Ecography 40: 365–375, 2017
doi: 10.1111/ecog.02209

Subject Editor: Susanne Fritz. Editor-in-Chief: Miguel Araújo. Accepted 18 March 2016

When Bergmann's rule fails: evidences of environmental selection pressures shaping phenotypic diversification in a widespread seabird

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Organisms tend to exhibit phenotypes that can be shaped by climate, commonly demonstrating clinal variations along latitudinal gradients. In vertebrates, air temperature plays a major role in shaping body size in both ectothermic and endothermic animals. However, additional small-scale environmental factors can also act as selection pressures in the marine ecosystem (e.g. primary productivity), evidencing multi-scale processes acting on marine organisms. In this study, we tested Bergmann's rule in a widely distributed seabird, the brown booby *Sula leucogaster*, in addition to evaluating the relationship of sea surface temperature and chlorophyll α with phenotypes. We used traits from a morphometric dataset (culmen, wing chord, and tarsus length) and body mass of 276 brown boobies distributed on six breeding sites along a latitudinal gradient in the South Atlantic Ocean (0–27°S). We found significant differentiation among colonies, but phenotypic similarities were observed between colonies located at the extremes of the latitudinal gradient. As the colony nearest to the Equator, Saint Peter and Saint Paul archipelago, had the largest and heaviest individuals, the model containing only air temperature explained $< 5\%$ of the allometric variation, providing no substantial support for Bergmann's rule. However, when we added the interaction of chlorophyll α and sea surface temperature the deviance explained rose to over 80%. Primary productivity and sea surface temperature do not follow a latitudinal gradient in the ocean and, therefore, the role of small-scale oceanographic processes in shaping body size and the importance of considering additional environmental variables when testing Bergmann's rule in marine organisms are evident.

Birds tend to exhibit phenotypic diversity on an intraspecific level along a climatic gradient, with larger body sizes occurring in colder environments, a phenomenon referred to as Bergmann's rule (James 1970). In general, population structuring among conspecifics results from the selection of multiple pressures to which an organism is exposed (Mayr 1956), such as differences of local oceanographic features around distinct seabird colonies (Friesen 2015). Identifying these variations is relevant both to understanding evolutionary mechanisms of divergence, which may be the first step towards new races (Rensch 1938), and to developing successful conservation strategies, especially in the age of global climate change (Quillfeldt and Masello 2013, Brommer et al. 2015).

Intraspecific population differentiation in seabirds has been frequently observed, either in genotypes (Hailer et al. 2010, Morris-Pocock et al. 2011), foraging behavior (Grémillet et al. 2004, Wakefield et al. 2013), isotopic niche (Wiley et al. 2012, Mancini et al. 2014), or morphometrics (Le Corre and Jouventin 1999, Bertellotti et al. 2002). The majority of over 200 studies using molecular markers have demonstrated gene flow limitation among seabird populations, assuming physical (e.g. ice or land) and non-physical barriers (e.g. philopatry and/or non-breeding distribution) as causes of isolation (Friesen 2015). Although historical or contemporary land barriers are commonly assumed to be one cause of allopatric speciation among seabird sister species (Friesen et al. 2007), several studies have demonstrated intraspecific differentiation even among geographically close colonies with no land barriers (Hailer et al. 2010, Wiley et al. 2012; reviewed by Friesen 2015).

In a global perspective, the long-standing hypothesis on natural selection pressures for optimum body size suggests increasing size towards high latitudes in direct association with heat conservation/dissipation (Mayr 1956). Although the concordance of body size with air temperature may have no direct causal relationship, temperature has an indirect effect on the body primarily by influencing other environmental factors (e.g. food supply) (James 1970). This large-scale clinal pattern of variation has been tested in several terrestrial organisms, such as mammals (Clauss et al. 2013, Martinez et al. 2013), birds (James 1970, Ashton 2002), and even in ectothermic animals, such as lizards (Angilletta Jr et al. 2004). However, additional environmental parameters seem to be correlated with phenotypes distribution in the marine realm (e.g. sea surface temperature, primary productivity), as has been suggested for marine fishes (Fisher et al. 2010), molluscs (Berke et al. 2013), crustaceans (Timofeev 2001) and even for seabirds (Yamamoto et al. 2016). These small-scale variables can be influenced by local oceanographic processes and not follow a latitudinal gradient (Longhurst et al. 1995), causing deviations of intraspecific and interspecific phenotype differences from the pattern predicted by Bergmann's rule.

The terminology used to describe Bergmann's hypothesis has been a matter of controversy regarding its application in studies at different taxonomic levels. Originally, the existence of a body size–temperature relationship was raised by Bergmann (1847) by referring to the differences observed between 'similar organizations' (as translated by Clauss et al. 2013). However, Blackburn et al. (1999) suggested the use of 'James's rule' in studies performed at an intraspecific level, referring to James (1970), in which the author demonstrated intraspecific clinal variations in the wing measurements of 12 bird species. Here, we use the term 'Bergmann's rule' specifying the taxonomic level we are dealing with, as it represents an illustrative example of the pattern first identified by Carl Bergmann. In addition, confusing interpretations related to terminology can be avoided by following the 'traditional' use from similar studies.

