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Social effects of space availability on the breeding behaviour of elephant seals in Patagonia

R. BALDI*†, C. CAMPAGNA*‡, S. PEDRAZA* & BURNEY J. LE BOEUF§

**Centro Nacional Patagónico, Argentina*

†Universidad Nacional de la Patagonia, Argentina

‡Wildlife Conservation Society, New York, U.S.A.

§Institute of Marine Sciences and Department of Biology, University of California at Santa Cruz, U.S.A.

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Abstract. The Patagonian breeding colony of southern elephant seals, *Mirounga leonina*, of Península Valdés, Argentina is characterized by long, continuous, homogeneous and spacious beaches. Reproduction in this colony occurs at the lowest group densities reported for the species. The availability of ample space resulted in the dispersion of reproductive females along 160 km of coastline, with a range of 0–300 reproductive individuals per km. Females grouped together in small harems (median=11 females, range 2–122, N=432), and individual distance between females was one to two female body lengths. Body contact within the harem was rare. Consequently, agonistic interactions (AIs) between females and female aggression (Ag) towards alien pups occurred infrequently (median rate=4 AIs/female per 100 h and 1 Ag/pup per 100 h, respectively). Pup mortality rate was low for an elephant seal rookery (3.5% for 3487 pups). Most dead pups were stillborn, and only three of 38 pups whose cause of mortality could be determined died from trauma or starvation following mother–pup separation. Female dispersal allowed many males to have access to females. About 45% of all males of reproductive size in the colony (about 1000 individuals) had a harem. Most adult males mated with receptive females. Low-density breeding conditions benefited female reproductive success through an increase in pup survival. Female dispersal resulted in small harem size, however, and limited the potential for polygyny.

The most polygynous mammalian species are found among the pinnipeds (Riedman 1990). The degree of pinniped polygyny is affected by ecological variables (Bartholomew 1970; Boness 1991). Availability of space in the breeding area is a key ecological aspect affecting the mating system. Space availability may determine female distribution and the degree of female aggregation (Emlen & Oring 1977). Female density during reproduction, in turn, affects the mating behaviour and reproductive success of both sexes (Bartholomew 1970; Boness & James 1979; Stirling 1983). This paper is about the effect of having ample space for breeding on female distribution and reproductive success and on male mating success for southern elephant seals, *Mirounga leonina*, at Península Valdés, Argentina.

Elephant seals, the most polygynous of all pinnipeds, typically reproduce on islands with restricted space to give birth and mate (Laws 1956; Carrick et al. 1962; Le Boeuf & Laws 1994). Breeding occurs in dense harems where density-dependent mother–pup separation, pup starvation and pup mortality are high (Carrick et al. 1962; Le Boeuf & Briggs 1977; Condy 1979; Van Aarde 1980; McCann 1982; Riedman & Le Boeuf 1982).

Conversely, elephant seals in Patagonia breed at the lowest density conditions reported for the species (Campagna & Lewis 1992). The long, continuous, homogeneous and spacious beaches of Península Valdés do not confine females to restricted places along the coast (Le Boeuf &

Correspondence: R. Baldi, Centro Nacional Patagónico, 9120 Puerto Madryn, Chubut, Argentina (email: UNBALDI@CENPAT.EDU.AR). B. J. Le Boeuf is at the Institute of Marine Sciences and Department of Biology, University of California, Santa Cruz, CA 95064, U.S.A.

