

# Testing Bergmann's rule and the Rosenzweig hypothesis with craniometric studies of the South American sea lion

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**Abstract** We tested the validity of Bergmann's rule and Rosenzweig's hypothesis through an analysis of the geographical variation of the skull size of *Otaria flavescens* along the entire distribution range of the species (except Brazil). We quantified the sizes of 606 adult South American sea lion skulls measured in seven localities of Peru, Chile, Uruguay, Argentina, and the Falkland/Malvinas Islands. Geographical and environmental variables included latitude, longitude, and monthly minimum, maximum, and mean air and ocean temperatures. We also included information on fish landings as a proxy for productivity. Males showed a positive relationship between

condylobasal length (CBL) and latitude, and between CBL and the six temperature variables. By contrast, females showed a negative relationship between CBL and the same variables. Finally, female skull size showed a significant and positive correlation with fish landings, while males did not show any relationship with this variable. The body size of males conformed to Bergmann's rule, with larger individuals found in southern localities of South America. Females followed the converse of Bergmann's rule at the intraspecific level, but showed a positive relationship with the proxy for productivity, thus supporting Rosenzweig's hypothesis. Differences in the factors that drive body size in females and males may be explained by their different life-history strategies. Our analyses demonstrate that latitude and temperature are not the only factors that explain spatial variation in body size: others such as food availability are also important for explaining the ecogeographical patterns found in *O. flavescens*.

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## Introduction

Studies of the geographic variations of different organism traits have been of particular interest in the fields of ecology and evolution, partly because of their utility for finding adaptive divergence within species (Futuyma 1998). Several ecogeographic rules that relate morphological variation to the environment have been developed (Ashton et al. 2000). One of the best-known ecological generalizations is Bergmann's rule (1847, translated by James 1970), which states that larger homeotherms are found at higher latitudes or in colder climates than closely related smaller ones

(Mayr 1963; Meiri 2011). Although this rule was originally intended to apply to different assemblages (e.g., Ashton et al. 2000; Meiri and Dayan 2003; Yom-Tov et al. 2006; Medina et al. 2007), it has mostly been studied at the intraspecific level, correlating size variation with temperature, latitude, or altitude (e.g., Aldrich and James 1991; Wiggington and Dobson 1999; Yom-Tov et al. 2003).

Support for Bergmann's rule has usually come from studies of size versus latitude, using latitude as a proxy for temperature (Ashton et al. 2000). Although several authors have found a relationship between latitude and/or temperature with body size in different species of mammals and birds (e.g., Ashton et al. 2000; Gaston and Blackburn 2000; Meiri and Dayan 2003), others found no relationship at all (e.g., McNab 1971; Dayan et al. 1991; but see criticisms of these studies made by Ashton et al. 2000). The differences found between the different studies may be due, at least in part, to the diversity of the compared taxa, since each of them has different traits or ecological characters (Oliifiers et al. 2004). Meiri et al. (2004) tried to overcome those "methodological errors" by comparing only carnivorous species and by including a phylogenetic framework. Meiri (2011) suggested that Bergmann's rule would be better proven at an intraspecific level, because the degree of geographic variation in body size within a species might be expected to closely parallel geographic differences in environmental variables, all other things being equal.

Although Bergmann's rule is an empirical pattern that is largely accepted by the scientific community, the mechanisms that operate in geographical body size patterns have clearly not been settled. The classical thermoregulatory interpretation of Bergmann's rule is that the small body surface relative to volume in larger individuals results in more efficient retention of body heat per unit mass, which could be an advantage in cold-climate zones (Mayr 1963; Boyce 1978). Furthermore, for smaller animals a greater surface to volume ratio allows better heat dissipation, which could be an advantage for warmer climatic zones (Yom-Tov et al. 2003). Some mechanisms other than thermoregulation have also been proposed to account for latitudinal variation in body size, such as primary productivity (Rosenzweig 1968), heat load (James 1970) and seasonality (Boyce 1978). Primary regional production has been considered as one of the main potential mechanisms for Bergmann's rule (Rosenzweig 1968; Case 1978; Lindsay 1986). The so-called Rosenzweig productivity hypothesis indicates that the sizes of carnivorous mammals can be better explained by environmental productivity (a prey abundance index), suggesting that productivity in an environment might be positively correlated with the body sizes of the individuals living there (Wiggington and Dobson 1999; Yom-Tov and Geffen 2006). Thus, some of the mammal species that corroborate Bergmann's rule,

such as some carnivores and granivores, would do so due to food availability rather than thermal interchange (Khokhlova et al. 2000; Yom-Tov et al. 2003).

