Multiple origins of vagrant Subantarctic fur seals: a long journey to the Brazilian coast detected by molecular markers

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Abstract

In this study, we present the first data about putative source populations of the vagrant Subantarctic fur seal, *Arctocephalus tropicalis*, found on the Brazilian coast, through the comparison of their mitochondrial DNA control sequences to exclusive haplotypes from the main breeding colonies of the species. The results indicated that, despite the majority of the vagrant individuals are from Gough Island (the closest breeding site to the Brazilian coast), they also come from other reproductive colonies, such as Crozet Island, a distance around 16,500 km from the Brazilian coast. Furthermore, the molecular data identified three possible management units: (1) Gough, (2) Amsterdam, and (3) Marion, Macquarie and Crozet. This significant genetic subdivision must be taken into account in any future management plan for the species conservation, including rehabilitation and even reintroduction of vagrant fur seals.

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Introduction

The Subantarctic or Amsterdam fur seal, *Arctocephalus tropicalis* (Gray *1872*), breeds on islands north of the Antarctic Convergence (Fig. 1) at Gough/Tristan da Cunha (40°20′S, 09°54′W), Amsterdam/Saint Paul (37°50′S, 77°31′E), Prince Edward/Marion (46°38′S, 37°57′E), Crozet (45°57′S, 50°33′E), and Macquarie (54°30′S, 158°57′E) (e.g., Bester *1980*; Wynen et al. *2000*). The largest breeding populations of this species are concentrated at Gough Island and Prince Edward Islands, with a yearly pup production of approximately of 50,000 (Bester *1987*, *1990)* and 30,000, respectively (Bester et al. *2003*).

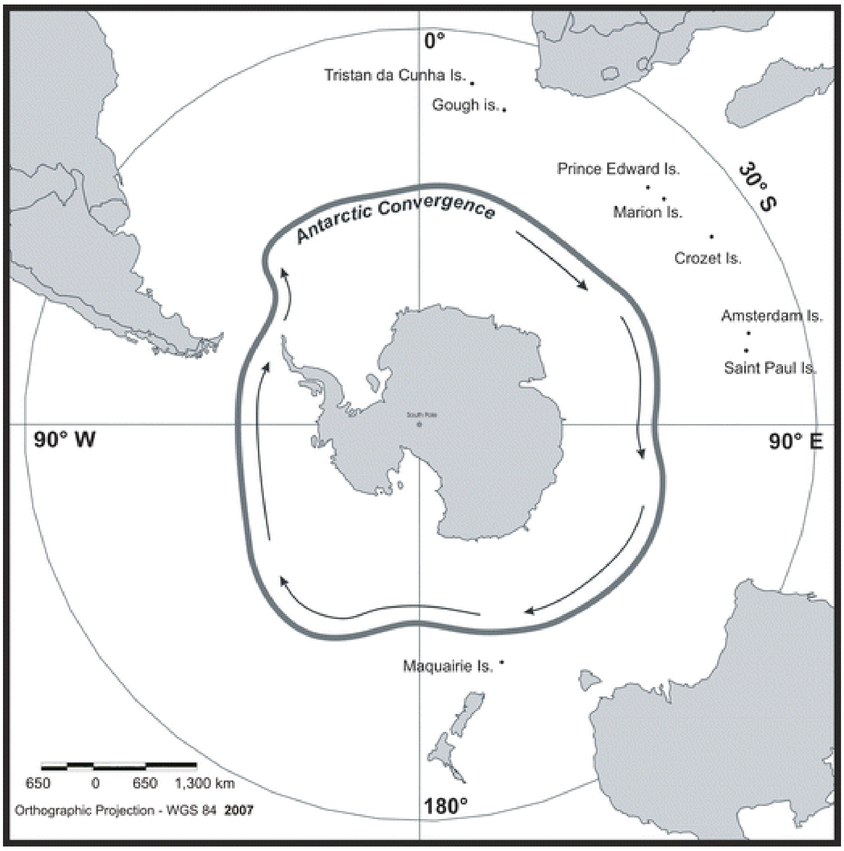

Fig. 1 Main breeding colonies of Subantarctic fur seal, *Arctcephalus tropicalis. Grey line* is the Antarctic Convergence (Polar Front) and the *arrows* indicate the direction of the West Wind Drift. Source: Ricardo Burgo Braga

