Mammalian Biology 80 (2015) 316–327

Contents lists available at ScienceDirect

Mammalian Biology

journal homepage: www.elsevier.com/locate/mambio

Original Investigation

Variability and sexual dimorphism in skull morphometry of California Sea Lions (*Zalophus californianus*) in Mexico

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ARTICLE INFO

Article history:
Received 15 October 2014
Accepted 8 April 2015
Handled by Daisuke Koyabu
Available online 25 April 2015

Keywords:
Classification
Population units
Sexual dimorphism
Skull morphometry
Zalophus californianus

ABSTRACT

A crucial question in wildlife management concerns the definition of ecologically meaningful population units. For the California sea lion (*Zalophus californianus*), three population units are recognized in Mexico based on mitochondrial DNA and geographical distances; these units are thought to be genetically isolated. In the present study, we quantitatively compare patterns of shape variation and evaluate different classification approaches to confirm this regional fragmentation among the Mexican colonies and assess sexual dimorphism in skull morphometry. We employed 20 linear measurements of 368 skulls of specimens from the Mexican Pacific (including the Gulf of California), evaluated correlation among the features, and performed multivariate analyses. To provide robustness to the classification by sex and region, we evaluated the use of kernel-based classifiers. According to skull morphometry, the classification of individuals to sex is very reliable, and there is a phenotypic regionalization among colonies that coincides with the proposed regional population structure. We suggest that inside the Gulf, there is gene flow between females but that it is reduced with geographic distance. The phenotypic differences between the Gulf of California and Pacific for both sexes are consistent with the hypothesis of little or no gene flow between these regions.

Introduction

Natural selection affects population structure substantially over time, complicating the prediction of the long-term phenotypic patterns that are generated as a result. Assumptions about the spatial structure of populations can significantly affect estimates of species vulnerability, which is the basis for defining management units and evaluating their status (Dizon et al., 1992; Fraser and Bernatchez, 2001; González-Suárez et al., 2009). Thus, such assumptions are particularly important for species that require special protection. Traditionally, systematic and taxonomic studies have involved analysis of three types of variation within and between species: geographical, sexual, and individual (Mayr, 1963). The California sea lion, *Zalophus californianus* (Lesson, 1828), has a wide breeding distribution that extends from California's Channel Islands to the west coast of Baja California and the Gulf of California (Lowry and Maravilla, 2005; Szteren et al., 2006). Some of the differences between the interior of the Gulf of California and the west coast of Baja California arise from the fact that the peninsula acts as a physical barrier, limiting the influence of the Pacific Ocean and the California Current (cold and rich in nutrients; Roden, 1964; Roden and Emilsson, 1980). Moreover, local variation in productivity within the Gulf is another important distinction (Alvarez-Borrego, 1983).

The geographic distance between breeding colonies and the environmental differences along the latitudinal gradient (13°), which include various patterns of productivity and temperature, foster great potential for diversification, which is evident in food resources (García-Rodriguez and Aurioles-Gamboa, 2004;

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http://dx.doi.org/10.1016/j.mambio.2015.04.001
1616-5047/

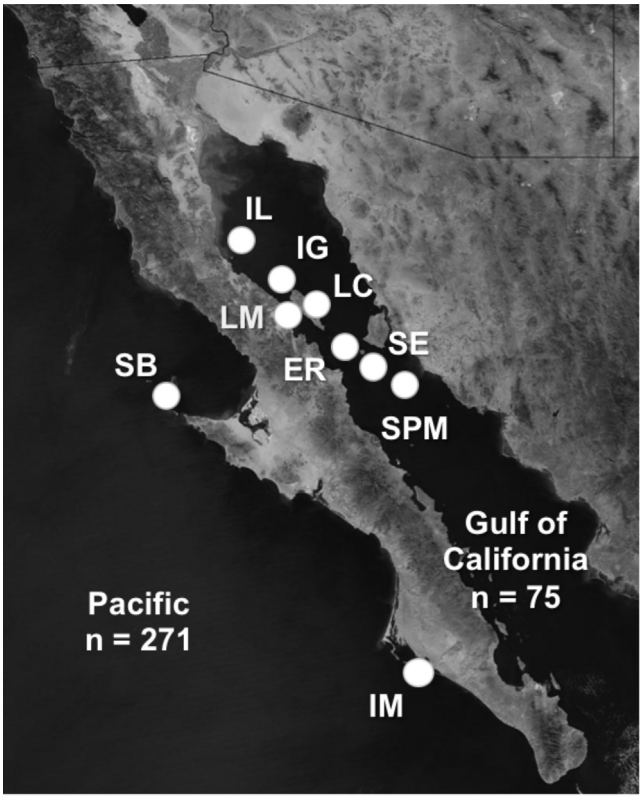

Fig. 1. Colonies from the northern Gulf of California (IL: Isla Lobos; IG: ISla Granito; LM: Los Machos; LC: Los Cantiles; ER: El Rasito; SE: San Esteban; SPM: San Pedro Martir) and Pacific (SB: San Benito; IM: Isla Margarita).