Predictions about latitudinal trends in body size have been tested primarily in terrestrial vertebrates, with relatively little work focusing on the latitudinal distribution of body size for marine vertebrates such as marine mammals. Studies in cetaceans suggest that water temperature and primary productivity are environmental factors that affect body size at an intraspecific level (Ross and Cockcroft 1990; Amano and Miyazaki 1992). In Otariidae (sea lions and fur seals), Brunner et al. (2002) found that most of the species follow Bergmann's rule: that populations of a given species tend to be smaller in the tropics; they increase in size with increasing latitude, reaching a maximum in subpolar regions. These authors also mentioned that this phenomenon could be due to greater primary productivity in high-latitude regions. Although both temperature and primary productivity seem to influence the body sizes of marine mammals, Ashton et al. (2000) and Meiri and Dayan (2003) indicated that it is hard to prove whether one or both factors can explain the geographic differences in body size, since these variables are usually correlated. This could be resolved by analyzing species with wide distribution areas that allow the concurrent evaluation of thermal (latitudinal) and productivity variations.

In South America, the South American sea lion *Otaria flavescens* (Shaw 1800) is a good model to test the effects of the environment on the geographical distribution of body size, because it has one of the widest geographic distributions among the Otariidae, from Peru (4°S) to the southernmost extreme of Chile (55°S) along the Pacific coast, and from Brazil (23°S) to the southern extreme of Argentina (54°S), including the Falkland/Malvinas Islands on the Atlantic side (Vaz-Ferreira 1982; King 1983). Studies of geographic patterns of body size in *O. flavescens* have demonstrated that significant variation occurs over its geographic range (Oliveira et al. 1999; Brunner et al. 2002). Brunner et al. (2002) found that male skulls from the mainland are generally larger than those from the Falkland/Malvinas Islands. By contrast, skulls of females from the mainland are smaller than those from the Falkland/Malvinas Islands.

South America is marked by large differences in primary productivity between the Pacific and the Atlantic oceans, due principally to the influence of the Humboldt Current near the coast in the Pacific Ocean (Neira and Arancibia 2004). The primary productivity in this system sustains a remarkably high fish biomass which, in turns, sustains one of the most productive fishing zones in the world (Neira and Arancibia 2004). Because a relationship between the maximum level of primary productivity and the catch of fisheries has been suggested (Beddington 1995;

Pauly and Christensen 1995), differences in primary productivity should be reflected in differences in fish landings between the oceans. From 1960 to 2002, fish landings in the southeastern Pacific Ocean averaged 8 million ton year<sup>-1</sup>, and was never less than 2.5 million tons (FAO 2003). By contrast, fish landings in the southwestern Atlantic Ocean average 500,000 ton year<sup>-1</sup>, and never exceeds 700,000 t.

The above information about *O. flavescens*—a wide species distribution (both latitudinal and longitudinal), evidence of geographic variation in body size, and a marked difference in primary productivity between the Pacific and Atlantic coasts—led us to select it as a suitable species. The aim of the study described in this paper was thus to test the validity of Bergmann's rule and Rosenzweig's productivity hypothesis by analyzing the geographical variation in the skull sizes of *O. flavescens* individuals from five areas: Peru, Chile, Uruguay, Argentina, and the Falkland/Malvinas Islands. The length of the skull correlates well with the body size of an individual, validating its usefulness as a measure of overall size (Cruwys and Friday 1995; Meiri et al. 2005; Blois et al. 2008). We tested two alternative predictions: (1) if there is a relationship between body size and latitude, then the skulls from Chile, Argentina, and the Falkland/Malvinas Islands should be larger than those from Peru and Uruguay; (2) if there is a relationship between body size and primary production, then the skulls of sea lions from the Pacific Ocean should be larger than the skulls of sea lions from the Atlantic Ocean.

