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ORIGINAL PAPER

Intra-sexual female agonistic behaviour of the South American sea lion (*Otaria flavescens*) in two colonies with different breeding substrates

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Abstract Female agonistic behaviour during pregnancy and lactation is common in several pinnipeds and has been associated to pup or territory defence. Previous studies on female agonistic behaviour in pinniped breeding groups have not usually considered the number of females per breeding group, which could influence the degree of aggressiveness. We compared female agonistic behaviour (open-mouth displays and bites) within two colonies with different breeding substrates (homogeneous, Punta Norte; heterogeneous, Pirámide) of South American sea lions using two methods: weighted means and general linear models. We found that both aggressive interaction rates were significantly affected by female density, which accounted for a greater proportion on the variability in bite rates than in open-mouth rates. Controlling for the number of females, we found with both methods that open-mouth rates were higher than bite rates within the Pirámide colony; however, no differences were found within the Punta Norte colony. In Pirámide, open-mouth rates could be used more often as threats to minimise the chances of more severe aggressions. The conclusion is that females vary their use of agonistic interactions in relation to their density in the colony with heterogeneous substrate, which may be related to the presence of limited numbers of tide pools that heightens competition for thermoregulatory resources.

Keywords *Otaria flavescens* · Pinnipeds · Breeding groups · Female aggression · Otariids · Patagonia

Introduction

Female agonistic behaviour during pregnancy and lactation is relatively widespread in otariids (Le Boeuf and Campagna 1994). Several studies point out that females after parturition exhibit increasing levels of intra-sexual agonistic behaviour, defending areas of about one body length around their pups (Francis 1987; Carey 1992; Harcourt 1991, 1992; Phillips 2003). Such behaviour may increase the survival probabilities of newborns during the first days after birth, as mothers stand out for their pups against physical aggression from females and attempts from other pups to steal milk (Christenson and Le Boeuf 1978; Svare 1990; Bowen 1991; Harcourt 1992; Maestripieri 1992; Le Boeuf and Campagna 1994; Ebensperger 1998). Female aggression in otariids has also been related to competition for space in breeding colonies, particularly in species breeding at high densities or in colonies with limited availability of high-quality substrates (e.g. tide pools; Doidge et al. 1984; Francis 1987; Campagna and Le Boeuf 1988a; Carey 1992; Maestripieri 1992; Majluf 1992).

Previous comparisons of different levels of female aggressiveness within and between colonies have generally employed the mean rate of female agonistic inter-

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actions (e.g. Harcourt 1992; Cassini 2001). However, such comparisons may be biased if the number of females per breeding group (e.g. males that defend a group of females or a territory with females) varies considerably between colonies or between different quality areas within colonies, simply because denser female aggregations could trigger more aggressive interactions. Another potential problem is that different types of female aggressive interactions have usually been lumped and studied together (e.g. Harcourt 1991, 1992; Boness et al. 1998; Cassini 2001; but see Phillips and Stirling 2001). This could reduce the analytical power of comparisons because some interactions could have contrasting or synergistic effects, which could modify the resulting patterns of female aggressiveness.

In this study, we compared the degree of female aggressiveness within two breeding colonies of South American sea lions (*Otaria flavescens*) with different substrates (Pirámide: heterogeneous substrate because of the presence of thermoregulatory resources, tide pools, that are distributed patchily; Punta Norte: homogeneous substrate because of the lack of thermoregulatory resources) by contrasting the rates of two types of common female–female agonistic interactions (open mouth and bites) having different levels of aggressiveness (Carey 1992). We predicted that (a) the rate of aggression would increase with the number of females per breeding group, and (b) bites would generate higher interaction rates controlling for the number of females per breeding group because of their greater level of aggressiveness.