Despite this large-scale well-established rule, seabirds have great flight capability and can travel thousands of kilometers during their seasonal movements, crossing environments with very different conditions (Shaffer et al. 2006, Egevang et al. 2010). For example, Arctic terns *Sterna paradisaea* travel ~ 90 000 km during the non-breeding period, holding the longest animal migration ever reported (Fijn et al. 2013). Furthermore, foraging trips of breeding Cory's shearwater *Calonectris borealis* can exceed 7000 km in just a few days (Ceia et al. 2014). This peculiar high mobility and gene flow limitation, even among geographically close colonies (Friesen 2015), represent a paradox that sheds light on other mechanisms of population differentiation.

Dispersal to other colonies is widely known to be reduced in seabirds due to the high natal philopatry observed in this group (Schreiber and Burger 2001). Resident birds have been observed to present even stronger natal philopatry compared to migratory species, illustrating the influence of ecological factors (i.e. local adaptation) on the dispersal costs (Weatherhead and Forbes 1994). Therefore, remaining in the colony surroundings throughout the year could avoid contact with distinct environmental conditions, positively selecting individuals best fitted to the local conditions and generating diversity from phenotype and genotype shaping (Greenwood 1980, Friesen 2015). Ocean turbulence at very small spatial scale has long been shown to aggregate seabirds (Haney 1987), by modifying the seascape structure and providing food concentration that support top predators through bottom-up processes (Bertrand et al. 2014). Therefore, small-scale ecological hotspots around colonies of resident seabirds would be expected to intensify specialization for local resources, which in turn could lead to the divergence even between nearby populations facing distinct environmental pressures.

Currently, it is recognized that local adaptation is the main barrier to gene flow in animals (Sexton et al. 2014), owing to the fact that organisms facing distinct environmental conditions are subject to different selection pressures (Wright 1943). In the marine realm, local primary productivity tends to influence energy transfer patterns, with productive environments having fewer trophic levels and larger top predators, because there is less energy loss along the trophic web (Pinet 2009). However, marine primary productivity has not a direct relationship with latitude (Longhurst et al. 1995), being influenced primarily by multi-scale physical processes which shape seascape structure (Bertrand et al. 2014). In this context, it would be expected body size and mass are driven both by large-scale (e.g. air temperature) and small-scale (e.g. primary productivity) environmental variables, with larger and heavier individuals occurring in productive and high latitude areas.

Furthermore, it has been a long-standing theory that ecology drives evolution (Darwin 1859); however, the importance of eco-evolutionary feedback, a reciprocal causal pathway between ecology and evolution, has only recently been demonstrated (Agrawal et al. 2013, Duckworth and Aguillon 2015). For instance, global ocean warming would be expected initially to affect baseline trophic levels of the marine ecosystem (Grémillet and Boulinier 2009), favoring seabirds with warm-water preferences and increasing predation on their preferential prey (Quillfeldt and Masello 2013). This should lead to top-down and bottom-up controlling processes occurring simultaneously (Chambers et al. 2011). Therefore, knowing both the extant biodiversity (Taylor and Friesen 2012) and the mechanisms of diversification, which are still poorly understood in seabirds (Friesen 2015), is critical to understand how seabirds and other organisms interact with the seascape structure, and also how they will respond to environmental changes.

In this context, seabirds arise as great organisms to test population differentiation, because they are distributed in breeding aggregations (colonies, mostly on islands) and present high natal philopatry. Furthermore, they depend directly on the marine resources (e.g. fish predation), making it possible to test relationships of multi-scale environmental variables on phenotypes. For this, we used body size and mass from brown booby (Suliformes: *Sula leucogaster*) colonies distributed along the Southwest Atlantic Ocean, to test clinal phenotypic variations related both to large-scale (latitude and air temperature) and small-scale variables (primary productivity and sea surface temperature). Brown boobies are seabirds distributed in tropical and subtropical regions of all ocean basins, which do not perform true migration (i.e. directed seasonal movements), remaining around their colonies throughout the year (Nelson 2005). In the Southwest Atlantic Ocean they breed in colonies along a latitudinal gradient, but with distinct characteristics regarding seascape structure. Therefore, given the broad latitudinal variation, which implies air temperature variations, we would expect to find strong population differentiation with larger individuals at higher latitudes, consistent with Bergmann's rule. Nevertheless, small-scale oceanographic parameters (i.e. primary productivity and sea surface temperature) can cause deviations in phenotypes from the clinal pattern expected, illustrating the influence of small-scale environmental variables in shaping organisms in the marine ecosystem.

Methods

Study area

We sampled six colonies distributed along a latitudinal gradient ranging from 0–27°S in the Southwestern Atlantic Ocean. Colonies presented distinct distances from the continental coast, ranging from ~ 4 km to ~ 1100 km, and distinct abundances of brown boobies, ranging from ~ 140 to ~ 2500 individuals (Table 1; Fig. 1). Moleques do Sul, Cagarras, and Abrolhos are located over the continental shelf, while Fernando de Noronha, Rocas Atoll, and Saint Peter and Saint Paul archipelago are volcanic in origin, with the latter being part of the Mid-Atlantic ridge. Distances between archipelagos range from ~ 150 km (Rocas Atoll/Fernando de Noronha) to ~ 3900 km (Saint Peter and Saint Paul/Moleques do Sul). All archipelagos are protected by the Brazilian government, and only on Cagarras and on Moleques do Sul there is no permanent human presence. Hereinafter, we refer to Moleques do Sul as 'Moleques', to Rocas Atoll as 'Rocas', to Fernando de Noronha as 'FN', and to Saint Peter and Saint Paul as 'SPSP'.