## Materials and methods

This study is based on morphological measurements of 606 South American sea lion skulls (217 males and 389 females), measured in seven localities along the entire range of the species (except for Brazil). Collections of skulls were examined at: (1) Punta San Juan, Marcona, Peru ( $N = 253$ ); (2) Museos de Historia Natural de Santiago and Valparaíso, central Chile ( $N = 46$ ); (3) Instituto de la Patagonia, Punta Arenas, south Chile ( $N = 4$ ); (4) Universidad de la República and Museo Nacional de Historia Natural, Montevideo, Uruguay ( $N = 30$ ); (5) Centro Nacional Patagónico, Puerto Madryn, Argentina ( $N = 217$ ); (6) Museo del Fin del Mundo, Ushuaia, Argentina ( $N = 16$ ); and (7) British Museum of Natural History, London, England (skulls from the Falkland/Malvinas Islands,  $N = 40$ ). To ensure that measurements were minimally affected by growth, only adult individuals were considered (Guill et al. 2003). Relative age was estimated by applying a suture ageing index (SI) (Sivertsen 1954). Based on the degree of closure of nine sutures,  $SI > 23$  for

males and  $SI > 18$  for females were considered to indicate adult individuals, following the criteria of Brunner et al. (2002). We measured the condylobasal length (CBL) of each skull using a 500 mm Mitutoyo caliper and a 200 mm digital caliper (accuracy 0.1 mm).

We focused on the influences of different geographical and environmental variables that may explain the intra-specific variation in body size. We examined the relationships between CBL and the geographical variables latitude and longitude, which have been used as a proxy for climate in other studies (e.g., Ashton et al. 2000; Blois et al. 2008). Latitude was included because the presence or lack of a positive correlation between body size and latitude indicates whether or not Bergmann's rule applies to a species (Meiri and Dayan 2003; Medina et al. 2007). Longitude was also included because this variable may be related to differences in primary productivity between the Pacific and Atlantic coasts. Latitude (LAT) and longitude (LON) were converted to decimal units.

We also examined the influences of some independent environmental variables: temperature and productivity. While sea lions show a combination of marine feeding and terrestrial breeding and resting behaviors, we considered that both the ocean temperature and the ambient temperature could potentially affect their body size. For each locality, we therefore calculated the average minimum ocean temperature in June (TSEA<sub>min</sub>), the average maximum ocean temperature in January (TSEA<sub>max</sub>), and the mean temperature over all months (TSEA<sub>mean</sub>) at the surface level for the entire dataset available. Different sources of information were used for different countries. For Peru (locality of San Juan de Marcona), Argentina (Chubut and Ushuaia), Uruguay (Isla de Lobos), and the Falkland/Malvinas Islands, data were obtained from the IRI/LDEO Climate Data Library at <http://iridl.ldeo.columbia.edu/SOURCES/NOAA/NCEP-NCAR/CDAS-1> from 1981 to 2010. Chilean data were obtained from the Servicio Hidrográfico y Oceanográfico of the Armada de Chile (SHOA) at [http://www.shoa.cl/cendhoc\\_php/index.htm](http://www.shoa.cl/cendhoc_php/index.htm) from 1945 to 2006 in central Chile and from 1961 to 2005 in Punta Arenas. We also considered air temperature. For this variable, we calculated the average minimum temperature in June (TAIR<sub>min</sub>), the average maximum temperature in January (TAIR<sub>max</sub>), and the mean temperature over all months (TAIR<sub>mean</sub>). Temperatures in Peru (in Vitor) and Chile (in Coquimbo, Valparaíso, Talcahuano, and Punta Arenas) were obtained from the NOAA Central Library at <http://docs.lib.noaa.gov/rescue/> from 1935 to 1963 for Peru and from 1928 to 1970 for Chile. For Uruguay, Argentina, and the Falkland/Malvinas Islands, data were obtained from the IRI/LDEO Climate Data Library from 1949 to 2011.

