

# Analysis of environmental correlates of sexual segregation in northern elephant seals using species distribution models

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**Abstract** Elephant seals are among the most sexually dimorphic and polygynous species of all mammals. Their foraging grounds occupy a wide area of the world oceans, where they show spatial segregation between males and females. The objective of this paper was to correlate female and male foraging distributions of *Mirounga angustirostris* with main climatic variables at a biogeographical scale. We used website and bibliographical sources to obtain information on adult elephant seal distribution and environmental predictors (surface and bottom sea temperatures, productivity and bathymetry) and three species distribution models [maximum entropy model, environmental niche factor analysis and based on climatic envelopes (BIOCLIM)] to predict the habitat suitability of ocean regions. BIOCLIM provided the best fit. Sea surface and bottom temperatures were the variables with the highest explanatory power for females, while bathymetry was for males. Predictive maps suggest that low temperatures constrain female, but not male, distribution at high latitudes. We suggest that large size increases foraging efficiency of males because, among other benefits, it augments thermal insulation, improving the use of cold, rich sectors of the ocean. Different thermoregulatory abilities between sexes due to size dimorphism should be a complementary explanation of sexual segregation in elephant seals.

## Introduction

The spatial segregation of sexes outside the mating season has been documented in a wide variety of mammals (Ruckstuhl and Neuhaus 2002). The differential use of space by sexes is intimately linked to sexual size dimorphism, being more common among more dimorphic species (Myserud 2000). In mammals, most studies have been conducted with ungulates, and hypotheses on the evolutionary ecology of sexual segregation in mammals have mostly been developed for this taxonomic group (Main and Coblenz 1996; Ruckstuhl and Neuhaus 2002; Bowyer 2004). Sexual segregation has been described in several dimorphic species of seals and sea lions, including *Arctocephalus gazella* (Staniland and Robinson 2008), *A. forsteri* (Page et al. 2006), *Halichoerus grypus* (Breed et al. 2006) and *Mirounga spp.* (see below). Staniland (2005) reviewed the literature in pinnipeds and concluded that, because of their diversity, the sexes segregate in many different ways and to varying extents, meaning that it is impossible to generalize the entire group.

Elephant seals are among the most sexually dimorphic of all mammals (McCann 1981; Le Boeuf and Reiter 1988). Estimations of size differences range from four to ten times, depending on species, populations and metric used (Bonner 1990; Boyd et al. 1994; Ralls and Mesnick 2009; Bailleul et al. 2010). Elephant seals forage exclusively at sea and dive continuously and deeply throughout their foraging trips (Costa 1991; Hindell et al. 1991; Le Boeuf et al. 1996; Campagna et al. 2000; Bailleul et al. 2007; McIntyre et al. 2010). There have been many studies on migration (Bailleul et al. 2007; Reisinger et al. 2010), foraging behaviour (Le Boeuf 2000; Bradshaw et al. 2002; Field et al. 2004; Biuw et al. 2007; Simmons et al. 2007) and diet (Van den Hoff et al. 2003). Many of these studies

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show sexual segregation at sea. Combining high sexual dimorphism and high sexual segregation, this species is an excellent model for the study of causes and consequences of sexual differences in habitat utilization.

At least six hypotheses have been proposed to explain sexual segregation in elephant seals: different predation efficiency (Le Boeuf et al. 2000), different energetic requirements during growing stages (Stewart 1999), different response to predation risk (Le Boeuf et al. 2000), niche competition (Field et al. 2005; Bailleul et al. 2010; McIntyre et al. 2010), and genetic drift and fixation (Stewart 1999). At present, there is not agreement on the ecological forces that govern ocean distribution, including sexual segregation, in elephant seals.

In recent years, there has been a steady increase in the application of species distribution models (SDMs) to investigate ecological and biogeographical issues (Ladle and Whittaker 2011). These associative models relate occurrence or abundance data at known locations of individual species (distribution data) to information on the environmental characteristics of those locations. Several publications have reviewed the available SDMs (Austin 2002; Hirzel et al. 2002; Guisan and Thuiller 2005; Elith and Leathwick 2009; Cassini 2013). These reviews found that SDMs have been used with good results to characterize the natural distributions of species and to apply this information to investigate a variety of scientific and applied issues. SDMs have two main uses: identifying predictors or key factors of the environment that affect species distributions and predicting distributions in new scenarios, assuming that the variables included in the model are relevant factors (Cassini 2013).