Study animal

To better understand the study design, it is important to summarise briefly the breeding biology of South American sea lions in light of previous research (Campagna 1985). Males defend a position where females give birth and mate (Campagna and Le Boeuf 1988a,b; Vilá and Cassini 1990), which is a female-defence polygyny system. In Península Valdés, Argentina, during most of the second week of January, breeding females give birth to one pup and nurse it for 1 week (Campagna and Le Boeuf 1988b). Females are in oestrus for approximately 1 day, and mating occurs during the third week of January, when the proportion of adult males to receptive females peaks (Campagna and Le Boeuf 1988b). After copulating, females alternate 1–5 days foraging at sea and 2–5 days nursing their pups in the colony (Campagna and Le Boeuf 1988b; Werner and Campagna 1995). The probability of mother–pup separation in this species is high, taking into account that the occurrence of pup abductions by sub-adult males can be greater than 21% of the pups (Campagna et al. 1988).

Materials and methods

The Punta Norte (42°04′S and 63°47′W) and Pirámide (42°35′S and 64°17′W) colonies are both located in Península Valdés. Sampling took place in Punta Norte in January 1995 (25 days) and in Pirámide in January 1985 (20 days). The data for this study were gathered with the same methodological procedures (see below).

Differences in breeding substrates between colonies have been reported to influence the distribution of breeding individuals (Campagna and Le Boeuf 1988a). In Punta Norte, about 100 adult males and 500 adult females grouped along the shoreline on a uniform pebble beach, without tide pools or vegetation (Campagna 1985; Campagna and Le Boeuf 1988a). Two areas of varying density were formed: the centre (area of the highest female density and closer to the watermark, as described in Campagna and Le Boeuf 1988b) and the periphery. The Pirámide colony lay on flat rocky shelves bordered by high cliffs that formed a steep wall. About 650 adult individuals (males and females) were distributed in areas with and without thermoregulatory resources (tide pools and areas shaded by boulders or the cliff; Campagna and Le Boeuf 1988a; Vilá and Cassini 1990). We sampled a portion of the Pirámide colony with a maximum of 55 adult males and 245 adult females.

Twenty-four females in Punta Norte and 17 females in Pirámide were studied during the reproductive period. Females were marked, along with their pups, with paint pellets (Campagna and Le Boeuf 1988b). Marking took place mainly during the first week of the breeding season, before the density of the colony reached the peak number of individuals, which allowed us to mark individuals in different areas of each colony. We observed only adult females but not wandering females that did not engage in reproductive activities. We recorded daily the position of marked individuals in the colony using a grid system. The maximum number of marked females per male was two, which happened seven times during the breeding season. We conducted 30-min focal observations on four to five marked females per day. The selection of females for sampling on a given day was based on their availability in the colony (some females were on foraging trips). In this study, we included similar numbers of focal observations per week per individual. On average, the individuals included in our data set were sampled 7.07 times (SD=3.04 times) in Punta Norte and 7.47 times (SD=2.98 times) in Pirámide.

We considered agonistic interactions between adult females but not mother–pup interactions, as our purpose was to assess the degree of intra-sexual agonistic behaviour in relation to members of the same age class. We studied two common types of female agonistic interactions within the behavioural repertoire of this species (Cassini 1985; Campagna and Le Boeuf 1988b; Fernández-Juricic et al. 1999): open-mouth displays (the female's head was oriented towards her opponent with the lower canines and vibrissae pulled back) and bites (quick biting motions with body contact at the opponent's head or neck). These agonistic interactions indicate increasing levels of aggression (Carey 1992): open mouth<bite. Female sea lions may also display a third type of agonistic interaction: grunts (a low-intensity, low-frequency, brief call directed towards the opponent; Fernández-Juricic et al. 1999). We did not include grunts in our analyses because they were difficult to hear in Pirámide from the observation point located 20 m above the animals, which could be a source of bias. Grunts were recorded in Punta Norte, but a preliminary analysis indicated no significant effects of female density (data available from the authors).