Primary productivity was also included because this variable has been hypothesized to be relevant to the

generation of geographical body size clines (Rosenzweig's hypothesis). However, we only have information for the Southwest Atlantic and Southeast Pacific zones, which is not differentiated by country or locality. For this reason, and as a proxy for primary productivity, we also included information on fish landings. Data were taken from a compilation of the Food and Agriculture Organization of the United Nations (FAO) at: <http://fao.org/fishery/statistics/software/fishstat/en> over a 57-year period, from 1950 to 2006. The entire dataset was averaged for each country. The information is presented by country and not by locality, so we assigned the same fish landings for specimens from Chubut and Ushuaia (Argentina) and for specimens from central Chile and Punta Arenas (Chile).

We examined the relationships of these environmental variables to variation in skull size using linear regression models. The Bonferroni correction for multiple comparisons was applied when necessary. Multiple regression analyses were discarded because climatic variables are highly correlated, and standard multiple regression analysis is not appropriate because of this multicollinearity (Ashton 2001). To satisfy assumptions of normality, the data were transformed using the Box–Cox transformation ( $\lambda = 4.999$ ). To analyze differences among localities, a one-way analysis of variance (ANOVA) with the Tukey post hoc test was applied. Males and females were analyzed separately, because skulls of South American sea lions showed pronounced sexual dimorphism (one-way ANOVA:  $F_{(1,604)} = 1097.13$ ,  $P < 0.0001$ ). The statistical analyses were performed using the statistical software

Statistica 7.0 (Statsoft Inc., 2004). All values are reported as the mean  $\pm$  SD.

## Results

### Latitudinal and longitudinal variations in skull size

Wide variation in skull size occurred within this species. Skull length ranged from 237 to 369 mm in males and from 214 to 288 mm in females. Male skulls showed greater size variation than females; the coefficients of variation were 9.4 for males and 4.6 for females.

South American sea lions showed a significant variation in CBL over their geographical range. In males there was a positive relationship between CBL and latitude, and the correlation accounted for nearly 18 % of the variation in body size (Table 1; Fig. 1a). Females showed a significant negative relationship between these variables; the correlation of CBL with latitude accounted for about 27 % of the variation in body size (Table 1; Fig. 1a). In the case of longitude, a significant positive relationship was obtained with female skull size—increased longitude was positively related to larger body size (Table 1; Fig. 1b). However, this relationship was not found in males.

### Body size and climatic variables

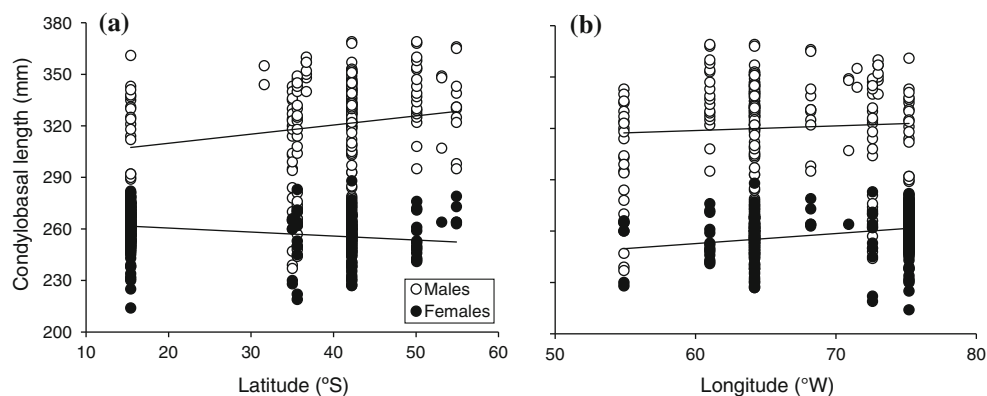
Condylbasal length showed basically the same relationship to different climatic variables when linear regressions

