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Fine-Scale Breeding Habitat Preferences of Southern Elephant Seals (*Mirounga leonina*) on Península Valdés

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Abstract

This study analyzed fine-scale habitat selection of southern elephant seals (*Mirounga leonina*) on Península Valdés, Patagonia, Argentina, during a decade of population stability. The results showed repeatability and consistency in harem formation in a predictable manner and according to specific environmental characteristics. Censuses were conducted during the peak of the breeding seasons (2001 to 2007 and 2010), and ten topographic variables were surveyed along 12 km of coast. The breeding social context was associated with certain topographic variables. Reproductive groups tended to occur in bays sheltered by cliffs with accessible beaches of slope less than 4º and unconsolidated substrates. The nonreproductive groups were found on shelf points. The spatial distribution reported herein will contribute to the understanding of the large-scale distribution of breeding groups on Península Valdés and other breeding colonies of southern elephant seals.

Key Words: habitat selection, breeding distribution, social structure, Península Valdés, southern elephant seal, *Mirounga leonina*

Introduction

Southern elephant seals (SES) (*Mirounga leonina*) may be found on most of the islands in the Southern Ocean, with breeding colonies located surrounding the Antarctic continent and in Patagonia, Argentina. There are four recognized and distinct large SES populations: the South Georgia population in the South Atlantic Ocean, the Kerguelen population in the southern Indian Ocean, the Macquarie Island population in the southern Pacific Ocean, and the Península Valdés (PV) population in Argentina (Slade et al., 1998; Hoelzel et al., 2001). Of the 22 sub-Antarctic SES breeding colonies that have been described, the PV population is the only one that occurs on a continent in lower latitude, and it is the fourth largest in terms of number of pups produced (Lewis et al., 1998; McMahon et al., 2005).

The PV population is a unique breeding colony in which the number of SES increased consistently throughout the last century without expanding the extent of their distribution on land (Campagna & Lewis, 1992; Lewis et al., 1998), but the population has essentially stabilized over the last decade (Ferrari et al., 2012). Two demographic subunits were identified in the north and south of PV with different trends in birth numbers, sex ratios, and harem sizes (see Ferrari et al., 2009, Figure 1).The only apparent difference between the northern and southern subunit is the physical characteristics of the habitat. In the north, there are pebble beaches with steep slopes; while in the southern area, there are mainly sandy beaches of irregular topography, with bays separated by natural barriers making access at the shoreline from open water difficult (Lewis et al., 2004). The relationship between social groups and topographic characteristics has not been previously reported.

SES have an annual cycle characterized by two well-defined pelagic phases at sea which alternate with moult and reproduction on land (Le Boeuf & Laws, 1994). The breeding phase of the adult cycle has been thoroughly described for several populations in the southern hemisphere (e.g., Carrick et al., 1962; Skinner & van Aarde, 1983; McCann, 1985; Guinet et al., 1992; Campagna et al., 1993; Galimberti & Boitani, 1999). The haulout pattern seems to differ little as a function of population size and colony latitude. In PV, the reproductive period was indicated by a gradual increase in the number of adults of both sexes starting in early September, a brief peak by the end of the first week of October, and a gradual decline that extended up to mid-November (Campagna et al., 1993). Latitude may have an effect on the date of peak number of breeding females (Condy, 1979; Campagna et al., 1993; Galimberti & Boitani, 1999) via a physiological response to day length (see Campagna et al., 1993, Figure 7). The photoperiod is known to influence implantation of the blastocyst and therefore the synchronization of breeding (Daniel, 1981; Boyd & Arnbom, 1991).

