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Regional factors associated with the distribution of South American fur seals along the Atlantic coast of South America

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Breeding colonies of the South American fur seal (*Arctocephalus australis*) are not homogeneously distributed along the coast of the Atlantic Ocean, but show an unusual patchiness, with colonies located only at the northern and southern extremities of the breeding range. We used bibliographic data of censuses carried out in the mid- and late 20th century, along with a Geographic Information System, to compare the pattern of distribution of colonies during these two periods, and to identify the anthropogenic and natural factors associated with the present pattern at a regional scale, using principal components analysis. The distribution of colonies did not vary in the period analysed even when the population abundance increased tenfold. The distribution was associated with the distance to the continental shelf break, and the availability of island and protected areas. We conclude that *A. australis* colonies are located in places where the continental shelf is narrow and there is no human disturbance.

Keywords: *Arctocephalus australis*, distribution, environmental factors, GIS.

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Introduction

The South American fur seal (*Arctocephalus australis*) is distributed along ~10 000 km of the coast of South America, from Isla del Marco (34°20′S 53°46′W) in Uruguay to Cape Horn at the extreme south of the continent, and from Cape Horn to Paracas Peninsula (13°55′S 76°15′W), central Peru, in the Pacific Ocean (King, 1983). Along the Atlantic coast, breeding colonies are not homogeneously distributed but show an unusual patchiness, with colonies located only at the northern and southern extremities of the range. In the north, there are six breeding colonies along the coast of Uruguay, at Isla de Lobos, Cabo Polonio, and La Coronilla (Vaz-Ferreira, 1982). In the south, there are colonies in the Beagle Channel and on Isla de los Estados (Schiavini, 1987). These two groups of colonies are separated by 4800 km of coast, and between them, there are just a few non-breeding colonies and one with very little reproductive activity (Crespo *et al.*, 1999). This rather clumped distribution contrasts with the patterns shown by other species of fur seal (reviewed by Bonner, 1999), which have a more homogeneous distribution at a similar geographic scale.

In Argentina, the first two extensive censuses of pinnipeds were performed in 1946–1949 and 1952–1954 by Carrara (1952, 1954), and they covered most of the 3500 km of Patagonian coastline, from 38°30′S to 55°01′S. In the first survey, Carrara (1952) found three *A. australis* colonies with an estimated population of 1850 animals. The same colonies were found in the second survey, but the population was estimated to number 2700 animals (Carrara, 1954). Bastida and Rodríguez (1994) documented a new colony of 1000 animals at Cabo Blanco (47°12′S 65°45′W), found in 1961 by Bastida. No further censuses were carried out until the end of the 1980s (Schiavini, 1987; Crespo *et al.*, 1999), and those authors censused the coast between Isla Escondida (43°43′S 65°17′W) and the islands of the Beagle Channel (55°S) between 1987 and 1998. *Arctocephalus australis* was located in 15 colonies south of 43°S, with an estimated total population size of ~20 000 animals.

In 1953, the Uruguayan population was estimated at 26 444 animals located in six colonies (Vaz-Ferreira, 1982), but by 1995, the estimate had risen to ~280 000 animals in the same six colonies, an annual growth rate of 1.4% (Bastida and Rodríguez, 1994; Lima and Páez, 1997; Naya *et al.*, 2002).

Our objectives with this work were to (i) compile and process the bibliographic information available on censuses, location of colonies, and breeding activity of *A. australis* along the Atlantic coast, (ii) compare the pattern of distribution of colonies in the mid- (1946–1961) with that in the late 20th century (1987–1998), and (iii) identify the anthropogenic and natural factors associated with the present pattern, on a regional scale.

We related some of the associations between population distribution and environmental factors with the behaviour at sea of *A. australis*. York *et al.* (1998) showed that all lactating females on Isla de Lobos (35°02′S 54°54′W), Uruguay, foraged between 40 and 100 km from the coast. Vaz-Ferreira and Ponce de León (1984) and Bastida and Rodríguez (1994) stated that *A. australis* foraged in deep water off the continental shelf. Thompson *et al.* (2003) documented the results of a study of the movements and foraging behaviour of 14 South American fur seals around Islas Malvinas (Falkland Islands), based on satellite telemetry. The results showed that (i) most foraging sites (>90%) during the breeding season were within 100 km of the breeding site, (ii) seals performed sequences of short, local trips, and (iii) trip distances and durations and the lengths of visits increased throughout the season. Thompson *et al.* (2003) further suggested that the last increase would be a response to a change in metabolic requirements of pups and females. In other work, Naya *et al.* (2002) found that 30% of the wet mass of prey consumed by fur seals at Isla de Lobos was cutlassfish (*Trichiurus lepturus*), an outer shelf species distributed worldwide in tropical and warm-temperate waters (Cousseau and Perrotta, 2000). This percentage wet mass peaked at 75% in January, early in the lactating period of fur seals.