**Table 1** Simple linear regressions and their statistical significance ( $P$ ) for male and female skull size CBL with latitude (LAT) and longitude (LON)

	Males				Females			
	$df$	$F$	$r$	$P$	$df$	$F$	$r$	$P$
Latitude	215	7.25	0.18	<b>0.0076</b>	387	29.24	-0.27	<b>&lt;0.0001</b>
Longitude	215	0.63	0.05	0.4287	387	34.62	0.29	<b>&lt;0.0001</b>

Significant terms are in bold

**Fig. 1** Relationships between condylbasal length (CBL) and **a** latitude and **b** longitude for male and female sea lion (*Otaria flavescens*) skulls



**Table 2** Linear regressions and their statistical significance (*P*) for male and female skull size and climatic variables

	Males				Females			
	<i>df</i>	<i>F</i>	<i>r</i>	<i>P</i>	<i>df</i>	<i>F</i>	<i>r</i>	<i>P</i>
TAIR <sub>max</sub>	215	11.17	-0.22	<b>0.0010</b>	387	10.09	0.16	<b>0.0016</b>
TAIR <sub>min</sub>	215	7.30	-0.18	<b>0.0070</b>	387	24.74	0.25	<b>&lt;0.0001</b>
TAIR <sub>mean</sub>	215	10.11	-0.21	<b>0.0017</b>	387	21.52	0.23	<b>&lt;0.0001</b>
TSEA <sub>max</sub>	215	18.70	-0.28	<b>&lt;0.0001</b>	387	14.84	0.19	<b>0.0001</b>
TSEA <sub>min</sub>	215	11.44	-0.22	<b>0.0008</b>	387	26.41	0.25	<b>&lt;0.0001</b>
TSEA <sub>mean</sub>	215	14.85	-0.25	<b>0.0002</b>	387	19.23	0.22	<b>&lt;0.0001</b>
Fish landings	215	0.55	-0.05	0.4592	387	33.13	0.28	<b>&lt;0.0001</b>

See “Materials and methods” for abbreviations of variables. A Bonferroni correction was applied and *P* values of <0.0071 were considered significant  
 TAIR air temperature, TSEA sea temperature

Significant terms are in bold

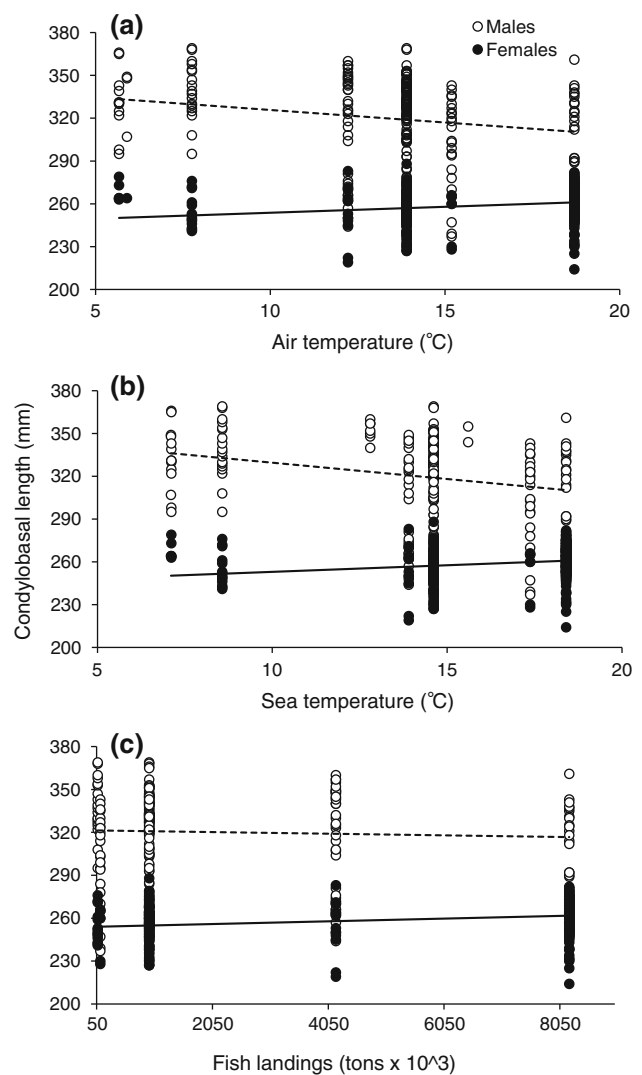
were performed (Table 2). With respect to temperature, male skull size showed significant and similar negative correlations with both TAIR and TSEA (min, max, and mean): male sea lions were larger when TAIR and TSEA were lower (Fig. 2a, b). On the contrary, females showed an inverse relationship, with positive and significant correlations between skull size and the six temperature variables, indicating that larger females tended to be found in warmer localities (Fig. 2a, b).