During 30-min focal observations, we recorded and classified all agonistic interactions initiated by the target female and the number of adult females defended per male. Females were considered associated with a male when they were less than two female body lengths from the focal male in Punta Norte (Campagna and Le Boeuf 1988b). Topographic features were used as landmarks to define territorial boundaries and number of adult females defended by males in Pirámide (Campagna and Le Boeuf 1988a). A male was considered a neighbour when he had defended an adjacent position for at least 3 days (Fernández-Juricic et al. 2001).

We calculated open-mouth and bite rates per female by averaging the number of each type of agonistic interaction per 30 min for each adult female across the breeding period; hence, our sample size equalled the number of marked females. We preferred this approach to using several samples from each marked female, because we reduced the confounding effects of individual variations (which would lead to pseudoreplication), because our observations took place when females were focussed upon breeding activities only (reducing the chances of non-breeding time budget variations), and because taking the average of raw-count data (number of behavioural events in 30-min focal samples) increased the normality of the studied variables.

Before performing statistical tests, we checked all variables for normality with the Kolmogorov–Smirnov test. We found that in Pirámide, the three factors studied followed a normal distribution (number of females defended by a male: d=0.12306, P>0.20; open-mouth rate: d=0.15482, P>0.20; bite rate: d=0.18109, P>0.20). In Punta Norte, two of the three factors followed a normal distribution (female density: d=0.16238, P>0.20; bite rate: d=0. 16111, P>0.20), but open-mouth rates did not (d=0.27667, P<0.05). A close examination at the normal probability plot of that variable showed minor deviations from normality, but we ran generalised linear models with this variable (McCulloch and Searle 2001) and got the same results as those with general linear models (GLMs; see below), so we decided to present the latter. Furthermore, we checked for equality of variances considering the two studied colonies and found homogenous variances in the dependent factors (Levene's test; open-mouth rates: W=3.62, P=0.064; bite rates: W=0.48, P=0.492).

We first analysed the effects of density on each aggressive interaction across colonies. We used two GLMs (one for open-mouth rates and one for bite rates), with density as a fixed factor and colony as a random factor to account for the variance attributed to inter-site differences.

We used two alternative ways of comparing female aggressiveness within colonies: (a) weighting the data to take into account the number of females in a breeding group and (b) conducting a GLM that considers simultaneously the levels of the categorical factor (type of aggressive interaction) and the number of females in the analysis.

We weighted the aggression rates by dividing them by $n-1$, where n = mean number of females defended by a male. To analyse the difference between mean-weighted agonistic interaction rates within colonies and mean number of adult females defended by males between colonies, we employed a t test for independent samples. We used GLMs (McCulloch and Searle 2001) including the rates of agonistic interaction as the dependent factor, type of aggression as the categorical independent factor and number of females as the continuous independent factor. We used linear models because most of our variables tended towards normality, and GLMs are robust to variations in normality (Underwood 1997), variances were homogeneous and each data point corresponded to a different female, which minimised non-independence problems. We also checked the distribution of the residuals in all GLM analyses, and they all approached normality. It should be noted that our goal in this study is *not* to characterise the shape of the relationship between female aggressiveness and female density (see Cassini and Fernández-Juricic 2003) but to assess whether agonistic interaction rates differ within colonies, controlling for density effects.

Results

The mean number of females defended by males was significantly higher in Pirámide (10.21±6.19) than in Punta Norte (3.84±1.98; t_{32}=4.72, P<0.001).

Open-mouth rates increased significantly with an increase in the density of females in the breeding group in both colonies (intercept: $F_{1,\ 38}$=0.82, P=0.467; density:

$F_{1,\ 38}$=13.81, $P<0.001$; partial η^2=0.26), controlling for the difference in open-mouth rates between colonies ($F_{1,\ 38}$= 4.09, $P<0.05$) (Fig. 1). Density also increased bite rates in both colonies (intercept: $F_{1,\ 38}$=0.06, P=0.837; density: $F_{1,\ 38}$=35.97, $P<0.001$; partial η^2=0.49), controlling for inter-colony differences (colony: $F_{1,\ 38}$=10.32, $P<0.01$; Fig. 1).