The haulout pattern shows a high degree of synchronization and is regular between years (Condy, 1979; Hindell & Burton, 1988; Galimberti & Boitani, 1999; Lewis et al., 2004). Females arrive at the beaches gradually and typically join a harem where they give birth, nurse, and wean their pup, and then mate with one or more males before returning to sea. Virtually all females spend 28 ± 2.5 d ashore. Each "alpha" male (i.e., beach master) has almost complete control of its group of females; the rest of the males remain peripheral and may gain access to oestrus females when they are returning to sea (Laws, 1956; Carrick et al., 1962). Only about 7 to 9% of females breed outside of harems, where they form a pair with a male (Campagna et al., 1993).

At PV, breeding occurs at specific sites along the 200 km coastline. There is a wide range of habitats available, and the factors that determine which beaches are the favorites are unknown but could involve social and environmental factors that influence breeding. In situations where suitable habitat is limited, environmental factors may be more important than interactions between males and females. The objective of this study was to identify the topographic characteristics that influence the distribution of the SES during the peak of the breeding season for the elephant seal population at PV. The study classified terrestrial habitats that are available for settlement by the breeding SES and surveyed the location during seven consecutive breeding seasons to test the preferences in site selection of the reproductive and nonreproductive groups during a period of population stability.

Methods

Study Area

The target sector was a stretch of approximately 12 km of coastline with high density groups, around Punta Delgada (PD, 42° 45' 57" S, 63° 38' 16" W) in southeast Península Valdés (Figure 1).