Material and methods

Our study covered ~5400 km of the known distribution of fur seals along the Atlantic coast of Uruguay and Argentina, from Isla del Marco, Uruguay (34°20′S 53°46′W), to Les Eclaireurs Islets, Argentina (54°52′S 68°07′W) (Figure 1a). The study area (5400 km) was subdivided using Geographic Information System (GIS) with ARCVIEW® software (license provided by PRODITEL group, University of Luján, Argentina) into 27 segments of

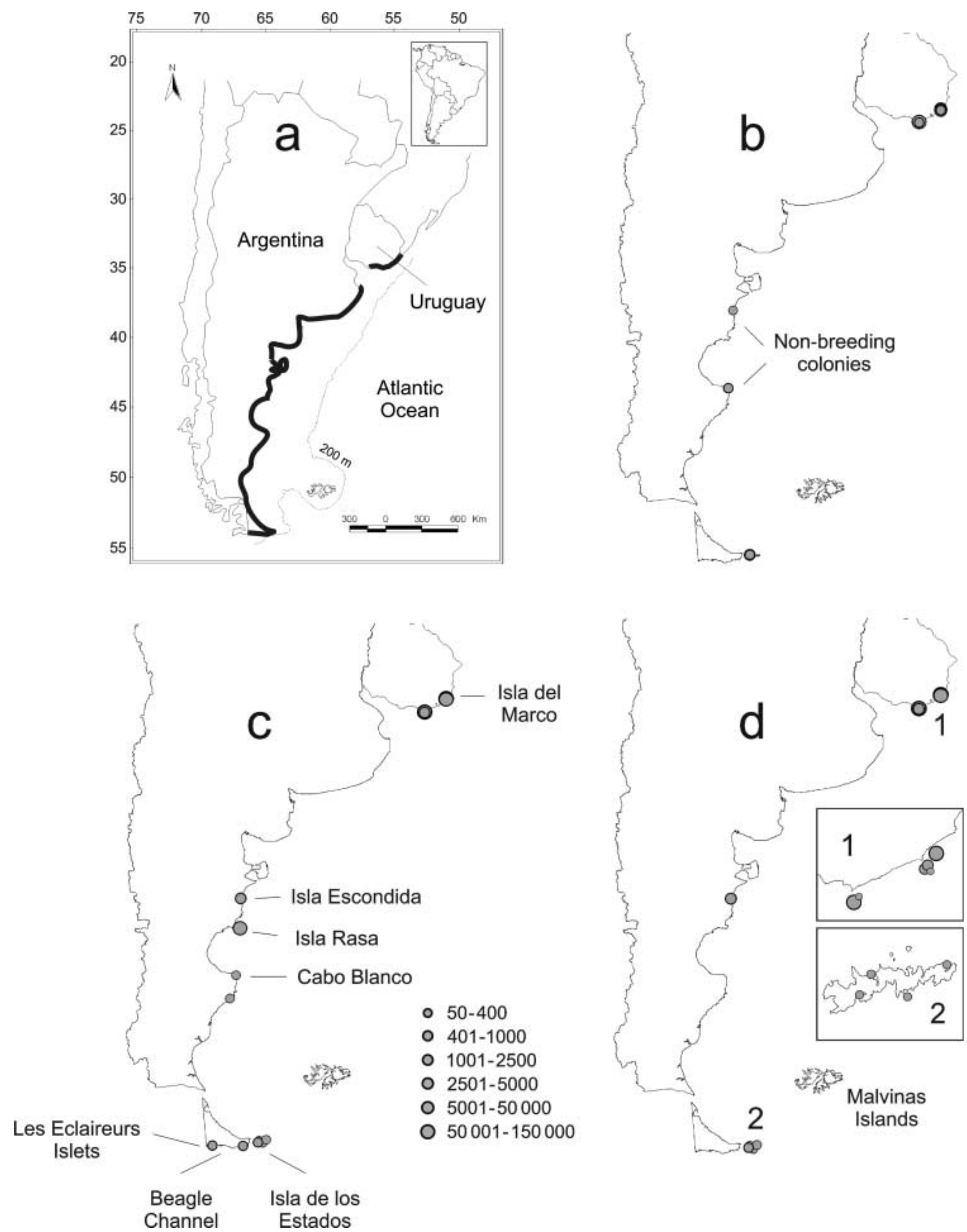

Figure 1. Study area and distribution of colonies along the Atlantic coast of South America. (a) The study area, showing 5400 km of the coast analysed here (dark line) and the continental shelf break, (b) past distribution, (c and d) present distribution of (c) all colonies and (d) breeding colonies, (1) along the Uruguayan coast and (2) at Isla de los Estados. The sizes of the circles reflect the number of fur seals in each colony.

~200 km each, but with one segment slightly longer owing to the interruption of the coastline by the Rio de la Plata, and the most southerly one measuring 110 km. In each segment, the variables measured were as listed below (with the information source in parenthesis).

(i) *Total colonies*—the number of breeding and non-breeding colonies (Carrara, 1952, 1954; Vaz-Ferreira, 1982; Schiavini, 1987; Bastida and Rodríguez, 1994; Crespo *et al*., 1999; E. Páez, pers. comm.).

(ii) *Breeding colonies*—the number of breeding colonies (same sources as the number of colonies).

(iii) *Islands*—the number of islands (INAPE, 2000; IGM, 2006).

(iv) *Cities*—the number of cities (Clearinghouse, 2006; IGM, 2006).

(v) *People*—the number of inhabitants (INDEC, 2006; INE, 2006).

(vi) *Harbours*—the number of fishing harbours (DINARA, 2006; SAGPA, 2006).

(vii) *Fish landings*—the mean landed weight (t) of fish per year of those species that are part of the fur seal diet. Landings do not necessarily represent the relative abundance of prey in a particular area. The variable was used only as an indirect measure of anthropogenic disturbance in the area (diet: Vaz-Ferreira, 1982; Ponce de León *et al*., 1988; Naya *et al*., 2002; Thompson *et al*., 2003; Szteren *et al*., 2004; landings: DINARA, 2006; SAGPA, 2006).