Tagging and its associated tracks have been used recently with SDMs (Redfern et al. 2006). Baumgartner and Mate (2005) inferred summer and fall habitat of North Atlantic right whales (*Eubalaena glacialis*) using satellite tagging, Kaschner et al. (2006) used long-term averages of three habitat variables to generate hypotheses about global cetacean distributions with environmental niche factor analysis (ENFA) model, Friedlaender et al. (2011) used the maximum entropy model (MaxEnt model) in tracking data of crabeater seals (*Lobodon carcinophaga*) and humpback whales (*Megaptera novaeangliae*) in western Antarctic Peninsula, Edren et al. (2010) applied MaxEnt to harbour porpoises (*Phocoena phocoena*) in European waters and Ballard et al. (2012) applied MaxEnt to meso-predators in Sea Ross, including satellite tagging of Weddell seals (*Leponychotes weddellii*).

In this paper, we applied SDMs to the distribution of northern elephant seals to search for differences in the effect of climatic variables on male and female distributions that can help to elucidate the ecological factors that cause sexual segregation in this species.

## Methods

Año Nuevo Island is a small island on the outskirts of Año Nuevo's coastal point (37.1086°N, 122.3378°W) in Northern California, 31 km north to Santa Cruz (Le Boeuf 2000). This colony is located near oceanic fronts or edges of shelves, which are highly productive areas (Le Boeuf 2000). Elephant seals locations in the ocean and environmental variable estimations were incorporated into a grid containing 300 × 300 km cells. This cell size was based on the study by Bradshaw et al. (2002), who evaluated the optimal spatial scale for the analysis of elephant seal distribution.

Locations of elephant seals in the ocean were obtained from a total of 153 tracks (36 adult males and 117 adult females) corresponding to the period 1991/2010 and were extracted from the studies of Stewart and DeLong (1995), Simmons et al. (2010), and Le Boeuf et al. (2000). Georeferencing was performed by extracting data through the method of control points provided in the SantiTools extension of ArcView V.3.3 software. In each case, 60–100 control points were taken.

The predictor variables used to calibrate the model included sea surface and bottom (seafloor) temperatures, bathymetry depth and productivity. Sea temperatures were obtained from the graphical interface POET (<http://poet.jpl.nada.gov/>) of Pathfinder AVHRR-source with a spatial resolution of 4 km. Bottom temperatures were obtained from the 'World Ocean Atlas' with a resolution of one degree of latitude by one degree longitude through the website 'ODV home' ([www.odv.awi.de](http://www.odv.awi.de)) and associated software Ocean Data View v.4. Bathymetry values were obtained from the website of the National Geophysical Data Center (<http://www.ngdc.noaa.gov/mgg/global/globla.html>) ETOPO1 through a global model of 1 arc minute surface, which integrates the land surface and topography of the ocean. Productivity was estimated from chlorophyll concentration (CHLO). Data on CHLO were obtained from the Web application 'Giovanni' (<http://disc.sci.gsfc.nasa.gov/giovanni>). The 'Ocean Color Radiometry' interface was used to access the sensor information SeaWiFS. R2009. In six of 276 cells in which coverage was incomplete, the interface 'Ocean Model Monthly' was used, in which the NOBM model (NASA Ocean Biogeochemical Model) offers coverage. Data on environmental variables were matched with specific tracks, in a way that each tracking data were associated to the closest environmental data available in web bases. Data were reprocessed to ASCII format for cell size.