As a consequence of the commercial seal hunt for fur, meat, and oil that took place between the eighteenth and the twentieth centuries, this species suffered very severe population reductions, even with local extinctions. After the cessation of sealing in the middle of the twentieth century, there were pronounced population expansions with the recolonization of historical sites and probable colonization of new breeding sites (Wynen et al. *2000* and references therein). Along with the population expansions, researchers registered several extra limital occurrences of the species in South America, Angola, New Zealand, Australia, South Africa, and on islands such as Madagascar and Juan Fernandez, The Comores and Bouvetøya (e.g., Shaughenessy and Ross *1980*; Bester *1981*; Orstom *1996*; Oliveira *1999*; Hofmeyr et al. *2006*; Seal Conservation Society *2007*). The large number of these occurrences in any given year is believed to result from the production of large numbers of young (Veit *2000*). Among the extra limital records mentioned above, several were made on the Brazilian coast (Pinedo *1990*); and in most of these cases, the records were in some particular years, mainly during the winter and spring months of the southern hemisphere (Oliveira *1999*; Oliveira et al. *2001*). The Subantarctic fur seals found in these extra limital occurrences are referred to in this paper as vagrant individuals, which are found very far from their breeding sites, and that are not likely to return to the breeding colonies.

Pinedo (*1990*) and Bester (*1981*) suggested that the high number of vagrant individuals found on South America may also be linked to the restriction of ideal breeding sites at Gough, the closest breeding site to Brazilian coast, at a distance of approximately 4,200 km. Recently, it has also been proposed that the number of vagrant of *A. tropicalis*, as well as of *A. gazella* (Antarctic fur seal), found on the Brazilian coast may also be related to anomalies in ocean currents or other oceanographic phenomena, such as the El Niño Southern Oscillation (ENSO) (Oliveira et al. *2001*).

There are both juveniles and adults among the vagrant individuals found on the Brazilian coast. This can be explained by the fact that in many pinniped species, juveniles are not generally present at the colonies during the breeding season, probably remaining at sea (Riedman *1990*). Moreover, during the post-reproductive period of the species (March–November), some adults can range great distances, far from the breeding colonies (King *1983*; Riedman *1990*). Still, the periods spent out of the colonies correspond to the least known phase of the life cycle, not only in terms of behavior and duration, but also in terms of distances covered and location (Bastida and Rodriguez *1990*; Riedman *1990*). In this sense, it is relevant to understand the aspects related to the wanderer and to the post-reproductive movements for a better comprehension of the Subantarctic fur seal biology; once learning about vagrant individuals can potentially lead to new insights on the biology of the species outside the breeding season, and the very existence of a large number of vagrant individuals could open the possibility of the colonization of new sites. However, when they die on the beach in extra limital regions, their importance resides in the fact that they are a noninvasive source of information about biology, natural history, and the areas, which the animals that move further than average are exploring. Nevertheless, it does not mean that the process will take place specifically on the Brazilian coast. As mentioned above, there are no breeding colonies of pinnipeds on the Brazilian coast.

To better understand the post-reproductive movements of the Subantarctic fur seal, marking methods including tagging and branding (Erickson et al. *1993*), as well as satellite telemetry (Matthiopoulos et al. *2004*) have been employed. However, satellite telemetry is very expensive and can only be applied to few individuals at a time and tagging/branding requires an enormous effort to mark a representative part of each population of a particular species, and the chances of recapturing or sighting these tagged individuals outside of the breeding colonies is low. An alternative means of addressing the issues surrounding the putative origin of individuals is provided through the use of molecular markers (Paetkau et al. *1995*; Fabiani et al. *2003*).