The six sampling locations present differences regarding oceanographic dynamics in their surroundings. Coastal sites (Moleques, Cagarras, and Abrolhos) are influenced mainly by shelf waters, such as Tropical Water, which flows southward and is a coastal branch of the Brazil Current (Möller Jr et al. 2008). During winter, Moleques is also influenced by the Subtropical Shelf Water, which is generated by the mixing of the Tropical Water with the northward flowing Río de la Plata Plume (Piola et al. 2008). On the other hand, FN, Rocas, and SPSP are influenced by the South Equatorial Current, which flows westward and reaches these archipelagos with distinct characteristics (e.g. velocity) (Richardson and Walsh 1986). SPSP is also influenced by the Equatorial Undercurrent, which flows in the opposite direction (eastward), approximately 80 m deep (Veleda et al. 2012). It decelerates when it reaches the SPSP archipelago, generating vortices on the east side and increasing the residence time of nutrients around the SPSP (Araujo and Cintra 2009), as commonly observed around seamounts (Mullineaux and Mills 1997).

Sampling

We captured 276 adult brown boobies on their nests by hand or hand net, and obtained the following body measurements of each individual: culmen length (exposed culmen), tarsus length (from middle of the midtarsal joint to the distal end of the tarsometatarsus), wing chord (carpal joint to the tip of the longest primary; unflattened wing), and body mass. We measured wing chord using a metal rule with stop (± 1 mm) and the remaining measurements using vernier calipers (± 0.01 mm). We obtained body mass using a digital balance and Pesola® spring scales, with precisions of 5 and 10 g, respectively. We distinguished adults from juveniles by plumage coloration and gender by skin coloration differences around the eyes (Nelson 2005). Each bird received an individually numbered tarsal metal band to avoid resampling. Samplings were carried out both by the authors GTN and PLM. Data were obtained between August 2010 and December 2014 (Table 1).

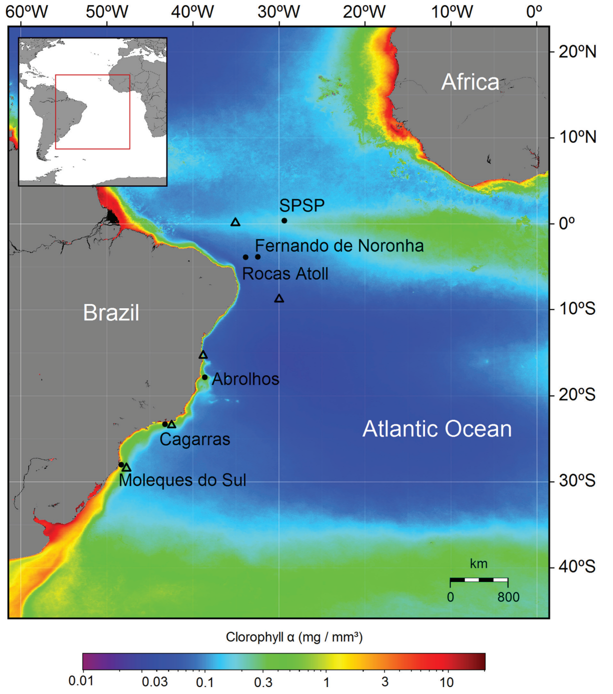

Figure 1. Geographic locations of the six brown booby *Sula leucogaster* colonies superimposed on data representing the average chlorophyll α concentration (mg m^{-2}) layer during the past 15 yr. Archipelagos are identified by closed circles, while oceanographic buoys are identified by open triangles. Data was extracted and modified from <www.oceancolor.gsfc.nasa.gov/SeaWiFS/>. SPSP = Saint Peter and Saint Paul archipelago.

Environmental data

We obtained sea surface and air temperature data for SPSP, FN, and Rocas from the nearest oceanographic buoys

Table 1. Approximate distances from the coast (km), abundance, and location of the six colonies of brown boobies sampled.

Sampling places	Abundance (number of individuals)	Location	Sampling events
Saint Peter and Saint Paul	600[1]	0°55′51″N, 29°20′45″W	May 2013 and 2014, Jul 2015
Fernando de Noronha	870[2]	3°51′15″S, 32°25′44″W	Mar, Apr 2011
Rocas Atoll	140[3]	3°52′30″S, 33°48′20″W	Sep 2010, Feb 2012
Abrolhos	550[1]	17°57′46″S, 38°42′10″W	Feb, Aug 2011
Cagarras	2500[4]	23°01′35″S, 43°11′33″W	Dec 2014
Moleques do Sul	1700[5]	27°50′46″S, 48°25′53″W	Feb 2014

[1]Mancini et al. (Unpubl.), [2]Antas (1991), [3]Schulz-Neto (2004), [4]Cunha et al. (2013), [5]Branco et al. (2010).