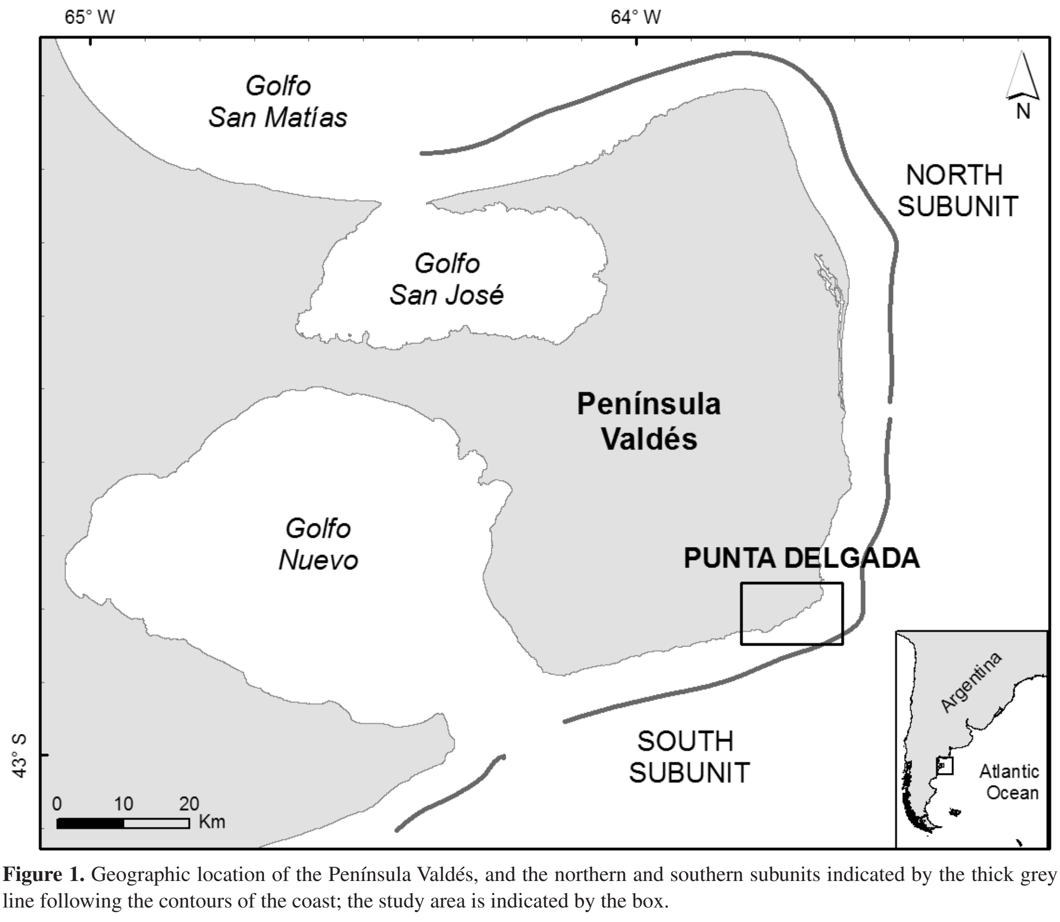

Figure 1. Geographic location of the Península Valdés, and the northern and southern subunits indicated by the thick grey line following the contours of the coast; the study area is indicated by the box.

The PD area encompasses different topographical features that are typical of the coastline of PV, alternating between stretches of land with bays of sandy and pebble beaches separated by extensive cliffs and rocky shelf areas (Lewis et al., 2004). Although PD represents 5% of the total coastline of PV occupied by the colony, more than 25% of the breeding population is concentrated in that area. The width of the beach at high tide varied between 0 and 250 m. Seven sites (8.25% of the total) that during high tide had minimal space for SES to settle were considered to be uninhabitable for breeding and were excluded from further analyses. The topography did not change appreciably over the last 10 y despite the high cliffs being prone to collapse periodically due to coastal erosion. In the past, PD was a restricted military area seldom visited by tourists. However, PV was named a World Heritage area in 1998, and this marked the onset of tourist activities leading to the present level of ecotourism development. Currently, approximately 25% of the PD area is open to visitors and remains accessible for 8 mo of the year, including the breeding and moulting seasons of the SES.

Data Collection

Censuses at PD were carried out between 2001 and 2007 when approximately 84% of breeders were ashore (3 to 7 October; see Lewis et al., 2004, Figure 4b). Since PD is accessible for viewing along 12 km, all individuals ashore were observed (Lewis et al., 2004). Censuses were conducted on foot on shoreline, and each animal was counted and categorized according to their sex and social status. With regard to the latter, the following categories were recognized: (1) *Grouped Harem* (GH), in which there is more than one male in the harem, and it is not clear which is the alpha male; (2) *Harem* (H), in which there is one alpha male and several females; (3) *Solitaries* (S), in which there are single adult males or females; and (4) *Mating Pairs* (MP), in which there is a pair of elephant seals: one male and one female.

Topographic data, including the size of the area available to settle on, type of coast, substrate, slope and protection of the beach, accessibility from the sea, and presence of tide pools, were collected at 109 sampling points evenly distributed along the study area in 2001 (Table 1). The whole area was then partitioned into 41 sites by combining consecutive points with similar topographic characteristics. For comparative purposes, the same sampling sites were surveyed again during the 2010 breeding season.

Data Analysis

At each site, Canonical Correspondence Analysis (CCA) was used to identify the relationship between social structure and topographic variables (ter Braak & Verdonschot, 1995). An ordination using two data matrices was performed. The first matrix encompassed biological data, namely the mean density of SES of each social class (GH, H, S, and MP) per 100 m^2 in each occupied area over the 7 y of the study (mean ± SE). The occupied area consisted of the 41 sites that were suitable for SES. This variable was log (x + 1), transformed prior to analysis in order to reduce the influence of extreme values and meet the assumption of the normal distribution criterion. The other matrix was composed of topographical data, including

Table 1. Description of the ten topographical variables used in Canonical Correspondence Analysis (CCA); 1-0 = presence-absence.