We tested three SDMs: MaxEnt, ENFA and BIOCLIM (based on climatic envelopes). MaxEnt technique has its roots in information theory and is a statistical modeling method in several fields. It has been widely used as a type of

SDM (Elith et al. 2006; Phillips and Dudik 2008). We used the MaxEnt program (version 3.3.1, [www.cs.princeton.edu/~schapire/maxent](http://www.cs.princeton.edu/~schapire/maxent)) as described in detail in Phillips et al. (2004). MaxEnt employs a maximum likelihood method that models species distributions by generating a probability distribution over the pixels in a grid of the study area. MaxEnt estimates a probability distribution that maximizes entropy (i.e. that is the closest to uniform) subject to a set of constraints derived from measurements of assumed suitable habitat values at species occurrence locations. For the MaxEnt analysis, we used a Java environment. We used the following settings of MaxEnt v.3.3.2: automatic feature selection, regularization multiplier at unity, maximum 500 iterations, 10 replicates and convergence threshold 10–5. We also used a random test percentage of 25 %. Maps of the potential distribution of the species using the logistic output format were produced, which is the easiest output to conceptualize and which provides an estimate of probability of presence between zero and one (Phillips and Dudik 2008).

Environmental niche factor analysis (Hirzel et al. 2002) uses a modified principal components analysis (PCA) to develop a model based on occurrence only data. The observed environment is compared to the background data of the study area. The analysis produces factors similar to a PCA. Model projection uses the geomeans method of Hirzel and Arlettaz (2003). ENFA analyses were performed using the BIOMAPPER software (<http://www2.unil.ch/biomapper/index.html>). A MacArthur's Broken-stick distribution analysis was used to establish factor significance (Hirzel et al. 2002). Distance geometric-mean algorithms were used for habitat suitability computations (Hirzel and Arlettaz 2003). These algorithms make no assumption about the shape of the species distribution, but the density of observations must be representative of the species niche. The geometric mean produces a smooth set of envelopes around the observation points and provides a good generalization of the niche (Hirzel and Arlettaz 2003).

Based on climatic envelopes, the algorithm uses means and standard deviations of each environmental variable separately to calculate bioclimatic envelopes. For each given variable, the algorithm calculates these two parameters (assuming normal distribution) for each point of occurrence (in these case centroids). Each variable has its own envelope represented by the interval  $[m - c * s, m + c * s]$ , where  $m$  is the mean,  $c$  is the cut off input parameter and  $s$  is the standard deviation. Besides the envelope, each environmental variable has additional upper and lower limits taken from the maximum and minimum values related to the set of occurrence (Nix 1986). For BIOCLIM analysis, we use DIVA-GIS software (version 7.1.7, [www.diva-gis.org](http://www.diva-gis.org)) and modeling module, with the option to run the model BIOCLIM.