Assuming that fish landings reflect productivity, female skull size showed a significant and positive correlation with productivity (Table 2; Fig. 2c). Males did not show any relationship with this variable.

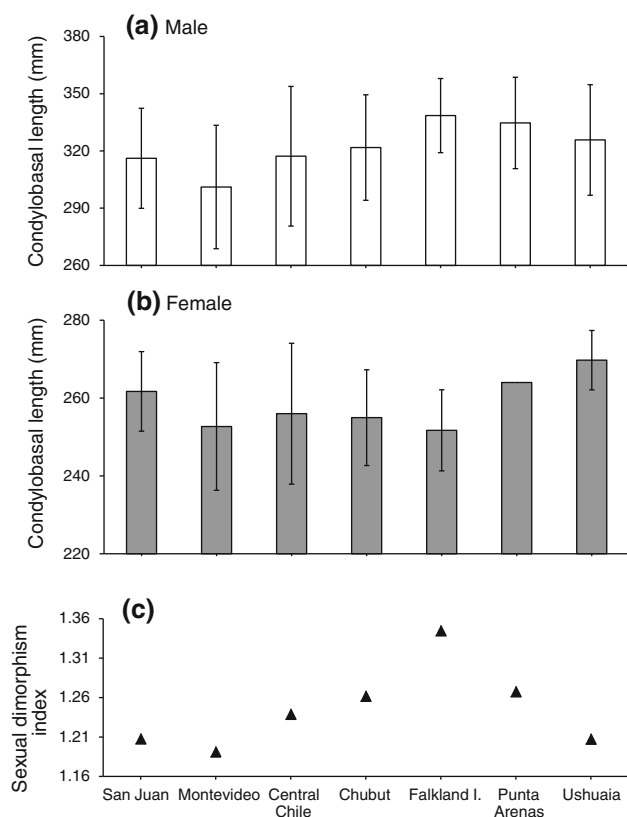
Differences between localities

Significant differences were found among males from different localities ( $F_{6,210} = 3.547, P = 0.0023$ ). CBLs of males from the Falkland/Malvinas Islands were significantly larger than those of individuals from Chubut ( $P = 0.009$ ), San Juan ( $P = 0.006$ ), Montevideo ( $P < 0.001$ ), and central Chile ( $P = 0.014$ ) (Fig. 3a). On the other hand, males from Montevideo were significantly smaller than sea lions from Chubut ( $P = 0.003$ ), Ushuaia ( $P = 0.016$ ), and central Chile ( $P = 0.022$ ). In the case of CBLs of females, significant differences among localities were found ( $F_{6,382} = 7.094, P < 0.0001$ ). Individuals from Ushuaia were significantly larger than individuals from Chubut ( $P = 0.007$ ), the Falkland/Malvinas Islands ( $P = 0.002$ ), Montevideo ( $P = 0.0154$ ), and central Chile ( $P = 0.037$ ) (Fig. 3b). Also, females from San Juan were significantly larger than females from Chubut ( $P < 0.0001$ ) and the Falkland/Malvinas Islands ( $P < 0.0001$ ).