Variables	Unit measured	Description
Coast	1-0	"Bay" (1) is defined as the area that is bordered on both sides and "Point" (0) as a piece of land that projects into a body of water.
Sand	1-0	Substrate with particles between 0.0625 and 2 mm
Pebble	1-0	Substrate with a of 4 to 64 mm
Mixed	1-0	A mixture of sand and pebbles
Shelf	1-0	Continuous solid rock platform sometimes extending into the sea
Tide pools	1-0	Deep pools filled with water during the low tide
Slope	Degrees	Inclination of the beach recorded using an inclinometer
Shelter	Percentage	The shelter is the elevation of the cliffs surrounding the beach and protected from observation or approach from land. The height was recorded by GPS to 10 m (0%), between 10 and 50 m (50%), and more than 50 m (100%).
Accessibility	Percentage	The accessibility is defined as the difficulty of access at the shoreline from open water. It is measured as the percentage of available area without obstacles (rocky platforms, rocks, and barriers) between low and high tide. The range varies in quartiles from totally accessible (100%) and not having access (0%).
Surface	Km^2	The area available on the shoreline between the coast and the high tide

Table 2. Summary of CCA ordination: eigenvalues, variance, and correlations between biological and environmental variables for the first two dimensions of the correspondence analysis

	Axis 1	Axis 2	Total inertia
Eigenvalues	0.43	0.21	1.69
Cumulative percentage variance			
of social group data	25.7	38.0	
of social group-environment relations	66.6	98.4	
Social group-environment correlations	0.80	0.57	

the variables scored for each of the occupied areas according to the criteria given in Table 1: "Coast," "Sand," "Pebble," "Mixed," "Shelf," "Tide Pools," "Slope," "Shelter," "Accessibility," and "Surface." The most important topographical variables obtained from the CCA were tested with data of density of SES (number of animals of a harem per 100 m^2 of occupied area) and the percentage of occupied and available area of the 2010 survey. The statistical procedures were performed with *Statistica 7.0* and *CANOCO* for Windows 4.5.

Results

Most of the sites around Punta Delgado (~60%) were characterized by sandy coves or beaches comprised of unconsolidated substrate with moderate slope (< 4º). The main type of substrate (about 90%) was sand, pebble, or a mixture of the two, and all sites of rocky substrate were consistent with promontories of the coastline or with points protruding out to sea. The beaches of only 36% of the sites were found to be accessible without difficulty for the southern elephant seals. More than half of the sites presented protection against wind and sun as a consequence of the high cliffs (> 50 m) that backed or partially surrounded the beaches.

The average number of SES across the study years was 4,203.43 ± 266.82 distributed in 47.43 ± 4.12 breeding groups. The number of SES per 100 m^2 of occupied area was 2.62 ± 0.21 and did not vary between different breeding seasons from 2001 to 2007 (Kruskal Wallis test $H_{6,266} = 1.04$; $p = 0.98$). The spatial distribution of SES was not consistent across the 12 km of coastline (Kruskal Wallis test $H_{34,212} = 149.39$; $p < 0.05$) and varied between 0.02 and 18.55 individuals per 100 m^2 in the sites where Hs were located. Seventeen of the 34 sites that were suitable were occupied by Hs every year. The mean H size (89.20 ± 11.46) was not homogenous across sites (Kruskal Wallis test $H_{16,119} = 56.97$; $p < 0.05$) and did not show differences between years (Kruskal Wallis test $H_{6,119} = 4.56$; $p = 0.60$).

Table 3. Canonical coefficients of topographic variables according to the first two axes of the CCA; canonical coefficient with absolute values > 0.25 are shown in bold.

	Canonical coefficients	
	Axis 1	Axis 2
Coast	-0.19	-0.08
Sand	**-0.31**	0.09
Pebble	0.07	-0.09
Mixed	0.01	**-0.25**
Shelf	**0.51**	0.12
Tide pools	-0.13	0.12
Slope	**-0.46**	-0.06
Shelter	**0.39**	**-0.28**
Accessibility	-0.17	-0.16
Surface	-0.23	0.19

The first two ordination axes in the CCA accounted for 38% of the total for the social structure data and 98.4% of the relationship between social structure and the environmental variables (Table 2). In Axis 1, the main environmental variables associated with the social structure distribution were "Sand," "Shelf," "Slope," and "Shelter." In Axis 2, the most important environmental variables were the "Mixed" substrate and "Shelter" (Table 3).