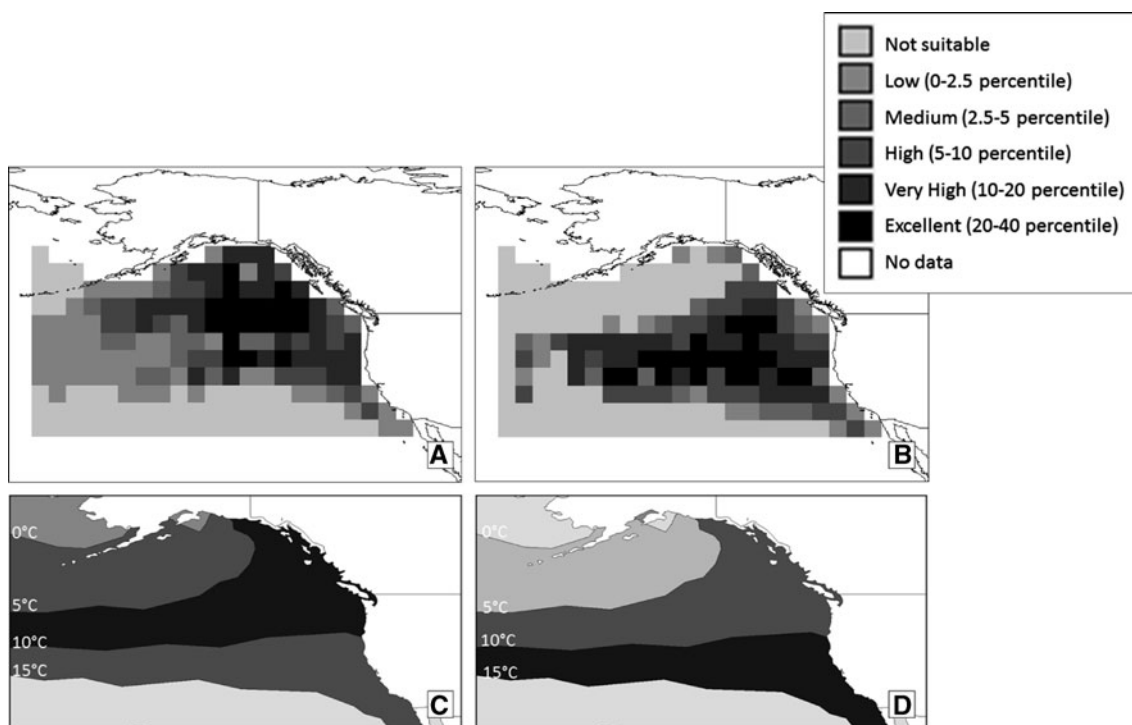
Model fit was measured using the area under the curve (AUC) from the receiver operating characteristic curve, which is the relationship between the sensitivity and the false positive fraction, with a value of 0.5 representing a random model (Woodward 1999). We used a threshold criteria proposed in the literature for deciding the quality of model outputs: values <0.8 represent poor fitted models, between 0.8 and 0.9 represent models with good fit and those over 0.9 being an excellent fit (Manel et al. 2001; Thuiller 2003). From the three SDMs applied to elephant seal data, we selected the model that reached an excellent fit. A jackknife test was used on AUC to determine the weight of each variable within each model.

## Results

The BIOCLIM model showed the highest AUC values ( $AUC_{\text{males}} = 0.927$ ,  $SD = 0.018$ ,  $AUC_{\text{females}} = 0.960$ ,  $SD = 0.014$ ), followed by ENFA ( $AUC_{\text{males}} = 0.887$ ,  $SD = 0.020$ ,  $AUC_{\text{females}} = 0.761$ ,  $SD = 0.028$ ). Although MaxEnt showed AUC values that are above chance, they did not exceed the threshold value of 0.8 ( $AUC_{\text{males}} = 0.712$ ,  $SD = 0.035$ ,  $AUC_{\text{females}} = 0.712$ ,  $SD = 0.022$ ). Habitat suitability maps generated by BIOCLIM showed a latitudinal segregation between males and females, where the highest probability of occurrence for males occurs in the highest latitudes, near the edge of the continental shelf (Fig. 1a). In contrast, females show high habitat suitability at low latitudes and open waters (Fig. 1b). When BIOCLIM predictions are mapped against isotherms, a clear pattern emerges with males using all temperature ranges (Fig. 1c), while females were almost absent from low-temperature waters (Fig. 1d).

The contribution of each environmental variable to BIOCLIM analyses using a jackknife method showed that both temperatures (sea surface and bottom) are the only variables that exceed the criterion of  $AUC > 0.8$  for females. For males, the highest AUC was for 'bathymetry' ( $AUC = 0.732$ ), i.e., that almost reaches this criterion. We used data provided by the ENFA model to complement the results of BIOCLIM. Values of AUC higher than 0.8 were only found for males. As with BIOCLIM, the analysis of the contribution of each variable to ENFA model revealed that 'bathymetry' was the only significant variable ( $AUC = 0.697$  when this variable is eliminated from the analysis). The influence direction was negative, meaning that males use shallow depths with high probability.