(Prediction and Research Moored Array in the Tropical Atlantic; PIRATA, located at 0°N, 35°W for SPSP and 8°S, 30°W for FN and Rocas) (data available on <www.goosbrasil.org/pirata/>). Sea surface and air temperature data for the remaining sites were obtained from the fixed buoys nearest to each archipelago (Santa Catarina's buoy for Moleques [28.52°S, 47.37°W], Guanabara's buoy for Cagarras [22.91°S, 43.15°W], and Porto Seguro's buoy for Abrolhos [15.99°S, 37.95°W]), through the National Program of Buoys (data available on <www.goosbrasil.org/pnboia/>) (Fig. 1). We used the average temperatures between 1 January 2000 and 1 January 2015 recorded by the PIRATA buoys, and mean temperatures recorded between the launching date (March 2011, April 2012, and July 2012 for Moleques, Cagarras, and Abrolhos, respectively) and 21 March 2015, by the remaining buoys. We used chlorophyll α concentration estimated for summers (seasonal climatology) between 2002–2014, extracted from the Aqua MODIS, NASA/GSFC, using the Ocean Color Index (OCI) algorithm (data available on <www.modis.gsfc.nasa.gov/>). We downloaded the data series with a resolution of 4 km/pixel and calculated the average chlorophyll α value within a 40-km radius surrounding each colony, following previously published maximum foraging range of brown boobies (Weimerskirch et al. 2009, Soanes et al. 2015). Chlorophyll α concentration was used as a proxy for primary productivity (Huot et al. 2007).

Statistical analyses

To identify outliers in morphometric variables, we defined ± 2 standard deviations from the mean as a criterion, in order to rule out possible sampling errors while avoiding losing within-population variability. For body mass, we defined as outliers the values with ± 1 standard deviation, to avoid biases caused by the large individual daily fluctuation, before and after feeding. We calculated the correlation between allometric variables using Pearson's test. We assessed phenotypic differences among all populations with a one-way MANOVA using the Wilk's lambda (λ), and a pairwise Hotelling's T-square as a post-hoc test. P-values were adjusted according to the Bonferroni procedure. We used residuals to test univariate normality using the Shapiro–Wilk's test, and multivariate normality with Mardia's test of skewness and kurtosis, Henze–Zirkler's, and Royston's tests, with the 'MVN' R package (Korkmaz et al. 2014). We assessed dissimilarity between populations using Euclidean distances based on a multivariate dataset (culmen, tarsus, wing, and body mass), with standardized values for all traits (subtracting the mean and dividing by the standard deviation). We generated dendrograms based on Euclidean distances by using the 'ggdendro' R package. We also used standardized values of culmen, wing, and tarsus to generate a body size index for each individual through a principal component analysis (adopting only the PC1 axis).

We used generalized linear models (GLM) with Gaussian family and identity link, to demonstrate which environmental variables better fitted the mass and body size data. We also tested correlations between all environmental variables (latitude, chlorophyll α, air and sea surface temperature) by using Spearman's ranking correlation with Bonferroni correction for multiple testing, in order to select uncorrelated variables for the regression model. High pairwise correlation values between morphometric variables (Pearson's r ranging from 0.49 to 0.74 for males and 0.61 to 0.65 for females; $DF = 2$ and $p < 0.01$ for both genders in all pairwise tests; Supplementary material Appendix 1, Fig. A1) allowed us to generate body size index adopting PC1, corresponding to 76.0 and 76.1% of the total variance for males and females, respectively. Culmen, tarsus, and wing lengths accounted for approximately 37.3, 27.9, and 34.7% for the male body size index, and 33.0, 32.7, and 34.1% for the female index, respectively. We did not include latitude in the regression models because this variable was significantly correlated to air temperature (Spearman's rho $= 0.75$; $DF = 3$; $p < 0.01$). Therefore, regression models were fitted only with air temperature (as the starting variable in a forward selection procedure), chlorophyll α and sea surface temperature as explanatory variables, and body size and mass as response variables. From this, we ran manual stepwise regressions, starting with air temperature (as postulated by Bergmann's rule) and adding the remaining variables through a forward procedure. We fitted models considering male body size index, male body mass, female body size index, and female body mass as distinct datasets. Moreover, we fitted models for these datasets in a scenario without SPSP, because it was an outlier to the clinal pattern (see 'Results'). We used Akaike's information criterion (AIC) as goodness-of-fit measure within datasets (the lower the better), and percentage of deviance explained to compare models fitted from distinct datasets (Burnham and Anderson 2002). All statistical analyses were performed with R software.

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.k713> (Nunes et al. 2016).

Results

In total, we sampled 135 male and 141 female brown boobies. We detected female-biased dimorphism in all traits (culmen, tarsus, wing and body mass) in all the six sampled populations, females being 5.2% larger and 21.9% heavier than males (Table 2). For both females and males, the smallest individuals were those from FN and Rocas. Contrary to prediction, the colony closest to Equator (SPSP) had the largest and the heaviest males as well as the heaviest females (Fig. 2).