The diagram of CCA showed two major groups in terms of the topography characteristics—(1) a group represented by shelf points with a pronounced slope and (2) other group bays with gentle slopes of different types of substrate. The spatial distribution of social groups identified clear segregation between the reproductive and nonreproductive groups. The highest densities of SES in the Hs were associated with bays of mixed substrate easily accessible from the sea and with gentle slopes. SES in GH occupied the sites of sandy beaches with tide pools surrounded by low cliffs. S and MPs exhibited a high association with rocky points with a pronounced slope (Figure 2).

The main variables of the CCA (substrate, slope, and shelter) showed a clear association with the percentage of occupancy and the density of SES observed in 2010 (Figure 3). There was a positive correlation between the number of SES and

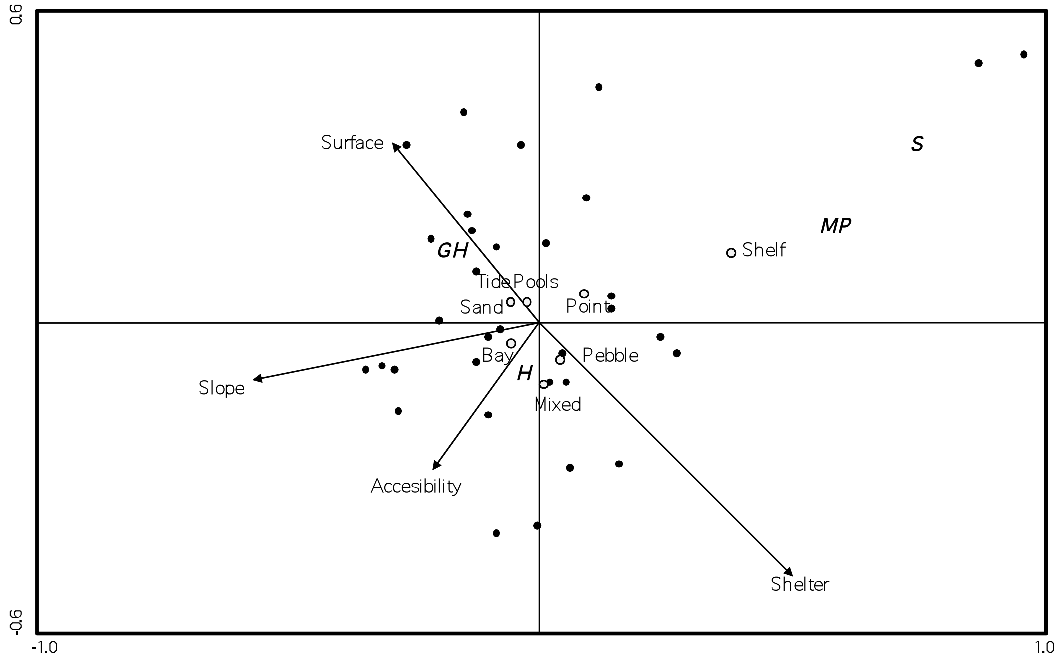

Figure 2. Plot of social structure scores, the environmental variables (○), and 34 samples sites (●) in the first two CCA axes. GH: Grouped Harem, H: Harem, S: Solitaries, and MP: Mating Pairs. The continuous environmental variables were represented as vectors and the nominal variables as points. The length of the environmental vectors indicates its importance for explaining the association between the social structure and the environment, and the direction of the arrow represents the way in which variables increase.

softness of the unconsolidated substrate ($r = 0.93$). The largest Hs were located on sand and mixed substrate (Figure 3a). Sites with more than 8º of inclination were not occupied; the highest density of SES were on beaches with slopes of less than 4º ($r = -0.99$; Figure 3b). The elevation of the cliffs had low incidence and negative correlation ($r = -0.93$) with the choice of the site; the largest GH was settled in the area without natural barriers to approach from land ($r = -0.82$). Most of the Hs were found on beaches with high cliffs that gave them protection from the wind and sun as well as shelter from the approach of other SES (Figure 3c).