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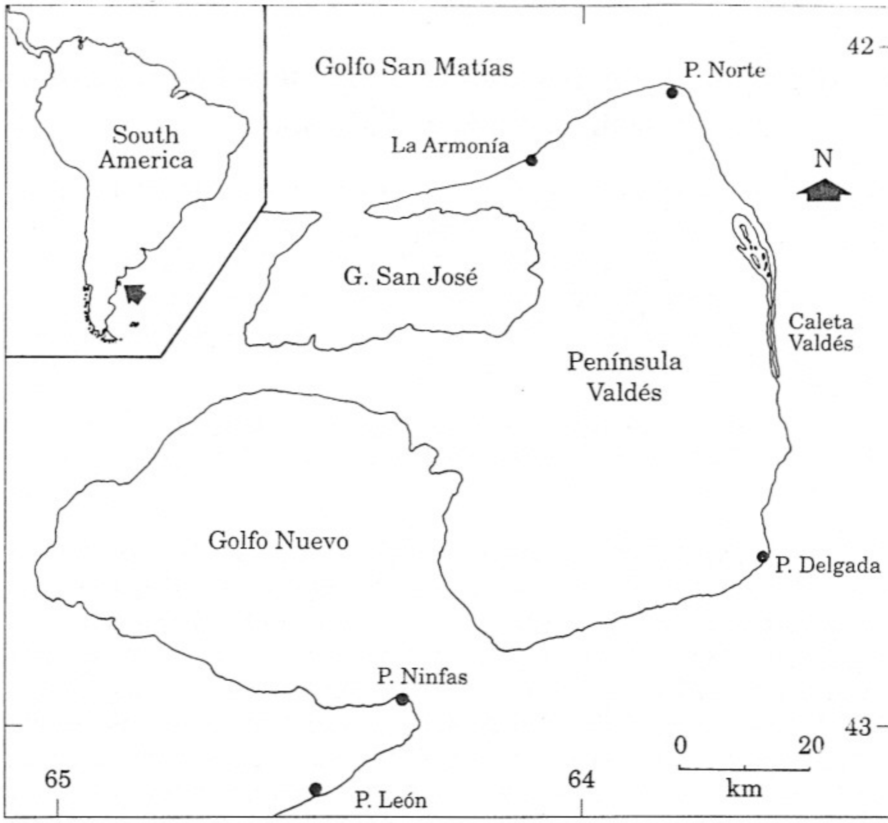

Figure 1. Geographic location of the areas of study.

Petrinovich 1974; Honigman 1988; Campagna et al. 1993). In this demographic study, the resulting small harem size and female dispersal increased female reproductive success through high pup survival, while limiting the polygyny potential of dominant bulls.

METHODS

This study was conducted during four reproductive seasons (mid-August to early November 1988 and 1990–1992) at two study areas of the extended southern elephant seal breeding rookery of Península Valdés (Campagna & Lewis 1992): La Armonia beach (1988) and Punta Delgada (1990–1992) (Fig. 1). Additional data on harem size and pup mortality were gathered at Caleta Valdés (October 1991, 1992) and other breeding beaches along the coast of the Península (Punta León to Punta Ninfas and Punta Norte; Fig. 1).

We determined the size of all harems in the rookery from photographs taken during aerial surveys (Campagna & Lewis 1992). We used data from the 1990 aerial census to describe demographic status. Terrestrial counts, preceding and following aerial censuses, were conducted every 2–3 weeks of stretches of coast along Caleta Valdés, Punta León to Punta Ninfas, and Punta Norte. Methods for aerial and terrestrial surveys are described elsewhere (Campagna & Lewis 1992; Campagna et al. 1993).

We defined a harem as a group of two or more females with an alpha bull in attendance (Le Boeuf 1974). Bachelors were males aggressively excluded from harems by the harem bull. We described the external two rows of females in a harem as peripheral. We measured the maximum width and length of two harems at Punta Delgada four times per day to obtain a rough estimate of variation in harem surface from tidal condition and female numbers. Mean surface of beach occupied per female was calculated by dividing total harem surface by harem size. We divided the breeding season into three periods: early (first 3 weeks of September), peak (last week of September and first 2 weeks of October) and end (late October and first week of November).

We kept serial records (Altmann 1974) of the following behavioural data during daylight hours throughout the 1990 and 1991 breeding seasons at three harems at Punta Delgada: (1) frequency and context of female agonistic interactions (AIs); (2) frequency and context of events of female–pup aggression (Ag) and individuals involved; (3) duration, context, place of occurrence and consequences of mother–pup separation; (4) number of copulations by males. We used the outcome of agonistic interactions to determine female dominance following McCann (1982). Agonistic interactions consisted of one or several of the following components: raised torso, repeated threat vocalizations accompanied by open mouth threat with the head extended rapidly toward the opponent and biting (Christenson & Le Boeuf 1978; McCann 1982). We recorded as mother–pup separation all events in which a mother was at least 10 m away from her pup, or as the disruption of the mother–pup bond because of the positioning of an adult male or female between them (modified from Riedman & Le Boeuf 1982).