All allometric variables were found to have a multivariate normal distribution from all populations, and global multivariate population differences were found to be significant for both genders (MANOVA: females, Wilk's $\lambda = 0.061$, $DF = 5$, $p < 0.001$; males, Wilk's $\lambda = 0.041$, $DF = 5$, $p < 0.001$). Despite this, the post-hoc test showed no significant difference between Cagarras and Moleques for both genders, and between Moleques and SPSP for females (Hotelling's T-square: $p < 0.001$; Table 3). We found the highest multivariate Euclidean distances between FN/Rocas and SPSP, the northernmost colonies (4.472 on average); and the lowest distances between Cagarras and Moleques (0.315 on average). We also found relatively low Euclidean distances among coastal colonies (0.912 on average), and between

Table 2. Means ± standard deviations of culmen, wing, tarsus, and body mass measurements from six colonies of brown boobies *Sula leucogaster* sampled in Brazil, from north to south. SPSP = Saint Peter and Saint Paul archipelago; FN = Fernando de Noronha archipelago; Rocas = Rocas Atoll; Moleques = Moleques do Sul.

	Culmen (mm)		Tarsus (mm)		Wing (mm)		Body mass (g)	
Locations and sample size (n)	♂	♀	♂	♀	♂	♀	♂	♀
SPSP (124)	103.04 ± 2.03	106.93 ± 2.63	48.13 ± 3.22	50.51 ± 1.75	410.92 ± 6.41	425.23 ± 6.14	1311.27 ± 80.11	1620.78 ± 87.92
FN (35)	92.45 ± 2.72	96.54 ± 3.03	42.49 ± 1.41	44.43 ± 2.14	382.76 ± 8.03	399.33 ± 11.13	867.05 ± 57.96	1061.33 ± 115.50
Rocas (31)	90.63 ± 2.31	95.09 ± 2.38	44.98 ± 1.69	47.11 ± 1.41	388.50 ± 4.05	403.53 ± 9.69	934.16 ± 65.01	1137.69 ± 85.16
Abrolhos (40)	99.91 ± 2.13	102.08 ± 2.14	46.33 ± 1.63	49.14 ± 1.75	404.38 ± 8.50	425.94 ± 9.18	1082.22 ± 98.49	1305.29 ± 179.30
Cagarras (28)	95.79 ± 1.05	103.77 ± 2.82	47.47 ± 0.95	51.01 ± 0.87	402.09 ± 6.64	426.01 ± 9.11	1210.45 ± 53.59	1465.45 ± 62.98
Moleques (18)	97.15 ± 2.21	103.68 ± 2.94	47.58 ± 1.23	51.32 ± 0.98	404.28 ± 4.46	426.14 ± 8.35	1235.71 ± 56.52	1511.42 ± 69.38

coastal colonies and SPSP (1.493 on average), demonstrating a phenotypic similarity between the colonies located in two geographical extremes of the area covered by the study (Table 3). Clustering using Euclidean distances based on multivariate data, generated dendrograms with two groups: a branch with the smallest and lightest individuals (FN/Rocas) and another branch with the remaining breeding sites (i.e. SPSP clustered with southern colonies; Fig. 3).

When using air temperature as the only explanatory variable in the regression models for all datasets, the explained percentage of deviance in body size and mass ranged from 0 to 2.3%, while in the scenario without SPSP the deviance explained of this model ranged from 50.6 to 72.9% (Fig. 4). In general, in both scenarios for all datasets, models improved (AIC decreasing and % deviance explained increasing) when we added chlorophyll α and SST (Supplementary material Appendix 2, Table A1). Finally, the model with air temperature and the interaction between chlorophyll α and sea surface temperature (air temperature + [chlorophyll $\alpha \times$ SST]) showed the highest percentage of deviance explained (80.4%) and the lowest AIC for all datasets in both scenarios.

Discussion

Environment shapes phenotypes

In the context of Bergmann's rule, we demonstrated seabird phenotype variations along a tropical-subtropical gradient. However, in the present study, allometric variables did not present a direct correspondence with air temperature and latitude, and therefore did not fit to the Bergmann's rule (Bergmann 1847), since boobies at the colony located nearest to the Equator (SPSP) were phenotypically similar to the southernmost colonies. Nonetheless, in a scenario without SPSP, all allometric traits measured were correlated with air temperature, perfectly illustrating Carl Bergmann's hypothesis. Although air temperature did not correlate with allometrics when we consider SPSP, adding oceanographic variables (i.e. the interaction between chlorophyll α and sea surface temperature) substantially improved this relationship, suggesting influence of relevant additional factors in shaping size and body mass of marine organisms.

The negative correlation between body size and air temperature, observed in the scenario without SPSP, is purely empirical, regardless of the possibility that it could be physiologically explained. This finding is in close agreement with the heat conservation hypothesis, where the 'surface area to body volume' ratio is smaller in larger varieties of birds and mammals, thereby decreasing heat loss, which confers a clear advantage in colder regions (Rensch 1938). Air temperature is most likely not the only factor involved in shaping phenotypes, since it varies on a large spatial scale. While the complexity of population differentiation mechanisms and environmental variables can make it difficult to fully understand phenotypic diversification, it may also help to explain deviations from expected outcomes, such as those observed in brown boobies from SPSP.