(viii) *Artisanal fishing*—the number of artisanal fishing vessels operating in the segment (Caille, 1996; DINARA, 2006). Artisanal fishing boats are 4–9 m long, with outboard motors, operating within 5–7 nautical miles of the coast (Caille, 1996; Szteren *et al*., 2004).

(ix) *Fish richness*—the number of fish species in each segment. We included only the species that are part of the fur seal diet (distribution data: Cousseau and Perrotta, 2000).

(x) *Protected areas*—the number of protected areas, including mainland areas and some islands near the coast (DINAMA, 2006; SAyDS, 2006).

(xi) *Surface area of protected areas*—in hectares (DINAMA, 2006; SAyDS 2006).

(xii) *Shelf break*—mean distance to the continental shelf break, estimated on a digital map as the distance (km) to the 200-m isobath from ten points of the coast. The points were 20 km apart to cover the 200 km of the segment (map source: Guerrero and Martos, 2000).

(xiii) *Productivity*—primary productivity, estimated in mg chlorophyll a m^{-3}, measured in a 100-km buffer from the breeding sites (SIMBIOS-NASDA-OCTS project-NASA, 2006). The selection of the radius of the buffer analysed was based on two studies of the foraging behaviour of *A. australis* which indicated that lactating females in Uruguay and the Malvinas foraged within 100 km of a breeding site (York *et al*., 1998; Thompson *et al*., 2003).

The datasets were used to build different georeferenced shape files with GIS. For estimates of primary productivity, monthly climatological images of satellite-derived ocean colour (chlorophyll *a* concentration), with a spatial resolution of 9.28 km, were used (SIMBIOS-NASDA-OCTS project-NASA, 2006). We used images corresponding to the November 1996 breeding season owing to the unavailability of images for years between 1990 and 1995. Comparisons with available images for the 1980s, using the program ArcView 3.2, showed no difference in the general pattern of monthly chlorophyll-*a* concentration, suggesting that the 1996 image was a good representation of the earlier years too. Ocean colour climatologies were derived from the Ocean Colour and Temperature Scanner (OCTS), which operated between November 1996 and June 1997 (SIMBIOS-NASDA-OCTS project-NASA, 2006).