Discussion

During the period of increasing population, southern elephant seals on Península Valdés reproduced in low density conditions in comparison to other circumpolar breeding localities that have similar topography (see Baldi et al., 1996, Table IV). The low density (2.6 elephant seals per 100 m^2) remained consistent in Punta Delgada, and the same number of females per km of coastline persisted between 2001 and 2010, during the apparent period of population stability (Ferrari et al., 2012).

Approximately 4,200 SES annually hauled out on 12 km of coast in the PD area. This study showed repeatability and consistency during several years in predicted localities for formation of Hs. In PD, the Hs with more than 30 females had a constant spatial and temporal distribution, while the small Hs (< 10 females) were less predictable in occurrence and localization.

Type of coast, substrate, slope, and shelter in each sector of the coast suggested that reproductive groups (GH and H) tend to settle in protected bays with beaches easily accessible from the sea with slopes less than 4º and unconsolidated substrate (mixed or sand). On the other hand, categories of animals less successful at reproduction, such as subordinate males, tend to haul out on shelf points, resulting in a spatial segregation between the different social structures. They remain on rocky platforms close to the beaches where the Hs are located in an attempt to gain access to some females. The topography also influenced the reproductive success of "alpha" males located in the bays insofar that it prevented females from being intercepted and mated by subordinate males. A similar effect on breeding success has been reported on Sea Lion Island (Malvinas/Falkland Islands) where there is small tidal amplitude. This

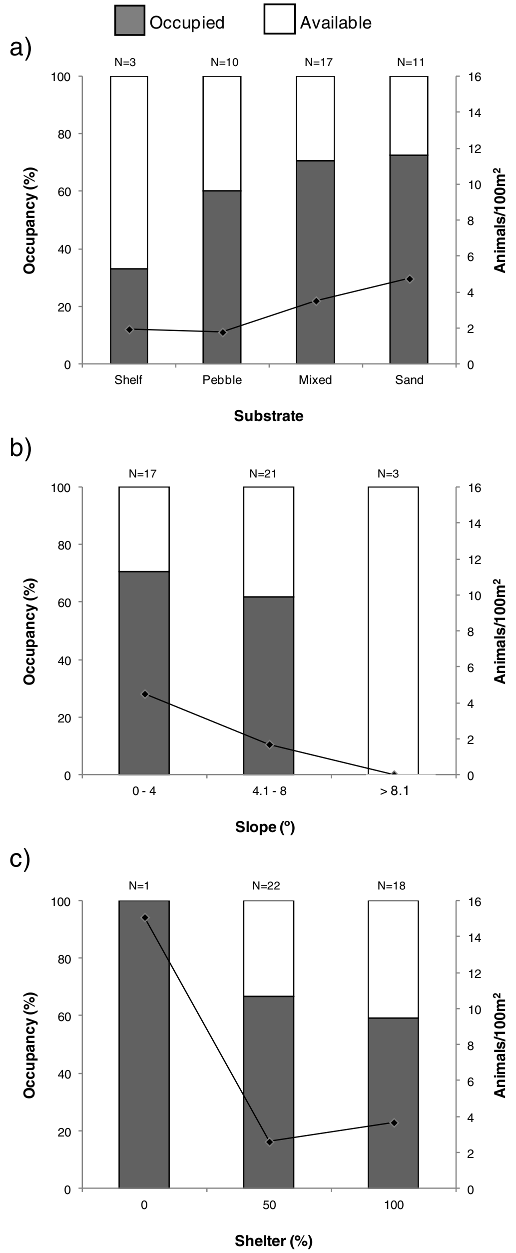

Figure 3. SES distributed during survey 2010 showed as percentage of available areas that were occupied (left axis), and the number of SES per 100 m^2 of occupied area in relation to the most important topographic variables obtained from the CCA: (a) substrate, (b) slope, and (c) shelter. N = total number of sites.