We obtained scan samples (Altmann 1974) every 2 h, recording: (1) position of marked females in a harem, (2) distance of marked females to their closest neighbours, expressed in female body lengths (one body length estimated as 2.5 m; Laws 1953), (3) distance between mothers and pups in pup body lengths (one body length estimated as 1 m) and (4) relative position of marked females in the harem (central or peripheral).

We recognized observed individuals (about 230 females and 60 males) by a name printed with a black dye or a bleaching agent (Le Boeuf & Peterson 1969). Marking efforts were similar between both studied areas and breeding seasons. Marked females were categorized according to body size, as large, medium or small, within 1 day after parturition (Campagna et al. 1992). We kept identification cards and a serial record of the daily presence and key activities of marked seals (i.e. arrival, parturition, copulation, weaning, departure). We categorized males as reproductively mature based on their size, behaviour and secondary sexual characteristics (Le Boeuf 1974). Dead pups were removed from the harems and marked. Pup mortality was calculated for the period from birth to weaning (about 1 month; Campagna et al. 1992).

Because dispersion of data points was typically high for most quantified variables, we used modes, medians and ranges instead of means and standard deviations as prevalent central tendency and variability measures. Tests are two-tailed unless otherwise specified. We set an alpha level of 0.05. Multi-sample median tests were performed following Zar (1984) (Table I).

RESULTS

Distribution of Individuals and Harems

Reproductive individuals were widely dispersed along 160 km of coastline (Table I). Individual dispersion was reflected in many scattered and small harems (Table I, Fig. 2). A median harem size of 11 was calculated for the entire breeding area (Table I). Ninety-one per cent of 432 harems were composed of less than 50 females (Fig. 2). Only two to three harems per season had more than 100 females.

Density of breeding groups in the most crowded part of the rookery (Punta Delgada and the southwest of Península Valdés) ranged from one to five harems/km (Table II). In low-density areas (north and northeast of the colony), harems were spaced up to 10 km apart from each other.

Within the harems, individuals were spread apart, and each harem took a large area of beach. For example, a group of 85 females at peak season occupied an area of 1000 m^2 at high tide, and 4000 m^2 at low tide. Harems of over 100 females took at least 12 000 m^2 of beach. Female density within harems remained low even when the number of females increased. A five-fold increase in size of one harem (from 17 to 85 females) matched a 13-fold increase in its surface (from 300 m^2 to near 4000 m^2 at low tide). Thus, minimum available area per female remained almost constant during the season (Fig. 3). Even during the most stringent conditions of space limitation (high tide and peak season), individual distance between females remained more than one body length (Table I).

Agonistic Behaviour

As females were dispersed, agonistic interactions occurred infrequently (Table I). The median rate of agonistic interactions did not vary significantly as a function of time within the season (early versus peak versus late = 3.9, 3.6, 4.2 AIs/female per 100 h, respectively; median

Table I. Summary of main variables, methodologies and results

Variable	Method	Results
Number of reproductive individuals per km of coastline	Aerial census	Mean=62 (range 0–300)
Harem size	Aerial census	Median=11, N=432 harems
Harem density	Terrestrial counts	See Table II
Individual distance between females within the harem	Scan samples of marked females	Mode=1–2 female body lengths (range 0.5–4), N=5331 scan samples
Rate of female agonistic interactions	Serial record	Median=4 AIs/female per 100 h (range 0–14), N=326 AIs observed in 140 h
Rate of female aggression towards alien pups	Serial record	Median=1 Ag/pup per 100 h (range 0–6), N=95 Ag observed in 140 h
Mother–pup distance	Scan samples	See Table III
Mother–pup separation	Serial record	N=216 separations for 112 marked pups at two harems during 473 h (rate=0.4 separations/pup per 100 h)
Pup mortality	Direct counts during terrestrial surveys	3.5% of 3487 pups
Proportion of males involved in reproduction	Aerial survey of the entire rookery	45% of 1000
Peripheral males per harem	Terrestrial survey	Mean=1.3 (range 0–8), N=123 harems
% Males that copulated at least once	Serial records of marked males	78% of 51 males observed during 10 consecutive days at peak season