In this study, we present the first data about the putative source populations of the vagrant Subantarctic fur seals, *A. tropicalis*, found on the Brazilian coast, through the analysis of mitochondrial DNA (mtDNA) sequences as population molecular markers.

Methods

To test the hypothesis that the vagrant Subantarctic fur seals found on the Brazilian coast are exclusively from Gough Island—the closest breeding site—we compared mtDNA sequences from tissue samples of *A. tropicalis* were collected from dead vagrant individuals on the southern Brazilian coast (29°59′S, 50°08′W) to those obtained from the most representative colonies of the species – Gough (40°20′S, 09°54′W), Amsterdam (37°50′S, 77°31′E), Marion (46°52′S, 37°51′E), Crozet (45°95′S, 50°33′E), and Macquarie (54°30′S, 158°57′E). Following Wynen et al. (*2000*), each island was considered as a distinct population.

We analyzed 31 samples from vagrant individuals from Rio Grande do Sul coast, southern Brazil (29°59′S, 50°08′W). We also analyzed a total of 169 samples from breeding colonies, namely 52 from Marion Island, 40 from Crozet Island, 40 from Amsterdam Island, 20 from Gough Island, and 17 from Macquarie Island. These samples comprised both new samples from the present study ($n = 72$) and sequences from Wynen et al. (*2000*) ($n = 97$) (see Electronic Supplementary Material). We compared, in total, 200 sequences corresponding to a segment of 274 bp of the mtDNA control region of *A. tropicalis*. The primers and the polymerase chain reaction conditions are described in Wynen et al. (*2000*).

According to Wynen et al. (*2000*) and Fabiani et al. (*2003*), exact matches of sequences from individuals to exclusive haplotypes from the breeding colonies suggested that the particular colony could be the source population.

In order to obtain a measure of confidence for this inference, the minimum frequency for detection ($P = 1 - e^{x}$ where $x = \log 0.05/N$; P. Otto, personal communication) was calculated. This measure determined the highest frequency in which the haplotype should be present in the colonies, and still not be detected by our sampling.

In order to identify exclusive haplotypes, to test for population structure within the species (population subdivision) and to ascertain whether each breeding colony represents distinct genetic sources, or whether all colonies should be considered panmictic, we performed population genetic analyses. We also analyzed the sequences from the breeding colonies to test against the null hypothesis of neutrality and infer possible events of population expansions, which could be related to the occurrence of vagrant individuals.

A haplotype network generated using TCS (Clement et al. *2000*) made it possible to determine which sequences from vagrant individuals were the same as the exclusive haplotypes observed in different breeding colonies. Tests of population differentiation [fixation indices Φst; Analysis of Molecular Variance (AMOVA)] and the neutrality tests were calculated using the software Arlequin 2.0 (Schneider et al. *2000*). The sequences from vagrant individuals that could not be identified with exclusive haplotypes were compared to the entire data set of *A. tropicalis* sequences.

Results

The results from the comparison of the 200 sequences from different individuals (present study and Wynen et al. *2000*) yielded 50 haplotypes (see Electronic Supplementary Material). Among these, ten were new for the species: two shared between Marion, Macquarie, and Crozet, two exclusive to Crozet, one to Amsterdam, and five found in the vagrant individuals from the Brazilian coast, meaning that they have not been described for any colony yet (GenBank accession numbers DQ313261, DQ313263, DQ313270, DQ313273, DQ313278, EF517383, DQ313293, DQ313307, DQ313308, EF526077). Although we did not perform a demographic or a sex-bias study, it is important to mention that the great majority of the vagrants found on the Brazilian coast were males (70%), what is in accordance with the natural history observed for the species, with little male phylopatry.

Both the Fu's Fs (Fu *1997*) and the Tajima's D (Tajima *1989*) did not indicate deviation from neutrality in the analyses conducted within each colony (Table 1), as well as in the analyses conducted with the species as a whole (Tajima's D: 1.46729, $P > 0.05$ and Fs: (−3.77152, $P > 0.05$). These results indicated that neither the populations, nor the species as a whole, went through a rapid population expansion from a small effective size.