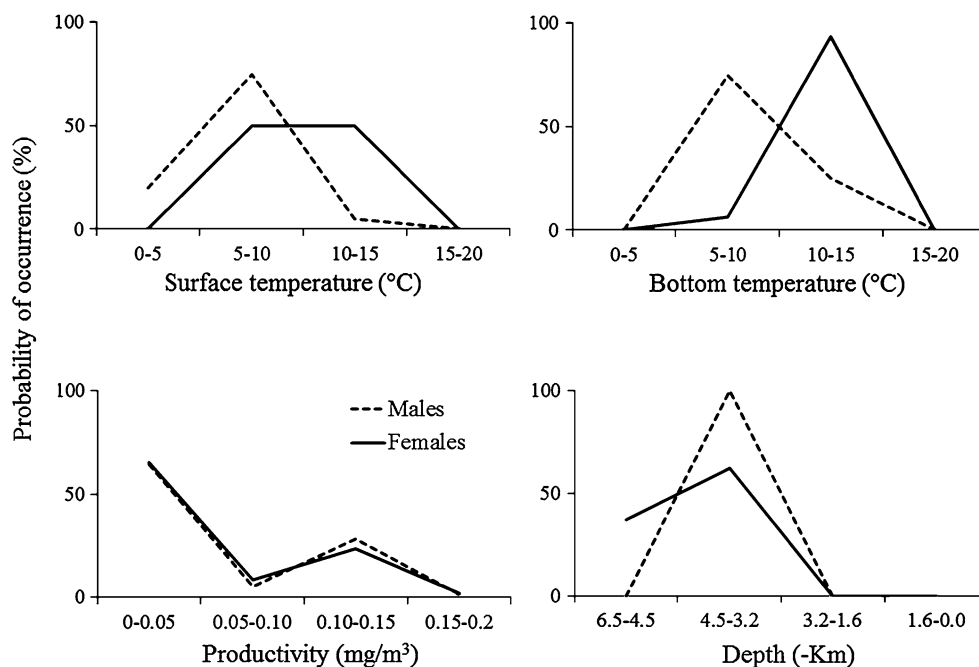
For each sex, we also analysed the relationship between the probability of occurrence and the values of each of the four environmental variables (Fig. 2). Males showed the highest values of suitability at lower temperatures than



**Fig. 1** Suitability maps for males (a) and females (b) obtained with BIOCLIM analysis. Maps c, d (males and females, respectively) showed another way to present the results of this analysis; different

shades of *grey* represent mean probabilities of occurrence obtained with BIOCLIM, within ranges defined by isotherms (for surface temperature, 5 degrees of amplitude)

**Fig. 2** Relationship between the probability of occurrence for model BIOCLIM and environmental variable values for males and females. We calculated frequency of occurrence of the probability values greater than zero divided into four categories for the four environmental variables: surface temperature, productivity, bottom temperature and depth. The probability values were transformed into 0–100 scale



females (Fig. 2a, c). At the deepest depths, females showed higher probabilities of occurrence than males (Fig. 2d), while no differences between sexes were found in relation to productivity (Fig. 2b).

## Discussion

Tracking data of northern elephant seals indicated that they foraged in a wide range of latitudes. Male and female

distributions showed some overlap, but there were still considerable differences that were associated to differential responses to oceanic factors. The results of the application of SDMs indicated that (1) female, but not male, distribution appears to be constraint by low ocean temperatures, while (2) male distribution is related to bathymetry. The influence of bathymetry on male distribution is not surprising as a number of papers have shown that male elephant seals tend to prefer performing benthic dives on shallow features (e.g. Hindell et al. 1991; Campagna et al. 2000). Previous studies also have reported a relationship between elephant seal movements, behaviour and ocean temperatures (Bestley et al. 2013; McIntyre et al. 2011; Simmons et al. 2007).

Although our results suggest different biogeographical responses of males and females to oceanographic variables, methodological improvements by increasing sampling size and environmental factors should be applied to confirm this trend. Satellite tracking data are usually obtained from relatively few individuals; hence, they could create a bias due to autocorrelation inherent in the behaviour of individuals when applied to SDMs (Gschweng et al. 2012). Even with this and other limitations, the use of this approach to the study of marine vertebrates can be very helpful to infer past distribution and likely refugial areas, predicting possible effects of future climate change on the ranges of species, or to visualize migration pathways and feeding grounds (Dambach and Rödder 2011). The following discussion attempts to relate different biogeographical patterns between sexes with hypotheses on the evolution of sexual segregation in elephant seals.