Considering the size differences between males and females, a sexual dimorphism index was calculated for each locality (CBL males:CBL females) (Fig. 3c). According to



**Fig. 2** Relationships between condylobasal length (CBL) and mean annual **a** air temperature, **b** sea temperature, and **c** fish landings for male and female South American sea lion skulls



**Fig. 3** Condylobasal length (CBL) (mean  $\pm$  SD) for **a** male and **b** female South American sea lion skulls from seven localities in South America. **c** Sexual dimorphism index for each locality

this index, sexual dimorphism was more pronounced in the Falkland/Malvinas Islands and less pronounced in San Juan, Montevideo and Ushuaia.

## Discussion

This study found a significant intraspecific variation in skull size among allopatric populations of *O. flavescens*. As in other studies, our results corroborate the importance of latitude and temperature in explaining body size variations. However, our analyses demonstrate that these are not the only factors that explain spatial variation in body size: others such as longitude and food availability are also important for explaining the ecogeographical patterns found in *O. flavescens*.

### Latitudinal and longitudinal variations in skull size

We found that males conform to Bergmann's rule, whereby individuals in colder regions are larger than conspecifics in warmer regions. Specifically, males from higher latitudes (and lower temperatures) such as Punta Arenas, Falkland/Malvinas and Ushuaia are larger than males from lower

latitudes such as Montevideo; males from Montevideo were the smallest. Similar results have been found for other species of mammals, providing extensive support for this rule in this group (e.g., Ashton et al. 2000; Meiri et al. 2004). In otariids, Brunner et al. (2002) found that most species conform to Bergmann's rule; populations from a given species tend to be smaller in the tropics, increasing in size with increasing latitude. Different results were found by Higdon (2011) in 34 species of pinnipeds (seals, sea lions, and the walrus). Using phylogenetic methods, this author did not find a positive interaction between body size and latitude. However, this study was performed at an interspecific level and thus may be not comparable with our results.

Females follow the converse of Bergmann's rule, since body size decreased with increasing latitude (and decreasing temperature). This pattern is more similar to what has been found in ectotherms, which also display converse Bergmann clines in which body size decreases toward the poles (Ashton 2004; Blanckenhorn and Demont 2004). In mammals, a similar pattern has only rarely been found—in the leaf warbler *Phylloscopus*, in which a single species showed the converse of Bergmann's rule (Katti and Price 2003), and in an interspecific study in a genus of subterranean mammals (*Ctenomys*, Medina et al. 2007). These contradictory results suggest that the body sizes of males and females may respond differently to climatic influences (Fleischer and Johnson 1982; Wiggington and Dobson 1999).

Although females do not seem to follow Bergmann's rule, they showed a positive significant relationship with our proxy for productivity, thus supporting Rosenzweig's hypothesis. Similarly, they also showed a positive relationship between longitude and body size, indicating that females from the Pacific coast are larger than females from the Atlantic coast. This positive relationship clearly suggests the crucial role of primary production in determining body size in females, also indicating that temperature is not the only factor behind the observed body size trend in females. Other studies have also found that primary production and food availability are important factors explaining spatial variation in body size (Yom-Tov et al. 2003; Meiri et al. 2007; Blois et al. 2008), and are more important than temperature (Yom-Tov and Geffen 2006). In males, however, there was no evidence of an association between primary productivity in the environment and body size that supports Rosenzweig's hypothesis, because the predicted association of body size and our proxy for mean annual productivity was not significant.

Differences in the factors that drive body size in females and males could be explained by their different life-history strategies. For example, South American sea lion females tend to remain in the same place and show a high degree of

philopatry (Feijoo et al. 2011). On the other hand, males are less philopatric and there is some evidence that high mobility of males exists among different colonies (Szapkievich et al. 1999; Feijoo et al. 2011). Females nurse their young on land for 8–10 months (Cappozzo and Perrin 2009), and evidence from satellite data indicates that they forage close to the breeding sites during their foraging trips (Thompson et al. 1998), so local productivity is an important factor for them.