Porras-Peters et al., 2008). Genetic studies based on differences in maternally inherited mitochondrial DNA have shown that the Gulf of California rookeries are differentiated from those of the Pacific (Maldonado et al., 1995); within the Gulf, it has been proposed that the population is structured into three genetically different groups (north, central, and south according to Schramm et al., 2009). It is currently unclear, if these units reflect true population subdivisions or only matrilineal structure in mtDNA that does fully represent patterns of gene flow. However, González-Suárez et al. (2009) proposed three groups based on nuclear DNA variation and geographical distances among colonies: Upper Gulf of California, Southern Baja Peninsula, and Upper Pacific Coast of Baja which suggests that there is true population subdivision even within the Gulf.

Using morphometric data, we tested whether phenotypic evidence supports the hypotheses that these four putative population units are genetically isolated: Gulf of California (Upper and Middle Riff) and Pacific (Upper Pacific coast and Southern Baja Peninsula) (Fig. 1). If these are reproductively isolated populations, then we would expect the phenotypic mean to differ among them because isolation would have allowed differences to accumulate by drift or selection. Alternatively, if there is gene flow, even at a reduced rate, we would expect phenotypic differences to arise from isolation by distance, which means that geographically closer samples would have more similar phenotypes.

Sex-specific differences in behavior complicate these hypotheses. In many mammalian species, dispersal is sex linked. This fact should be considered when making inferences regarding the impact of spatial dynamics on the genetic structure of a particular population. For example, pinnipeds are dispersed over considerable distances; however, movement is exclusively associated with males because females are typically philopatric (Burg et al., 1999; Hoffman et al., 2006). California sea lions exemplify this pattern with a breeding season that begins in late May with the birth of pups and ends in August with mating. At the end of this period, adult males migrate in search of food (to higher latitudes in Pacific populations and inside the Gulf of California in the colonies distributed in this area), while adult females remain at the breeding colonies, alternating between feeding trips and maternal care during the first year following the birth of a pup (García-Aguilar and Aurioles-Gamboa, 2003).

The sex differences in dispersal would therefore be expected to lead to sex-linked differences in morphological differentiation, especially if gene flow is reduced or absent. If the male dispersal pattern results in gene flow between adjacent regions, we would expect no phenotypic differences in either males or females because the phenotypes would spread to females through interbreeding. However, if there is no gene flow despite male dispersal, then males from the home region would be intermingled with males of the target region, which would increase within-region male variation and decrease differences between regions. Females, however, would be expected to differ between the two regions because restricted gene flow would preclude homogeneity. Furthermore, if male phenotypes differ between regions, then the populations are likely to be both genetically isolated and free from regular male dispersal events.

Morphometry allows these hypotheses to be tested using existing specimens available in natural history museums and scientific collections. This approach takes into account features reflecting a relatively long period of time, and ultimately, these traits are also related to the organism's life history, which in turn, may be affected by environmental variables. Thus, the approach represents an advantageous and informative analytical tool.

In this study, we made quantitative comparisons using shape variation and assessed different classification approaches to identify sex and geographical variation in the biometry of the skulls of California sea lions from different colonies (or groups of colonies) along the coasts of Mexico. We attempted to evaluate differences in the species phenotype using parametric and non-parametric methods, and based on the cranial features evaluated, we expected that the population units would emerge. This work constitutes the first characterization at the phenotypic level of population units of *Z. californianus* in Mexico in relation to specific morphometric features of the skull and mandibles, taking into account the Pacific and Gulf of California populations and the differences between sexes.

Material and methods

The area for this study corresponds to the colonies around the Peninsula of Baja California (Fig. 1). We selected these colonies based on previous work that highlighted the genetic, biological, ecological, and regional differences among them (Aurioles-Gamboa and Zavala, 1994; Aurioles-Gamboa et al., 2011; Garcia-Aguilar and Aurioles-Gamboa, 2003; González-Suárez et al., 2009; Schramm et al., 2009; Szteren and Aurioles-Gamboa, 2011; Zavaleta-Lizárraga, 2003). Colony selection resulted in the following three areas:

- Pacific (P), which corresponds to the west coast of the Peninsula: We selected individuals from Isla Santa Margarita (IM: 23°31′ N, 112°01′ W) in the south (PS) and San Benito (SB: 28°18′ N, 115°32′ W) in the north (PN). These are rocky, sandy, and pebble beaches (Zavaleta-Lizárraga, 2003).
- Gulf of California (GC), which is divided into North (GCN) and Central (GCC). GCN: We selected colony individuals from Isla Lobos (IL: 30°02′30″ N, 114°28′30″ W). GCC: We selected individuals from Isla Granito (IG), Los Machos (LM: 20°20′00″ N, 113°30′00″