Within the Punta Norte colony, no significant variation was found between weighted mean open-mouth and bite rates (0.28±0.41 open mouths per 30 min, 0.38±0.43 bites per 30 min, t_{46}=−0.73, P=0.473). The GLM yielded a similar result, with no variations between open-mouth and bite rates (1.13±1.64 open mouths per 30 min, 0.92±0.79 bites per 30 min; intercept: $F_{1,\ 45}$=2.77, P=0.103; agonistic display: $F_{1,\ 45}$=0.52, P=0.473), after controlling for the significant effects of the number of females defended by a male ($F_{1,\ 45}$ =29.82, $P<0.001$).

Within the Pirámide colony, weighted mean open-mouth rates were higher than bite rates (0.81±0.92 open mouths per 30 min, 0.09±0.07 bites per 30 min, t_{32}=3.20, $P<0.01$). Using the GLM, we also found higher open-mouth than bite rates (4.56±3.07 open mouths per 30 min, 1.04±1.14 bites per 30 min; intercept: $F_{1,\ 31}$=1.51, P=0.228; agonistic display: $F_{1,\ 31}$=25.90, $P<0.001$), controlling for the significant effects of the number of females defended by a male ($F_{1,\ 31}$=11.07, $P<0.01$).

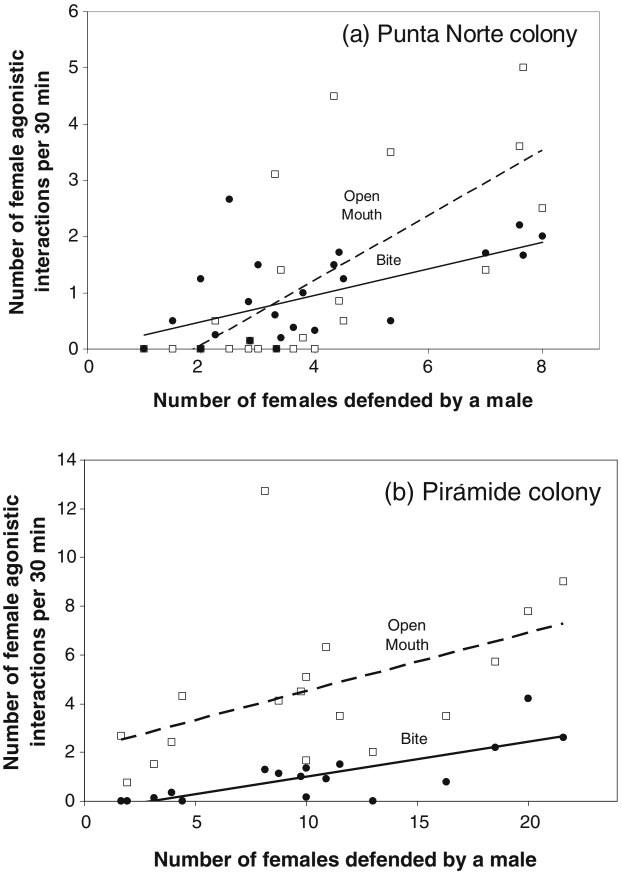

Fig. 1 Differences between South American sea lion female aggressive interaction rates within the **a** Punta Norte and the **b** Pirámide colonies. *Open squares* represent open mouth displays, whereas *filled circles* represent bites

Discussion

The number of females defended by a male affected significantly South American sea lion female–female interaction rates, as found in this (Cassini and Fernández-Juricic 2003) and other species (e.g. Harcourt 1991, 1992). Female density had a greater effect on bite rates than open-mouth rates (e.g. twice as much variability explained), which confirms the higher degree of aggressiveness of bites. Other studies also found that the number of females defended by a male could exert a substantial effect on other female breeding parameters, such as individual activity budgets (Twiss et al. 2000). These results indicate that care should be exercised when interpreting results that compare female aggressive interactions between colonies or areas within a colony with different number of females per breeding group without controlling for density effects (e.g. Cassini 2001).