A possible explanation for the inverse body size trend found in females in this study could be that the energetic cost of being larger is compensated by the ability to find and capture prey, and this explains their deviation from Bergmann's rule. Females from Peru face unpredictable fluctuations in food supply due to El Niño (ENSO) events (Majluf 1991). Such periodic stress may lead to selection for flexible patterns of behavior, and perhaps even for larger body size, to provide some level of buffering against lean years (Oliveira et al. 2008). The evolution of a larger body size in this unpredictable environment may thus provide females with a greater ability to overcome spatiotemporal fluctuations in food and mate availability (Ferguson and Lariviere 2008). A similar pattern was found in the South American fur seal (*Arctocephalus australis*) by Oliveira et al. (2008), a species also strongly affected by El Niño events. Also, according to Ralls (1976), "big mothers are better mothers," because they are better at defending their broods. It is possible that females from Peru are better mothers because, for them, the survival of their pups is critical and provides another buffer against El Niño years.

### Sexual dimorphism

One of the most remarkable results of this study is the observation of latitudinal differences in sexual dimorphism. Because females from low latitudes are larger than females from high latitudes, while males from high latitudes are larger than males from low latitudes, it could be expected that sea lions inhabiting high latitudes would display greater size dimorphism than sea lions from low latitudes (Ferguson and Lariviere 2008). Sexual dimorphism is very well documented in many species of pinnipeds and seems to be related to sexual selection (male competition) and highly polygynous mating systems (Berta and Sumich 1999; Lindenfors et al. 2002). The potential for polygyny varies greatly among pinnipeds, and there is a strong correlation between the degree of polygyny and the degree of sexual dimorphism (Lindenfors et al. 2002). The northern fur seal (*Callorhinus ursinus*) and the Steller sea lion (*Eumetopias jubatus*), for example, have the greatest relative dimorphism in body weight and defend the greatest number of females in their territories among dimorphic species (Ralls and Mesnick 2002).

Differences in body size and degree of sexual dimorphism may be reflected in more than one polygynic strategy within the same species (Oliveira et al. 2008). In otariids, Lindenfors et al. (2002) found that size dimorphism is positively correlated with harem size: the more polygynous the species, the more dimorphic in size it will be. In the *O. flavescens* populations from Argentina, a polygynous female-defense system has been described in which males defend positions in the central breeding area and later attract, defend, and copulate with females (Campagna and Le Boeuf 1988; Cappozzo and Perrin 2009). On the contrary, Soto and Trites (2011) described a lekking system in Punta Ballestas (Pisco, Perú). In this system, males positioned themselves along the waterline and allowed the free movement of females between the water and the beach. Movements of individual females were not random, and they tended to shift between a few preferred rocks or resting sites, associating with several territorial males during the day (Soto and Trites 2011). Thus there is no stable harem structure and males have to expend only a minimum level of effort to retrieve and copulate with the females. This absence of great effort to control females may be a consequence of smaller males in relation to females (i.e., a lesser degree of sexual dimorphism). By contrast, defense of females and/or territories that are characteristic of other places may act as a sexual pressure for high body size in males. A similar result was found in *A. australis* populations, in which more than one type of polygyny also occurs depending on the ecological conditions (Oliveira et al. 2008).

In summary, *O. flavescens* shows a strong pattern of body size variation over spatial gradients. Our results suggest that temperature and food availability are the principal factors driving body size patterns. Thus, it appears that the relationships between body size and temperature are not simple and should be related to other climatic factors (Yom-Tov and Geffen 2006). Because body size must be maintained by sufficient food supply, natural selection may adjust consumers to various rates of energy flow by modifying body size in accord with productivity (Wigginton and Dobson 1999). It appears that, at least for females, temperature alone (the classical physiological explanation for Bergmann's rule) was not a primary influence on variation of body size (Wigginton and Dobson 1999). We suggest that the effect of food availability on latitudinal body size variation has been underestimated, and that many of the observed trends that claimed conformity with Bergmann's rule (particularly those based on latitude alone) are also influenced by factors that determine food availability. Selection for female size is likely driven by a complex set of trade-offs between factors such as lactation patterns, prey availability, and a balance between the immediate costs of lactation (in terms

of energy depletion) and the future reproductive performance of females as well as their offspring.

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