highest significance for the growth of the pup—suckle bout durations during early and middle lactation and frequency of maternal aggression during late lactation—we were not able to detect any direct or indirect changes resulting from the presence of people.

We previously reported that, on average, mothers were longer and weaned pups heavier on remote Middle Beach than on human-accessible Isthmus East; however, there was no difference in the mass of pups at weaning in proportion to their mothers's mass (Engelhard et al. 2001). Moreover, the area difference in the size of mothers was already present at the start of the breeding season before the higher degree of human disturbance on Isthmus East took place (Engelhard et al. 2001). It remained unclear whether the apparent preference of larger females to breed on Middle Beach was due either to human activity near the research station in earlier years (cf. Thiel et al. 1992) or to natural differences between the areas, such as in the distribution of high-quality males or of male aggression (Cox 1981; Galimberti et al. 2000*a*, 2000*b*). However, the absence of any differences in pup weaning mass between sites other than that due to the size of mothers corresponded with the absence of any significant differences in behaviour during lactation and indicated no direct effect of human presence on lactational pup growth.

Hence, we find no evidence that human activity of the type and intensity investigated here will result in a decrease in fitness by affecting mother–pup behaviour and pup growth during the present lactation period. This study therefore lends credibility to the notion that the population decline observed at Macquarie Island is not due to human disturbance on land, including researcher activities, given that the absence of any significant effects is not due to the fairly moderate power of our analyses. As this southern elephant seal population has been investigated more extensively than any other of the species, it is postulated that the finding may also be applicable to other declining populations in the southern Indian and Pacific oceans (in accordance with Wilkinson and Bester 1988 and Engelhard et al. 2001).

Guidelines for disturbance research in pinnipeds

Behavioural studies investigating anthropogenic impacts on wildlife should focus on parameters with known or expected links to survival and (or) reproductive success (Hofer and East 1998; Gill et al. 2001). In southern elephant seals, suckling behaviour in young pups correlates with their mass at weaning (this study), and weaning mass influences their chances of survival (McMahon et al. 2000). Both of these links may also be present in other pinniped species, although the association between suckle bout duration and pup mass gain may well be restricted to phocid seals where females fast throughout lactation (see Oftedal et al. 1987). Associations between weaning mass and survival have also been shown for northern fur seals (*Callorhinus ursinus*; Baker and Fowler 1992), Hawaiian monk seals (*Monachus schauinslandi*; Craig and Ragen 1999), and grey seals (Hall et al. 2001). In the impact assessment of human disturbance on populations of pinniped species characterized by lactation fast, we suggest that detailed recordings on suckle bout durations are a more sensitive behavioural indicator than observations on the most conspicuous behavioural responses, such as the levels of alertness.

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