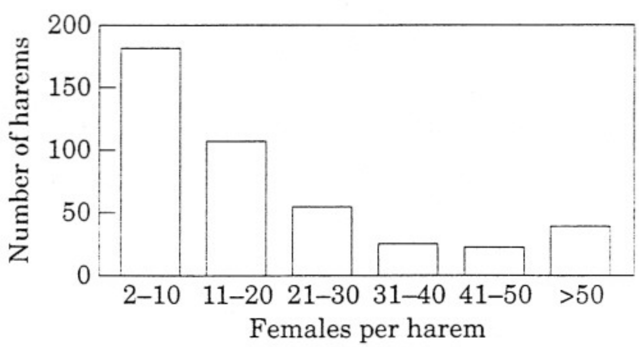

Figure 2. Frequency distribution of harems as a function of size for the entire breeding area (N=432 harems).

test: χ^2=0.34, df=2, P>0.05). Female aggression towards alien pups was also rare (Table I). The aggression rate was not significantly affected by time within the breeding season (early versus peak versus late=0, 0.8, 1.8 AIs/pup per 100 h, respectively; median test: χ^2=4.82, df=2, P>0.05).

Mother–Pup Distance and Separation

Mothers were typically at less than one pup body length from their offspring, regardless of tide, size of the mother, position in the harem and time in the breeding season (Table III). Low density and proximity to pups prevented mother–pup separations. We recorded 0.4 separations/pup per 100 h (Table I). Male harassment and herding of females caused 86% of the separations and aggression and movement of female neighbours caused 14%. We determined a median reunion time of 11 min for 161 separations (range 1–170 min). Only two separations were fatal to the pup.

Pup Mortality

We calculated pup mortality rate as 3.5% of 3487 pups born during 4 years at two study sites (La Armonia and Punta Delgada). We observed the deaths of 38 pups: 92% were stillborn and 8% died owing to trauma and starvation after mother–pup separation. Pup mortality was not significantly affected by harem size. Mortality recorded throughout the season of 609 pups born in six of the largest harems (>80 females) was 2.6%, which did not differ significantly from the 4.2% mortality rate of 288 pups born in nine

Table II. Comparison of number of harems per km and females counted during terrestrial surveys in different geographic areas of the Península Valdés rookery

Geographic area	Km of coastline	Number of harems	Number of females	Range of harems/km
Punta Delgada	30	65	2192 73/km.	1–5
Caleta Valdés	40	62	845 21	0–4
Punta Norte	14	23	274	0–3
Punta León to Punta Ninfas	25	9	56	0–2

Data for the 1992 breeding season except for Punta Norte (1989; see Fig. 1).

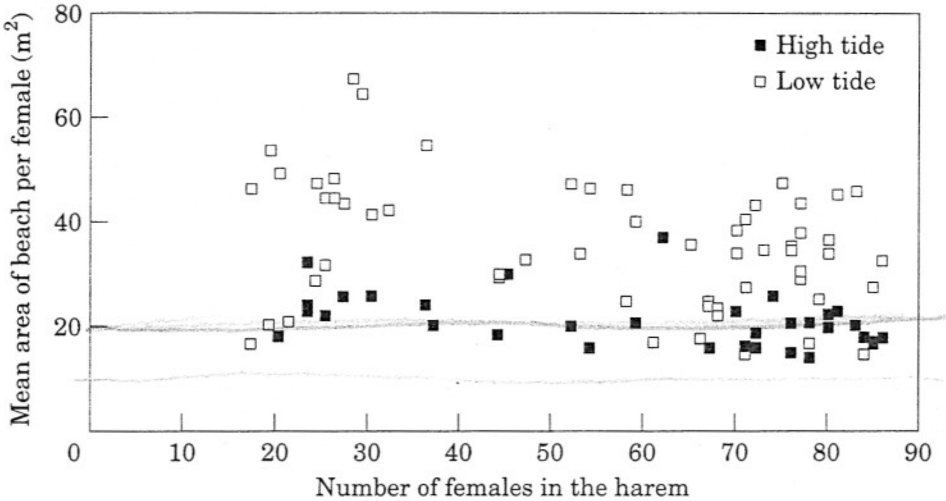

Figure 3. Mean area used by individual females as a function of harem size and tidal condition. Despite an increase in the number of females in the harem, the space available to each female at low and high tide remained about constant. Data points are samples of the same harem taken throughout the breeding season during different tidal conditions.

smaller harems (18–50 females; $\chi^2=0.98$, $df=1$, $P>0.05$).