Table 1 Tajima (*1989*) and Fu (*1997*) neutrality tests

	Tajima's *D*	***P*-value**	**Fu's Fs**	***P*-value**
Gough	–0.65144	0.274	0.18943	0.696
Macquarie	1.28535	0.928	1.35763	0.725
Crozet	1.41542	0.946	2.17815	0.802
Marion	1.91165	0.98	5.7184	0.952
Amsterdam	0.65131	0.792	0.47857	0.621

Positive values and statistical probability of divergence from 0 (*P*) indicate a deviation from expected values under neutral evolution model and an indicative of population expansion event

The first analyses of population structure were conducted considering five populations (one corresponding to each group of breeding colonies sampled), and a sixth one, in which we grouped all the vagrant individuals found on the Brazilian coast. The AMOVA indicated that 85.6% of the variation is within, rather than among the populations. However, the Φst values (Table 2) were generally statistically significant, suggesting that most of the populations analyzed are different from each other. The population differentiation analyses showed that Gough Island is the most genetically distinct population when compared to the others. The data also indicated that Gough and Amsterdam Islands are significantly different from each other and from the other colonies—Marion, Macquarie and Crozet—which form a substructured, yet unique group (from now on referred to as MMC). These differences allowed us to divide the species into three putative subgroups: Gough, Amsterdam, and the MMC group.

Table 2 Pairwise *Φ*st values of *Arctocephalus tropicalis* populations based on haplotype sequence data

Population	Vagrants	Amsterdam	Gough	Crozet	Macquarie	Marion
Vagrants	–					
Amsterdam	0.10353***	–				
Gough	**0.00498**	0.13785***	–			
Crozet	0.15169***	0.04796*	0.22190***	–		
Macquarie	0.18782***	0.07076*	0.28369***	**–0.01416**	–	
Marion	0.23826***	0.18956***	0.30713***	0.06114*	**0.03584**	–

Pairwise comparisons not statistically significant are in bold
*$P < 0.05$, ***$P < 0.001$

The significant *Φ*st results with the new subgroups showed that the populations are indeed different from each other. These results gave support for the comparative analyses performed with the samples from vagrant individuals and the exclusive haplotypes from the breeding colonies. The 31 screened vagrant individuals (Brazilian coast) presented 12 haplotypes (Table 3): five new ones (nine specimens, 29.03% – GenBank accession numbers DQ313261, DQ313263, DQ313270, DQ313273, DQ313278), four corresponding to unique haplotypes from Gough Island (eleven individuals, 35.48%) and two were identical to nonexclusive haplotypes distributed among different colonies (ten individuals, 32.26%), what prevented us from inferring the origin of the individuals that presented them. We have also identified one haplotype from one specimen (3.23%) collected on the southern Brazilian coast (GEMARS 907) unique from Crozet (in the MMC group, haplotype CI50T), which was highly unexpected.

Table 3 Haplotypes of the vagrant specimens (new and matching with haplotypes already described in the literature) and their inferred origin

Haplotype	Number of specimens	Percentage	Origin
GEMARS832, GEMARS834, GEMARS851, GEMARS866, GEMARS883	9	29.03	Undetermined
GI4T, GI14T, GI20T, GI5T	11	35.48	Gough
GI2T, CI44T	10	32.26	Undetermined
CI50T	1	3.23	Crozet (MMC)

Discussion

According to our results, the vagrant Subantarctic fur seals found on the Brazilian coast came from different source populations, with roughly 35% of the 31 studied vagrant individuals from Gough Island, and with the remaining individuals coming from further a field (Amsterdam and the MMC group). Therefore, we refute the hypothesis that the vagrant *A. tropicalis* found on the Brazilian coast were exclusively from Gough Island. In general, it is accepted that specimens from Gough and from Tristan da Cunha Islands could reach the Atlantic coast of South America taking advantage of the Anticyclone Currents System of the South Atlantic Ocean currents, which is a complex of marine currents, including the West Wind Drift, Benguela, South Equatorial, and Brazil currents (Rodriguez et al. *1995*; Queiroz and Pereira *1997*; Oliveira *1999*). We found, however, one vagrant individual, which presented a DNA sequence matching an exclusive haplotype from the Crozet Island (45°95′S, 50°33′E), located between the African and the Australian continents, in the Indian Southern Ocean. This individual probably moved west with assistance of the West Wind Drift, a clockwise movement around Antarctica (Fig. 1) and Falkland (Malvinas) cold current, arriving on the Brazilian coast after covering a distance of around 16,500 km. This result highlights the utility of molecular markers, and provides additional means of addressing the species' temporary movements alongside tagging studies. Therefore, molecular markers seek to expand on our current methods, rather than replace them.