Fur seal bibliographic census data were processed to obtain two distributional datasets: (i) the mid-20th century, containing Argentine census data from 1946 to 1961 and Uruguayan data from 1953, and (ii) the late 20th century, containing Argentine census data from 1987 to 1998 and Uruguay data from 1995. The ~200-km coastal segments in which breeding and non-breeding colonies were identified were used as sampling units for comparing the distribution of *A. australis* colonies over time (mid- vs. late 20th century). For this analysis, the total number of colonies and the number of breeding colonies in each study period (in each segment) were compared with a contingency analysis.

We performed a principal components analysis (PCA) to evaluate natural and anthropogenic variables measured in all segments and to associate them with fur seal distribution in the late 20th century. Variables with component loadings (s) >0.6 were considered to contribute high scores to the component or axis (Manly, 1986). A simple regression analysis was used to determine the effect of variables on fur seal distribution, using the first two factors of the PCA (which explained 53.96% of the variability in the data) as independent variables, and the total numbers of colonies and breeding colonies as dependent variables.

Results

In the late 20th century, there were 21 colonies of *A. australis* along the Atlantic coast of South America, all on islands near the coasts of Uruguay and Argentina (Figure 1c). There were two distinct areas with breeding activity: the coasts of Uruguay and Tierra del Fuego—Isla de los Estados. In Uruguay, there were six breeding colonies with a population of some 280 000 animals (Figure 1c and d), and at Tierra del Fuego—Isla de los Estados, there were four breeding and six non-breeding colonies with a total of 5000 animals (Figure 1c and d). Between these two groups of breeding activity, there were four non-breeding colonies and just one breeding colony at Isla Escondida (43°43′S 65°17′W) (Figure 1c and d), a total population of ~15 000 animals. Of those colonies, 11 000 fur seals at Isla Rasa (45°06′S 65°23′W) were the most populous (Figure 1c). There was a small amount of reproductive activity at Isla Escondida, some pups being seen and counted in the breeding period.

The almost 300 000 fur seals of the late 20th century constituted an almost tenfold increase in just 40–50 years over the estimated 29 719 *A. australis* censused along the Atlantic coast of South America in the mid-20th century. The increase in the numbers of fur seals was not, however, uniform along the Atlantic coast; it was a much bigger increase in Uruguay, where the population increased from 26 444 to 280 000 seals. Despite this large increase, though, the differences between the distributions of both total and breeding colonies in the mid- and late 20th century were not significant (Figure 1b–d; contingency analysis for total colonies, $\chi^2 = 4.61$, d.f. = 6, $p = 0.59$; and for breeding colonies, $\chi^2 = 2.49$, d.f. = 3, $p = 0.48$).

The first two factors of the PCA explained 53.96% of the variability in the data. Factor 1 had positive values on artisanal fishing ($s = 0.87$), people ($s = 0.86$), cities ($s = 0.81$), fish landings ($s = 0.79$), harbours ($s = 0.63$), and productivity ($s = 0.60$) (Figure 2). Factor 2 had a positive value on shelf break ($s = 0.68$), and negative values on islands ($s = -0.60$) and surface area of protected areas ($s = -0.83$; Figure 2). Regression analyses retained factor 2 as the predictor of the distribution of total colonies ($F_{1,\ 25} = 13.96$, $r = -0.60$, $p = 0.001$) and breeding colonies ($F_{1,\ 25} = 5.77$, $r = -0.43$, $p = 0.024$). However, regression analyses were not statistically significant between factor 1 loadings and these two variables (total colonies: $F_{1,25} = -0.62$, $r = -0.16$, $p = 0.44$; breeding colonies: $F_{1,\ 25} = 3.51$, $r = -0.35$, $p = 0.072$). The results suggest that colonies are more abundant where the continental shelf is narrow, where island space is available, and where there is some protection from extraneous impact.