Offspring survival until weaning did not vary as a function of female dominance. All of 31 marked females belonging to the same harem for which we recorded 234 agonistic interactions in 140 h weaned their pups, independently of the outcome of the confrontations when mothers engaged in agonistic interactions.

Male Access to Females

Female dispersal and small harems resulted in a relatively high proportion of males involved in reproduction as harem bulls (Table I). Subordinate males, unable to defend harems, managed to have access to females by remaining close to harems as peripheral males. The number of peripheral males was positively correlated with harem size ($N=123$ harems; Kendall's tau=0.69, $df=121$, $P<0.05$). Because subordinate males tended to be peripheral to large harems and most harems were small, a proportion of the harems (43% of 123) did not have subordinate males in attendance at peak season (Table I).

Most males observed during 10 consecutive days at peak season copulated at least once (Table I). Harem bulls ($N=13$ of 51 marked males) were still the most successful, achieving 67% of 698 copulations. The highest number of copulations were by bulls that defended harems larger than 50 females. Four of these males mated with different females at a mean rate of 37 copulations per 100 h (variance=28). Harems larger than 50 females, however, were difficult to control by a single male. Bachelors took advantage of large harems and mated at a mean rate of nine copulations per

Table III. Per cent of the scan samples in which marked females were at less than one pup body length from their offspring as a function of tide, mother body size, position of the mother in the harem and time in the breeding season

	% of scan samples	Number of scan samples	χ^2
Tide			
Low (87)	90	1084	0.01
High (87)	90	477	
Size			
Small (16)	83	390	4.30
Medium (43)	85	824	
Large (28)	80	378	
Position			
Central (41)	84	794	0.00
Peripheral (46)	84	1130	
Time in the breeding season			
Early	88	351	4.88
Peak	91	1011	
Late	87	199	

Number of females scan-sampled in parentheses. None of the chi-squared values are significant ($P>0.05$; $df=1$ for tide and position, and $df=2$ for size and time in the breeding season).

Table IV. Comparisons of southern elephant seal rookeries in terms of number of females per km and harem size

Colony	Females per km of coastline	Harem size (max)
South Georgia	175–250[1]	70–75[1]
Kerguelen	400[2] 520[3]	102 (1305)[2]
Heard	2188[4]	40–50[5]
Macquarie	1100[6]	100–300 (>1000)[6]
Marion		45[7]
Península Valdés	62[1]	11 (22)

References: 1. Dartmouth Point (McCann 1980); 2. Bester & Lenglart 1982; 3. Van Aarde 1980; 4. Carrick et al. 1962; 5. Gibbney 1957; 6. Carrick & Ingham 1960; 7. Condy 1979.

100 h with different females at peak season (variance=20, N=5 males).

DISCUSSION

We conclude that the ecological features of the southern elephant seal breeding colony of Península Valdés, characterized by homogeneous and spacious beaches (Campagna & Lewis 1992), allow breeding in the lowest density conditions reported for the species (Table IV). Low-density breeding in Patagonia increases female reproductive success through high pup survival. Because harems are small and widely separated, females keep inter-individual distances that result in low levels of aggression among themselves and towards alien pups. Contrary to seals breeding in high-density rookeries, mother–pup separations in Patagonia occur infrequently and are followed by successful and fast reunions.