The use of mtDNA haplotypes to infer the putative source populations of individuals with unknown origin was successfully used by Wynen et al. (*2000*) and by Fabiani et al. (*2003*). In the former, three of the six vagrant *A. tropicalis* individuals analyzed could be associated with a specific breeding colony. Among these, there was one individual found on the Juan Fernandez Islands off the Chilean coast (33°50′S, 80°00′W) whose mtDNA haplotype was exclusive to Amsterdam Island, approximately 15,000 km away. In this case, the individual probably reached the Chilean coast assisted by the east-flowing circulation generated by the West Wind Drift. Fabiani et al. (*2003*) also used this technique to show evidence of male-mediated genetic dispersal in Southern elephant seals, *Mirounga leonina*, over a geographic range of about 8,000 km (from one extreme of the species range to the other). Based on a tagging study and haplotype comparisons, the authors found that an adult male of elephant seal that was born in Macquarie Island had lately bred on Falkland Islands. They also suggested that Southern elephant seals traveled around Antarctica with the West Wind Drift to other breeding grounds or nourishment sources.

The tests used to analyze deviation from neutrality using the mtDNA fragment indicated that neither the populations, nor the species as a whole, went through a rapid population expansion from a small effective size. This result does not mean that demographic expansion (increase in census size population) from a small effective size did not occur; it just suggests that the mtDNA could not detect it. In this sense, we could not refute the hypothesis of population expansion to explain the high numbers of vagrant individuals currently being reported.

The highly differentiated populations of Gough and Amsterdam Islands stand in stark contrast to the substructured MMC group. The similarity within the MMC group may be explained by the pattern of recolonization after the cessation of sealing (Wynen et al. *2000*). The differentiation between the Amsterdam population and the MMC population group is difficult to explain. However, Wynen et al. (*2000*) suggested that both Macquarie and Crozet Islands were probably recolonized by females from Marion Island, and to a lesser extent Amsterdam Island.

These three groups (Gough, Amsterdam, and MMC) were not reciprocally monophyletic for mtDNA haplotypes (i.e., they share some mtDNA haplotypes), however they present statistically significant differences in mtDNA haplotype frequency. Based on these results, we believe that the three major groups described above may represent distinct Management Units (Moritz *1994*). These must be taken into account in any future management plan in relation to the conservation of this species, mainly due to the constant problems brought by fur seal translocation and reintroduction programs of vagrant individuals in the Brazilian coast.

The use of molecular markers was effective to identify putative populations of origin of vagrant Subantarctic fur seals. The occurrence of vagrant individuals with haplotypes from geographically distant localities is an indication of the multiple origins of the vagrant individuals found along the Brazilian coast, and corroborates previous studies that showed the great dispersal capacity of this species. Despite the fact that the neutrality tests could not detect signals of population expansions in the mtDNA, we could not deny that the reports on the increase of vagrant individuals in this region is probably a reflection of the increase in the population sizes for this species described in the literature (Bester *1980*, *1990*; Bester et al. *2003*).

Furthermore, it is important to mention that the mtDNA is a matrilineal molecular marker and can reveal only the evolutionary history and population structure of the female history. Nevertheless, further sampling at the breeding colonies and of vagrant animals, combined with the use of nuclear molecular markers (autossomic and heterossomic) and morphological studies, and also the increase of tagging and satellite telemetry studies, are essential to a better understanding of the patterns of movements of the species.

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