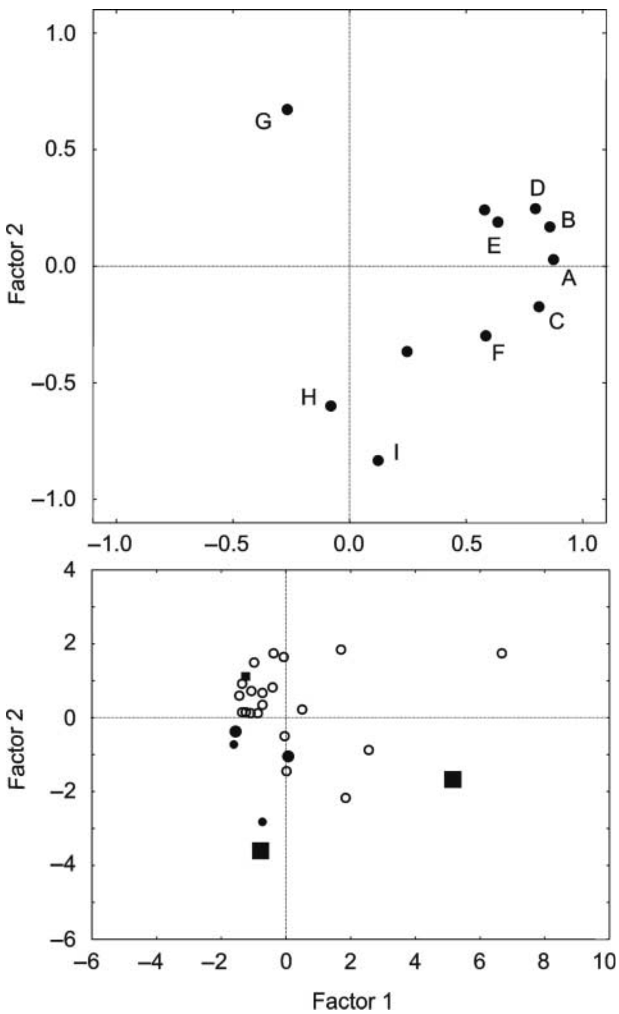

Figure 2. Factors 1 and 2 (top) of the PCA showing the arrangement of the environmental variables sampled. Variables with a large contribution to the components are labelled as follows: A, artisanal fishing; B, people; C, cities; D, fish landings; E, harbours; F, productivity; G, shelf break; H, islands; I, protected area. Factors 1 and 2 (bottom) showing the arrangement of the 27 segments sampled. Filled squares, segments with breeding colonies; filled circles, segments with non-breeding colonies; open circles, segments without colonies. The larger the symbol, the more numerous the colonies.

Discussion

The abundance of fur seals along the Atlantic coast of South America increased in the second half of the 20th century primarily as a consequence of an increase in the Uruguayan population. The increased abundance may well be attributable to the cessation of commercial harvesting there, as described for other fur seal species (reviewed by Bonner, 1999; Shaughnessy, 1999).

Arctocephalus australis has a patchy distribution of breeding and non-breeding colonies that was maintained during the second half of the 20th century even with a tenfold population increase. Breeding colonies are still grouped in two areas of the coast separated by thousands of kilometres, in Uruguay and in Tierra del Fuego—Isla de los Estados.

The scarce archaeological evidence in the region suggests that the distribution of *A. australis* along the Atlantic coast did not vary significantly over the past 5000 years. Castro *et al.* (2004) visited 12 archaeological sites between Punta Ninfas (42°56′S 64°19′W) and Cañadon Gapp (52°04′S 68°37′W) and found archaeological evidence of *A. australis* presence only at Cabo Blanco (47°12′S 65°44′W), at present a non-breeding colony. Schiavini (1993) recovered archaeofaunal fur seal material from sites occupied by ancient canoe-using humans near colonies in Tierra del Fuego. In contrast, Caracotche *et al.* (2005) found six pieces of *A. australis* teeth of unidentifiable age and sex at Monte León (50°21′S 68°53′W), the first and currently the only description of *A. australis* there.

Harvesting data from the 16th century in our study area suggest a fairly uniform distribution and abundance. All available records of exploitation came from colonies in which fur seals are now present (Cabrera and Yepes, 1940; Vaz-Ferreira, 1982; Bastida and Rodríguez, 1994), suggesting that the lack of fur seals between Uruguay and Tierra del Fuego—Isla de los Estados is not the result of local overexploitation before 1950.

Groups of breeding colonies are <150 km from the continental shelf break (Figure 1a and d). The other population of the species in the Atlantic Ocean is located at Islas Malvinas, 50–100 km away from the shelf break (Strange, 1973). Between the Uruguay and Tierra del Fuego—Isla de los Estados breeding colonies, there are 4800 km of coast with a wide continental shelf (171–571 km, mean 391 km; Figure 1a). Along that part of the coast, the number of colonies is small and reproductive activity virtually negligible, the exception in terms of breeding activity being the Isla Escondida colony with some reproductive activity but a high rate of pup mortality (Crespo *et al.*, 1999; HLC, unpublished). That colony is 450 km from the continental shelf break.