Female southern and northern elephant seals breeding in crowded conditions are frequently separated from their pups by neighbouring females or bulls, and reunions often do not occur (McCann 1982; Riedman & Le Boeuf 1982). Wandering pups starve to death or suffer injuries with fatal consequences (Le Boeuf & Briggs 1977). Up to 60% of pup deaths at Año Nuevo were due to trauma and starvation (Riedman & Le Boeuf 1982). Starvation caused by high-density conditions was also a majôr cause of pup mortality at Macquarie, Marion and South Georgia Islands (Carrick et al. 1962; Condy 1979). Trauma and starvation caused 57% of the pup deaths at South Georgia (McCann 1982). Density-dependent pup mortality, because of failure of the mother–pup bond, mother–pup separation and pup injury and starvation, also occurs in other pinnipeds that breed in crowded conditions, such as grey seals, *Halichoerus grypus* (Bonner & Hickling 1971; Anderson et al. 1979), South American fur seals, *Arctocephalus australis* (Harcourt 1992), and Antarctic fur seals, *A. gazella* (Doidge et al. 1984).

The competitive advantage of experienced mothers over younger ones is greatest when female density is high (Reiter et al. 1981). At Año Nuevo and South Georgia Islands, superior size, higher social dominance and greater experience markedly increases the chances of weaning a pup (Reiter et al. 1981; McCann 1982). Conversely, the probability of weaning a pup in Patagonia does not seem to be strongly associated with female dominance, because most females successfully wean their pups, independently of their size and position in the harem.

From a male perspective, small harem size and dispersed females limit the polygyny potential (Bartholomew 1970; Emlen & Oring 1977; Boness 1991). Consequently, variance in male mating success should be lower at Península Valdés, where proportionally more individuals have access to a harem than in other populations. Although copulation rate is only a rough estimator of reproductive success, it illustrates the effect of female dispersion on males. We roughly estimated variance in male mating success at Península Valdés based on the known size of all harems of the population at peak season, and assuming that only harem bulls would mate with all the females in their harems (i.e. peripheral males would not have access to females). This variance would hypothetically be 282 ($N=800$ males of which 432 are harem bulls). Because most peripheral males do achieve copulations, the actual variance should be even smaller than our estimate. Variance in male mating success at Año Nuevo, where females breed in crowded beaches and harems are dominated by a small number of males, may be up to five times larger than at Península Valdés (Le Boeuf & Reiter 1988). An indication of variance is the number of males that monopolize matings. As few as five of 180 northern elephant seal males were responsible for up to 92% of the matings (Le Boeuf & Reiter 1988). Similarly, five of 38 southern elephant seal males at South Georgia Island achieved 88% of 331 copulations (McCann 1981). At Península Valdés, 13 of 51 males achieved 67% of 698 copulations.

Dispersal of females and harems and distances between females within harems make it difficult for males to monopolize matings. Individual males at Península Valdés have a rich behavioural repertoire that augments their mating success (R. Baldi & C. Campagna, unpublished data). They recruit arriving females at the onset of the breeding season, herd females away from neighbouring harems, merge small harems into larger ones, simultaneously control more than one harem and shift to larger harems after changes in the dominance hierarchy. Some males defend the same harem during two consecutive seasons, increasing the number of females monopolized during the second year. Most interestingly, some males defending small harems abandon their females to become peripheral males of large harems.

Our observations of male behaviour at Península Valdés were similar to descriptions of the behaviour of southern elephant seals breeding on ice at Signy Island (South Orkney Islands; Laws 1956). In some particularly cold years, offshore ice prevents seals from reaching the breeding beaches. Harems then occur on ice where space is not restricted. These harems are found further apart than harems at South Georgia, where fast ice does not occur and breeding takes place on beaches where females form a continuum. Dominant males at South Georgia keep subordinates away from the harems (McCann 1981). These animals are confined to swimming back and forth, parallel to the beaches, attempting to intercept departing females and copulate with them in the surf. Conversely, when seals breed on ice, bachelors stay on the periphery of the harems, sneaking into them when opportunity arises (Laws 1956).

Seeking opportunities may be a generalized rule of thumb for males competing for females in all seal species. Even though males exploit opportunity, however, the ecological context in which breeding occurs in Patagonia clearly favours individual female reproductive success at a cost to the most successful males. Dominant harem bulls in Patagonia may be getting a lower reproductive outcome than their counterparts in high-density rookeries.

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