An explanation of sexual segregation in *Mirounga* spp. was proposed by Le Boeuf et al. (2000). They started by assuming that sexual dimorphism evolved by a sexual selection process. The larger size of males resulting from intra-sexual competition is conceived as a phylogenetic constraint on foraging behaviour. Males must acquire more resources to attain great size as well to maintain it. It has been estimated that the difference in size between the sexes determines that males must consume about three times as much prey energy as females (Le Boeuf et al. 1993; Boyd et al. 1994). Le Boeuf et al. (2000) concluded that these different requirements may be achieved using different foraging strategies. A more efficient foraging behaviour by males can lead to differences in diet composition and spatial segregation between sexes.

Le Boeuf et al. (2000) applied this ‘different predation efficiency’ hypothesis to data on ocean distribution of northern elephant seals. They found that the richest foraging areas were those furthest from the rookery and suggested that males, specially the largest ones, can take advantage of the abundance of prey in these rich sites

because they can swim faster and have sufficiently large fat reserves needed for the long trip.

There are at least four other hypotheses that complement this ‘different predations efficiency’ one. Firstly, in the same paper, Le Boeuf et al. (2000) suggested that females balance food acquisition with predation hazard avoidance. By foraging near the coast, male elephant seals risk greater exposure to their major predators than females feeding in the open ocean, although they can deal with this larger predation risk due to their body size. Secondly, Stewart (1997) proposed that sexual segregation of northern elephant seals is more precisely related to differential metabolic needs of males during the period of sexual maturation and accelerated growth rather than to sexual differences in gross energy requirements of adults. This author proposed that the direction of migration was established during the first year of life in both males and females. Several authors have further proposed that sexual spatial segregation may be explained by avoidance of inter-sexual competition (Field et al. 2004; McIntyre et al. 2010). Under this hypothesis, divergence in migration among age and sex groups has resulted from both temporal and spatial separation of resource use where individuals avoid intra-specific competition. Finally, food preferences may drive habitat selection. Elephant seals show sexual segregation in food niche, so differential use of regions of the ocean could be associated with different prey distributions. If prey distribute in accordance to oceanic features such as temperature, then the relationship between environmental variables and male and female distribution could be in fact an indirect effect of the response to prey distribution (for a discussion of this topic at a smaller ecological scale, see: McIntyre et al. 2011; Boersch-Supan et al. 2012; McIntyre et al. 2012). However, food preferences are closely associated to metabolic demands, predatory efficiency and intra-specific competition, so this hypothesis interlinks with the others.

We suggest a complementary hypothesis about the origin of sexual segregation in *Mirounga* spp., which could explain the different spatial responses to ocean temperature of males and females. Previous hypotheses are based on the assumption that large male size is a benefit during the reproductive season; however, it is an energetic cost outside this period because it requires more absolute energy than small size. We propose that large size can also represent a benefit for males as a means of improving thermoregulation. Numerous studies have demonstrated elevated metabolic costs in aquatic and semi-aquatic mammals (Irving and Hart 1957; Dawson and Fanning 1981; Williams 1986). While raising heat production through increased metabolism appears to be an effective mechanism by which to counteract heat loss, it also represents an added energetic expense to the animal, especially if employed over long periods (Liwanag 2009). As a consequence, an aquatic

mammal may suffer environmental stress if it spends sufficient time in water temperatures below a critical value (Watts et al. 1999). There are at least two morphological adaptations relevant to elephant seals that can reduce heat lost in marine mammals at low temperatures: (1) increased body size will decrease the surface-area-to-volume ratio, so the surface area through which heat can be transferred is reduced; and (2) increased thickness of the subcutaneous bubbler, so that insulation from environmental temperature is increased.

One possibility is that sexual segregation of elephant seals in the sea is influenced by different thermal requirements of males and females. Due to their relatively small body size and thin blubber layer (Gales and Burton 1987), females should be more likely to be metabolically constrained and have a thermal limit in water temperature while males are expected to exploit the colder areas because of their productivity. Our results support the hypothesis that males are more efficient foragers than females, as it was proposed by Le Boeuf et al. (2000), and should be validated with future studies that integrate research on bioenergetics, foraging behaviour and biogeographical distribution.

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