We used two methods to control for density effects. Weighted means do not allow for the partitioning of the variance between independent factors, which could render biased parameters under some conditions (e.g. Freckleton 2002). The GLM solves that problem by assessing the effect of an independent factor but controlling simultaneously for the number of females. Despite these differences, our results seem robust, as both methods yielded the same trends regarding differences in aggressive interaction rates.

The rates of open-mouth displays and bites were similar within the Punta Norte colony but differed in the Pirámide colony. This pattern of variation may be related to the presence of thermoregulatory resources. In Pirámide, tide pools reduce thermoregulatory stress during the breeding season (Campagna and Le Boeuf 1988a). The spatial limitation in the availability of tide pools can increase the number of females per breeding group and trigger differences in the use of aggressive interactions to compete for these resources.

In Pirámide, open-mouth rates were higher than bite rates, contrary to our prediction. This result can be explained by the fact that threats can function to minimise the likelihood of more severe aggressions (Bradbury and Vehrencamp 1998). Another factor related to this pattern may be the response of males to female–female agonistic interactions. Otariid males have a tendency to interrupt female interactions (Hamilton 1934; Miller 1974; Cassini 1985; Harcourt 1991; Fernández-Juricic et al. 1999), likely because such sort of disturbance within the breeding group may intensify activity levels in the surroundings and fights between males, with the potential risks for males of losing females or their positions in the breeding area (Campagna et al. 1988; Fernández-Juricic et al. 2001). South American sea lion males tend to react to an increase in the rate of female open-mouth displays but not to female bites (Fernández-Juricic and Cassini, unpublished data). Thus, by responding to open-mouth displays, males would reduce the probability that agonistic interactions escalate to greater levels of disturbance (e.g. bites).

Our results have implications for the relationship between male harassment, female–female competition and female reproductive success. Joining breeding groups is a profitable strategy in species in which adult females are harassed by adult males (Clutton-Brock et al. 1993; Boness et al. 1995; Carranza and Valencia 1999; Cassini 1999; Galimberti et al. 2000). Breeding groups can minimise the interactions between members of the opposite sex, but they can also arise intra-sexual agonistic behaviour (e.g. female–female), which can jeopardise offspring survival (Le Boeuf and Campagna 1994; Bradshaw et al. 2000). In pinniped species, pup mortality is known to be density dependent (Anderson et al. 1977; Doidge et al. 1984; Fowler 1987; Harcourt 1992; Le Boeuf and Briggs 1977; but see Twiss et al. 2003). Deaths of pups occur mainly when social events separate them from their mothers, and consequently they starve, are crushed by males or suffer aggression from alien females (Le Boeuf and Briggs 1977; McCann 1982; Doidge et al. 1984; Vilá and Cassini 1990; Bowen 1991; Campagna et al. 1992; Harcourt 1992). We found that females use agonistic interactions in different ways in a colony with heterogeneous substrates to probably reduce the risk of pup injuries and increase its survival. Future studies should compare female physiological strategies between colonies with different distribution of breeding resources to better understand the costs and benefits of female agonistic behaviour.

The cost/benefit relationship of different agonistic strategies can eventually influence how females distribute in areas with different quality of breeding resources. A recent model to explain the distribution of pinnipeds (Cassini 2000) predicts that females would form denser aggregations than expected according to the distribution of resources to minimise male harassment through dilution. However, the costs of female competition would reduce the size of breeding groups that maximises breeding success. The model assumes that the costs of female competition (f) are linearly related to female density (F) in the following way: $f = qF$, where q stands for the coefficient of female interference (Cassini 2000). The GLM approach used in this study can potentially be used to test some of its predictions because it estimates these parameters. For instance, species with different coefficients of female agonistic behaviour would exhibit variations in the different optimal female density per breeding group because of different levels of interference (see Cassini 1999, 2000). The differences in patterns of gregariousness between some otariid species (Gentry 1975; Trillmich and Trillmich 1984) may be a good case study. In this context, fur seals are expected to have higher coefficients of intra-sexual aggression (greater coefficients of interference) than sea lions, which are more tolerant to body contact. This prediction has yet to be tested.