Although the SPSP archipelago is on the Equator and its phytoplankton community is characteristic of oligotrophic

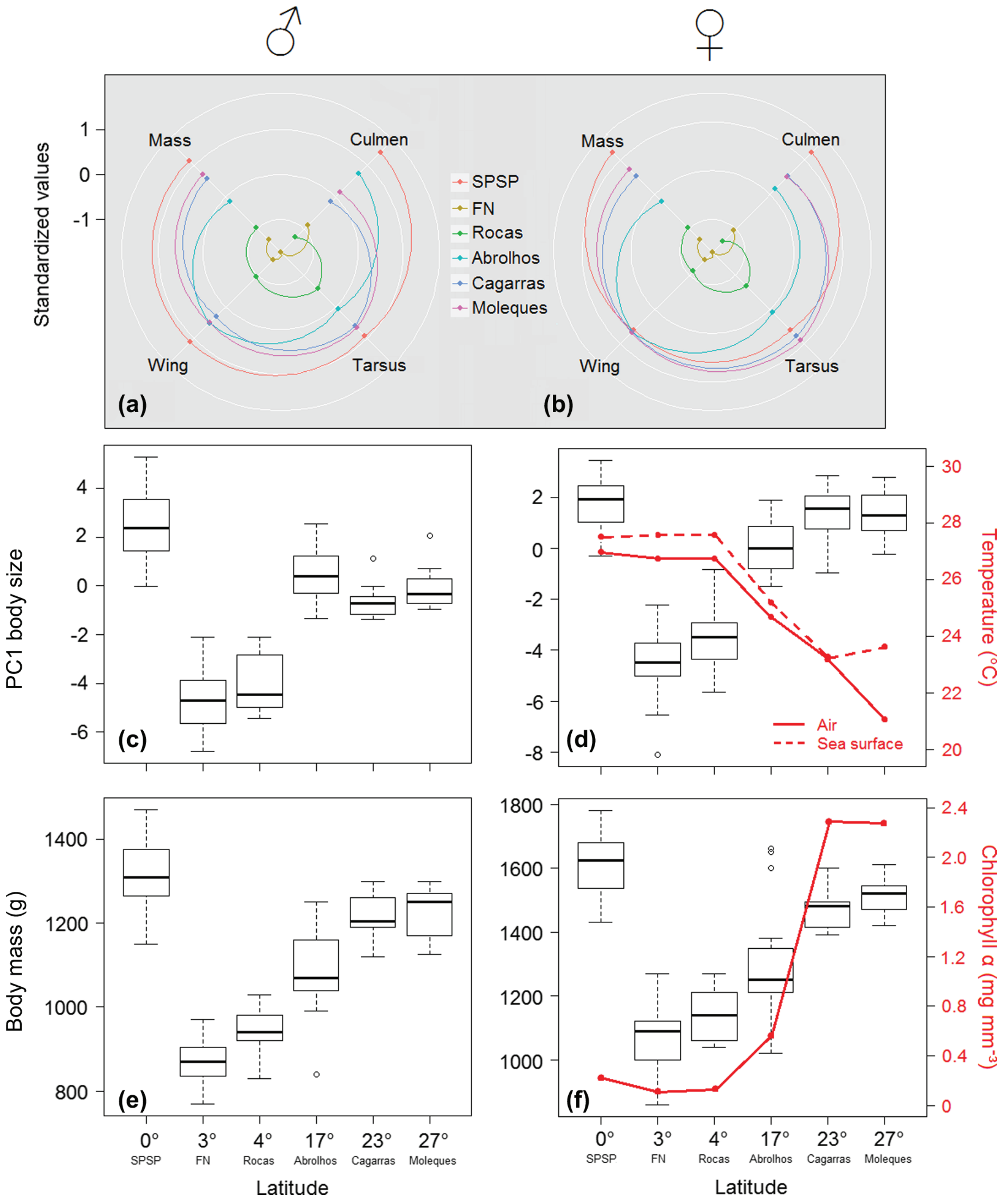

Figure 2. (a, b) Radial plots comparing standardized values (subtracting the mean and dividing by the standard deviation) of culmen, wing chord, tarsus, and body mass among all sampled colonies for males (left) and females (right). Radial lines correspond to quantitative variables, with values decreasing toward the center. Each color corresponds to one archipelago, and each point on radial lines corresponds to the population mean (the ellipse '0' corresponds to the mean for each variable). (c, d) Clinal variation of the intraspecific variation in the body size index (first principal component from culmen, tarsus, and wing measurements) within archipelagos; and (e, f) body mass values distributed on a latitudinal gradient. Air and sea surface temperatures (in red) are reported in (d) and chlorophyll α in (f). Males and females are represented by left and right panels, respectively.

tropical waters (Tiburcio et al. 2011), the interaction of the Equatorial Undercurrent with the archipelago topography slows the movement of the current at a local level and generates vortices, which increase the mixing of the water column (i.e. disrupting the surface thermocline) and the residence time of waters around the SPSP (Araujo and Cintra 2009). This process allows for the retention of nutrients from allochthonous or autochthonous sources (e.g. seabird guano), making the biomass and zooplankton productivity in the vicinity of SPSP similar to those observed around seamounts (Mullineaux and Mills 1997, Melo et al. 2014). A pattern of higher productivity and presence of relatively colder waters closer to the surface is more pronounced around SPSP than nearby tropical islands sampled for this study, i.e. FN (Souza et al. 2013) and Rocas (Jales et al. 2015). In addition, ichthyoplankton are more abundant around the SPSP than

Table 3. Euclidean distances based on a multivariate dataset of allometric variables (culmen, tarsus, wing, and body mass) between all brown booby colonies sampled along the Brazilian coast. Females are represented by values above the diagonal, and males by values below the diagonal. Bold values represent Hotelling's T-squared significant differences, with adjusted p-values based on the Bonferroni correction for multiple comparisons ($p < 0.01$).