reduces the time taken by females to depart at sea (Fabiani et al., 2004). The tidal amplitude is directly related to the slope and accessibility of the breeding beaches. Beaches with easy access and low slope encourage alpha male haul-out and beaches with less refuge encourage the peripheral males to haul out. These strategies to locate sites on a beach indicated that the spatial distribution was a consequence of the interaction between behavioral and environmental factors.

The SES is not the only polygynous species for which topography influences the reproductive success of males. Grey seal (*Halichoerus grypus*) males are better able to monopolize females in rugged and broken terrain that minimizes disturbance by bachelors when they are trying to copulate with the females (Twiss & Thomas, 1999). The physiognomy of breeding sites can affect breeding success in other ways—for example, through influencing thermoregulation (Twiss et al., 2002; Norris et al., 2010) and the effectiveness of the mother-pup bond (Twiss et al., 2001).

In the current study, females selected the beaches that were more accessible, with gentle slopes. The slope of the beach and the accessibility from the sea are likely to be important selection criteria for an animal that moves with difficulty on land such as the SES. In general, these beaches had substrates composed of fine particles, mix, or sand that may enhance the thermoregulatory abilities of individuals, especially in temperate areas including PV (Lewis & Campagna, 1998). Also, at sub-antarctic Iles Kerguelen, the surface structure of the breeding habitat influenced SES H size, with Hs located on sandy beaches being up to three times larger than those found on pebble beaches (van Aarde, 1980). The moisture contained in wet sand facilitates heat exchange by evaporation and conduction (Hillel, 1982), allowing SES to insulate themselves against high and low temperatures. The skin temperature of northern elephant seals (*Mirounga angustirostris*) has been shown to be highly responsive to environmental conditions, varying with ambient temperature, solar radiation, and vapor pressure (Noren, 2002; Norris et al., 2010). On PV, the mean air-temperature is usually around 17º C with peaks of 30º C during the breeding season; and at the same level of solar radiation, pebble substrates reached higher temperatures than sandy substrates (Lewis & Campagna, 1998). To compensate for temperature increases, female SES located on pebble beaches move to the shoreline where ambient temperature is lower; such movements increase the likelihood of mother-pup separations with implications for pup survival and, consequently, breeding success (Lewis & Campagna, 1998). Therefore, besides abilities of alpha males to attract females to Hs (Carrick et al., 1962; Campagna et al., 1993; Galimberti & Boitani, 1999), substrate could be influencing the decision for female haul-out at suitable sites.

The suite of environmental variables considered in this study on a fine spatial scale explained nearly 100% of the variability in social structure between sites. An understanding of habitat requirements and preferences for breeding is important for the purposes of conservation and helps to determine other potential areas for protection of natural populations that select patchy heterogeneous environments.

In this study, fine-scale analysis showed the influence of topographical variability in the selection of habitat of the southern elephant seals when arriving and settling on the beach for breeding. However, to extrapolate at a larger spatial scale (Bell et al., 1993), it is necessary to continue with studies on the behavior of each social group (GH, H, S, and MP) in the site identified as the favorite for the group. The variability between habitats occupied and behavior associated with the selection of suitable sites could then be extrapolated to areas beyond PV to help understand changes in distribution associated with the different trends. The northern area was the first to be colonized by SES (Ferrari et al., 2012) and is composed primarily of pebble beaches with pronounced slopes and unsheltered coast. At present, this area shows the lowest density of SES in the breeding area (Ferrari et al., 2009). Although changes cannot be explained completely, substrate, slope, and shelter appear to influence selection of the site for different cohorts throughout the decade studied.

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