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References

Anderson SS, Baker JR, Prime JH, Baird A (1977) Mortality in grey seal pups: incidences and causes. J Zool 189:407–417

Boness DJ, Bowen WD, Iverson SJ (1995) Does male harassment of females contribute to reproductive synchrony in the grey seal by affecting maternal performance? Behav Ecol Sociobiol 36:1–10

Boness DJ, Craig MP, Honigman L, Austin S (1998) Fostering behavior and the effect of female density in Hawaiian monk seals, *Monachus schauinslandi*. J Mammal 79:1060–1069

Bowen WD (1991) Behavioral ecology of pinniped neonates. In: Renouf D (ed) Behavior of pinnipeds. Chapman & Hall, London, pp 66–127

Bradbury JW, Vehrencamp SL (1998) Principles of animal communication. Sinauer, Sunderland

Bradshaw CJA, Davis LS, Lalas C, Harcourt RG (2000) Geographic and temporal variation in the condition of pups of the New Zealand fur seal (*Arctocephalus forsteri*): evidence for density dependence and differences in the marine environment. J Zool 252:41–51

Campagna C (1985) The breeding cycle of the southern sea lion, *Otaria byronia*. Mar Mamm Sci 1:210–218

Campagna C, Le Boeuf B (1988a) Thermoregulatory behaviour in the sea lion and its effect on the mating system. Behaviour 107:72–90

Campagna C, Le Boeuf B (1988b) Reproductive behaviour of southern sea lions. Behaviour 104:233–261

Campagna C, Le Boeuf B, Cappozzo HL (1988) Groups raids: a mating strategy of male Southern sea lions. Behaviour 105:224–249

Campagna C, Bisioli C, Quintana F, Perez F, Vila A (1992) Group breeding in sea lions: pups survive better in colonies. Anim Behav 43:541–548

Carey PW (1992) Agonistic behaviour in female New Zealand fur seals, *Arctocephalus forsteri*. Ethology 92:70–80

Carranza J, Valencia J (1999) Red deer females collect on male clumps at mating areas. Behav Ecol 10:525–532

Cassini MH (1985) Comportamiento social de las hembras adultas del Lobo Marino del Sur, *Otaria byronia* (Blainville, 1820) durante la temporada de cría. Rev Latinoam Psicol 17:339–350

Cassini MH (1999) The evolution of reproductive systems of pinnipeds. Behav Ecol 10:612–616

Cassini MH (2000) A model on female breeding dispersion and the reproductive systems of pinnipeds. Behav Processes 51:93–99

Cassini MH (2001) Aggression between females in the South American fur seal *Arctocephalus australis*. Mamm Rev 31:169–172

Cassini MH, Fernández-Juricic E (2003) Costs and benefits of joining South American sea lion breeding units: testing the assumptions of a model on female breeding dispersion. Can J Zool 81:1154–1160

Christenson TE, Le Boeuf BJ (1978) Aggression in the female northern elephant seal, *Mirounga angustirostris*. Behaviour 64:158–172

Clutton-Brock TH, Deutsch JC, Nefdt RJC (1993) The evolution of ungulate leks. Anim Behav 46:1121–1138

Doidge DW, Croxall JP, Baker JR (1984) Density-dependent pup mortality in the Antarctic fur seal *Arctocephalus gazella* at South Georgia. J Zool 202:449–460

Ebensperger LA (1998) Strategies and counterstrategies to infanticide in mammals. Biol Rev Camb Philos Soc 73:321–346

Fernández-Juricic E, Campagna C, Enriquez V, Ortiz CL (1999) Vocal communication and individual variation in breeding South American sea lions. Behaviour 136:495–517