SPSP	**4.567**	**3.998**	**1.851**	**1.005**	0.919
5.044	FN	**1.150**	**3.188**	**4.032**	**4.200**
4.279	**1.399**	Rocas	**2.568**	**3.321**	**3.466**
1.794	**3.374**	**2.706**	Abrolhos	**1.070**	**1.286**
1.889	**3.604**	**2.578**	**1.285**	Cagarras	0.240
1.504	**3.886**	**2.923**	**1.205**	0.390	Moleques

around FN, mainly because the former is a spawning area for Exocoetidae flyingfishes (Lessa et al. 1999), the preferential food item of brown boobies (Mancini and Bugoni 2014). Although spatially very restricted, local productivity around SPSP is increased by small-scale oceanographic dynamics, making it an oasis in a tropical oligotrophic area and sustaining migratory and resident endemic fishes, as well as fisheries production (Vaske Jr et al. 2005, 2008).

In general, productive areas in the ocean favor larger organisms, decreasing the energy path along the trophic web, so that energy transfer from the base to the top is optimized (Pinet 2009). We found larger boobies in coastal colonies and, therefore, near to more productive waters (Mann and Lazier 2006). Accordingly, smaller and lighter boobies were found at FN and Rocas, which are outside the Brazilian continental shelf and are influenced mainly by the oligotrophic waters of the South Equatorial Current (Garrison 2010). Therefore, chlorophyll α, here used as a proxy for primary productivity, and sea surface temperature, although they show no correlation with latitude and air temperature, sheds light on spatial small-scale processes shaping phenotypes. In this context, allometric variation in marine organisms could be better explained when combining air temperature with small-scale oceanographic parameters, as primary productivity and sea surface temperature.

Although the best model explained over 80% of the deviance for all datasets, the sharp deviation from the clinal pattern observed in SPSP could be enhanced by the relatively restricted area for breeding. The SPSP colony holds approximately 200 nests (Mancini et al. 2016) and a suitable nesting area of only about 200 m^2, where average distance between nests is 1 m and average nest diameter of 0.36 m, while the Rocas colony have an average distance of 11.2 m between nests and average nest diameter of 0.44 m (Kohlrausch 2003). The high density of nests at SPSP could favor larger and heavier boobies when competing for nesting areas. Furthermore, the crowded nesting colony at SPSP has also been postulated to alter behavior, resulting in frequent cannibalism in this colony, but not elsewhere (Neves et al. 2015). Thus, the restricted spatial area for nesting, along with environmental variables, could intensify phenotypic differences between boobies from SPSP in comparison with those from the nearby FN and Rocas, representing an example of ecology driving evolution and, consequently, isolation by environment as a mechanism of population divergence.

Phenotypic diversity

Our findings demonstrated a high phenotypic diversity of brown boobies along the Southwest Atlantic Ocean colonies. Coastal colonies were found to be similar, presenting boobies with intermediate body size and mass. Rocas and FN also proved to be quite similar to each other, consistent with limited distance between colonies (~ 150 km) and similar environmental constraints. Dietary differences between brown booby populations have been observed through regurgitates and stable isotopes ($\delta^{13}C$ and $\delta^{15}N$), as well as differences in isotopic niches among brown boobies from SPSP, Rocas, FN, and Abrolhos (Mancini et al. 2014). The wider isotopic niche observed from Abrolhos was thought to be related to higher baseline isotopic values and/or to a more generalist diet, as Abrolhos was the colony closest to the coast, where prey diversity could be also influenced by discards from demersal fisheries. The dependence of brown boobies on discards from demersal fisheries has been reported in other coastal colonies along the Brazilian continental shelf (Coelho et al. 2004, Krul 2004, Branco et al. 2005). Waters around coastal archipelagos have higher productivity than oceanic environments and, therefore, the isotopic range of brown boobies in Abrolhos could be similar to other coastal

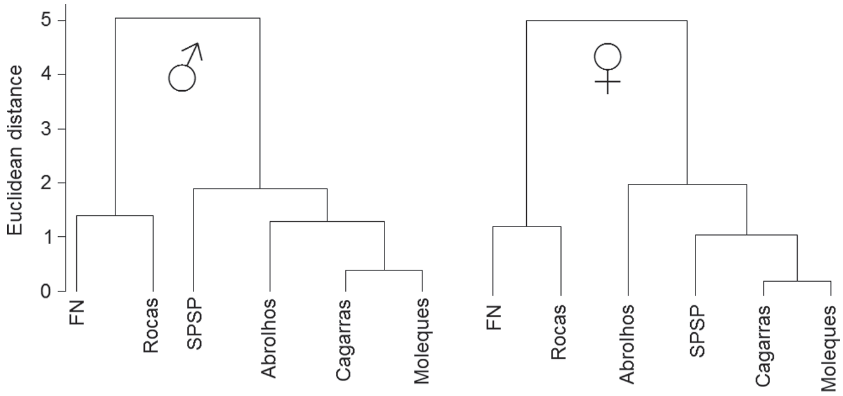

Figure 3. Dendrograms based on variation of the multivariate Euclidean distances (y-axis) from standardized values of culmen, tarsus, wing and body mass for males (left) and females (right). SPSP = Saint Peter and Saint Paul archipelago; FN = Fernando de Noronha archipelago; Rocas = Rocas Atoll; Moleques = Moleques do Sul.