South American fur seals feed mainly off the continental shelf (Vaz-Ferreira and Ponce de León, 1984; Bastida and Rodríguez, 1994), and an important part of the diet is outer shelf species (e.g. cutlassfish and cephalopods; Naya *et al.*, 2002). Hence, the need for colonies to be next to coastal waters with a narrow continental shelf appears to minimize the distance to foraging sites. The width of the local continental shelf may affect fur seals in several ways. First, the distance from shore to the nearest point of deep water (at the shelf break) is much greater at wide-shelf colonies, and fur seals are limited in the distance they can forage from their breeding sites (Costa, 1991; Boyd, 1998) owing to limits on the speed with which they can swim (Ponganis *et al.*, 1992) and a pup's ability to fast (Bonner, 1984). Second, the prey species taken and their relative abundance may differ as the distance offshore to the foraging sites changes (Knox, 1994; Gentry, 1998; Bradshaw *et al*., 2000). Colonies of northern fur seals (*Callorhinus ursinus*) occupying islands next to wide and narrow continental shelves tend to differ in their past population trends (Gentry, 1998). Most wide-shelf colonies declined between 1956 and 1981 (Saint George, Saint Paul, and Robben islands), whereas narrow-shelf colonies (Medny and Kuril islands) remained stable or increased over the same years (Gentry, 1998). Moreover, attendance behaviour at wide (Saint George Island) and narrow (Medny Island) shelf islands differs, females at narrow-shelf islands cycling faster between foraging at sea and nursing their pups. In a related work, Antonelis *et al*. (1997) showed differences in the diet between these two islands. New Zealand fur seals (*Arctocephalus forsteri*) forage mainly over the outer continental shelf over a bottom depth of 100–300 m (Harcourt *et al*., 1995; Fea *et al*., 1999), but they also forage beyond the continental slope in deep water (Harcourt and Davis, 1997). Bradshaw *et al*. (2002) developed a mathematical model to determine the most influential environmental factors in predicting coastline suitability to support breeding colonies. They found that the shorter the distance to the 1000-m isobath, the better the colony performance. This is consistent with the belief that steeper slopes facilitate local upwelling, which leads to higher local productivity (Trillmich and Ono, 1991; Vincent *et al*., 1991; Knox, 1994; Harcourt *et al*., 1995; Bradshaw *et al*., 2000). The South American sea lion (*Otaria flavescens*), the other otariid found in southern South America, has the same geographic range as *A. australis*, but its 131 colonies along the Atlantic coast cover almost the whole coast of Uruguay and Patagonia (Túnez *et al*., 2008). Continental shelf width appears not to be a critical factor in the distribution of sea lion colonies, therefore. Coincidently, *O. flavescens* tends to forage mainly in coastal waters (Campagna *et al*., 2001).

In the PCA, the number of colonies was also associated with the availability of islands and protected areas, suggesting that human disturbance could be another important influence on the distribution of fur seals. Isolated breeding sites appear to be a requirement of fur seals. Most species of fur seal breed at isolated islands (reviewed by Gentry, 1998; Bonner, 1999), the only exceptions appearing to be *A. australis* along the Peruvian Pacific coast, where mainland colonies are found in specially protected areas (Stevens and Boness, 2003), and Cape fur seals (*A. pusillus pusillus*) with four mainland colonies backed by the virtually unpopulated Namib Desert (Bonner, 1999). That species also had mainland colonies historically, so likely bred on the mainland for many millennia (Klein, 1974). Cape fur seals establish on the mainland despite the presence of predators such as black-backed jackal (*Canis mesomelas*) and brown hyaena (*Hyaena brunnea*; Oosthuizen and Meÿer, 1997; Kolar, 2005). Possible explanations for the existence of the mainland colonies are the narrow ($<$150 km) continental shelf along much of the Namibian coast, the very large population size of the species (now numbering in millions), and the fact that overexploitation of fur seals did not take place until the late 19th century and was then swiftly halted, owing to the strict diamond concession regulations that have curtailed human traffic along that coast for many years (Rand, 1972).

To summarize, we have identified environmental factors likely influencing the rather clumped distribution of *A. australis* along the South American Atlantic coast. Our results suggest that (i) this clumped distribution did not change during the second half of the 20th century, although the population abundance increased tenfold, and (ii) breeding and non-breeding colonies of *A. australis* are located in areas relatively near foraging sites in deep water, where islands are available, and where the coastal zone is protected.

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