Fernández-Juricic E, Campagna C, Enriquez V, Ortiz CL (2001) The effects of social contexts on South American sea lion male vocal rates. Mar Mamm Sci 17:387–396

Francis JM (1987) Interfemale aggression and spacing in the northern fur seal *Callorhinus ursinus* and the California sea lion *Zalophus californianus*. Ph.D. thesis, University of California, Santa Cruz

Fowler CW (1987) A review of density dependence in populations of large mammals. Curr Mammal 1:401–441

Freckleton RP (2002) On the misuse of residuals in ecology: regression of residuals vs. multiple regression. J Anim Ecol 71:542–545

Galimberti F, Boitani L, Marzetti I (2000) The frequency and costs of harassment in southern elephant seals. Ethol Ecol Evol 12:345–365

Gentry RL (1975) Comparative social behavior of eared seals. Rapp P-v Reun—Cons Int Explor Mer 169:164–189

Hamilton JE (1934) The Southern sea lion *Otaria byronia* (Blainville). Discov Rep 8:269–318

Harcourt R (1991) Maternal aggression in the South American fur seal in Peru. Can J Zool 70:320–325

Harcourt R (1992) Factors affecting early mortality in the South American fur seal (*Arctocephalus australis*) in Peru: density-related effects and predation. J Zool 226:259–270

Le Boeuf BJ, Briggs KT (1977) The cost of living in a seal harem. Mammalia 41:167–195

Le Boeuf BJ, Campagna C (1994) Protection and abuse of young in pinnipeds. In: Parmigiani S, vom Saal FS, Chur, R (eds) Infanticide and parental care. Academic, Harwood, pp 257–276

Maestripieri D (1992) Functional aspects of maternal aggression in mammals. Can J Zool 70:1069–1077

Majluf P (1992) Timing of births and juvenile mortality in the South American fur seal in Peru. J Zool 227:367–383

McCann TS (1982) Aggressive and maternal activities of female southern elephant seals (*Mirounga leonina*). Anim Behav 30:268–276

McCulloch CE, Searle SR (2001) Generalized, linear and mixed models. Wiley, New York

Miller EH (1974) Social behaviour between adult male and female New Zealand fur seals, *Arctocephalus forsteri* (Lesson) during the breeding season. Aust J Zool 22:155–173

Phillips AV (2003) Behavioral cues used in reunions between mother and pup south American fur seals (*Arctocephalus australis*). J Mammal 84:524–535

Phillips AV, Stirling I (2001) Vocal repertoire of South American fur seals, *Arctocephalus australis*: structure, function, and context. Can J Zool 79:420–437

Svare BB (1990) Maternal aggression: hormonal, genetic, and developmental determinants. In: Krasnegor NA, Bridges RS (eds) Mammalian parenting: biochemical, neurobiological, and behavioural determinants. Oxford Univ. Press, Oxford, pp 179–210

Trillmich F, Trillmich KGK (1984) Mating systems of pinnipeds and marine iguanas: convergent evolution of polygyny. Biol J Linn Soc 21:209–216

Twiss SD, Caudron A, Pomeroy PP, Thomas CJ, Mills JP (2000) Finescale topographical correlates of behavioural investment in offspring by female grey seals, *Halichoerus grypus*. Anim Behav 59:327–338

Twiss SD, Duck C, Pomeroy PP (2003) Grey seal (*Halichoerus grypus*) pup mortality not explained by local breeding density on North Rona, Scotland. J Zool (Lond) 259:83–91

Underwood AJ (1997) Experiments in ecology: their logical design and interpretation using analysis of variance. Cambridge Univ. Press, Cambridge

Vilá BL, Cassini MH (1990) Aggressiveness between females and mother–pup separation in the southern sea lion, in Chubut, Argentina. Rev Chil Hist Nat 63:169–176

Werner R, Campagna C (1995) Diving behavior of lactating southern sea lions in Patagonia. Can J Zool 73:1975–1982