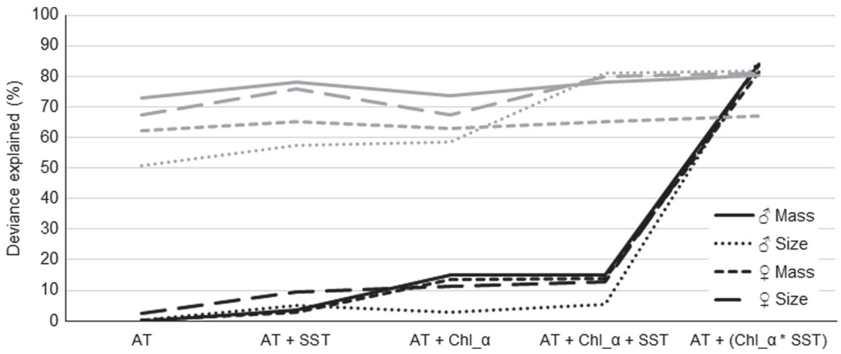

Figure 4. Gaussian regression models fitted with body mass and body size (culmen, tarsus, and wing integrated in a body size index) for both males and females as response variables, and air temperature (AT), sea surface temperature (SST), and chlorophyll α (Chl_α) as explanatory variables. Black lines refer to the scenario with the Saint Peter and Saint Paul archipelago, and grey lines refer to the scenario without the Saint Peter and Saint Paul archipelago.

sites. This could explain the phenotypic similarity among brown boobies sampled from coastal colonies (Abrolhos, Cagarras, and Moleques). Moreover, long-term climatic stability tends to promote genetic differentiation even among conspecific populations (Carnaval et al. 2009, Rodríguez-Robles et al. 2010). In this context, relatively stable climatic conditions of tropical regions (Evans et al. 2002, Tierney et al. 2015) could enhance population structure observed in our study, by keeping environmental conditions around colonies stable along an evolutionary time-scale and promoting genetic divergence according to the structuring based on phenotypes.

On the other hand, we observed an unexpected phenotypic similarity between SPSP and all other coastal colonies, particularly the southernmost one at Moleques, which are located in the extremes of latitude of our study area. Regarding distribution around colonies, tracking brown boobies during foraging trips throughout the breeding period at SPSP (Nunes unpubl.) has revealed a mean foraging trip duration of only ~ 1 h for both genders, and a mean maximum distance from colony of ~ 9 km. These values are much lower than those reported for other populations elsewhere (~ 2.5 h and ~ 28 km in the Gulf of California, Weimerskirch et al. 2009; ~ 5 h and ~ 38 km in the Caribbean, Soanes et al. 2015). Although there is no information on the distribution of these individuals during the non-breeding period, SPSP population shows constant adult abundance and breeding along the whole year (Barbosa-Filho and Vooren 2010), which, together with the brief trips observed, suggest that obtaining food close to SPSP may not be difficult. In this case, dispersal could not be beneficial, increasing philopatry of this population and strengthening the hypothesis of adaptive convergence in relation to the coastal colonies.

Divergences among brown booby colonies have already been observed in the Atlantic Ocean, although using a purely genotypic approach (Morris-Pocock et al. 2011). These authors revealed two clusters in the Atlantic Ocean (Ascension/Cape Verde and the Caribbean Isla Monito), suggesting natal philopatry as the mechanism of population differentiation. Additional mechanisms, such as nonbreeding distribution patterns, could also contribute to population isolation (Friesen 2015), although it remains unknown for brown boobies. Here, we proposed that the level of natal philopatry can be a consequence of distinct pressures (e.g. environmental variables) and it could be understood as dispersal cost, which is determined by the degree of adaptive diversification generated from ecological differences between colonies (Weatherhead and Forbes 1994). In this context, environmental variables with oceanographic parameters (both large and small spatial scales) should be a primer in explaining phenotypic diversity in the marine realm, since it also enables monitoring climate change effects on marine organisms considering intraspecific diversity (Quillfeldt and Masello 2013).

Tropical marine environments tend to be stable throughout the year, but an increase in sea surface temperature during the last 100 yr has been observed in tropical oceans (Hoegh-Guldberg 1999). Looking forward, the most extreme Representative Concentration Pathway (greenhouse gas concentration trajectory RCP 8.5) predicts mean global surface temperature increasing by 7–8°C between now and the year 2300 (IPCC 2014). This could have several implications for ecological processes, such as alterations in atmospheric and oceanic circulation. This phenomenon has already been observed in the Bering Sea, where the decreased recruitment of juvenile walleye pollock *Theragra chalcogramma*, a local key fish species, has affected other fish species, marine mammals, and seabirds (Wespestad et al. 2000). In this context, brown booby populations could be affected in distinct ways, as breeding sites with low prey diversity (i.e. dependence on a few key prey species) could be impacted earlier by rapid climate change.

Conclusions

This study demonstrates that Bergmann's rule does not apply to brown boobies nesting on islands along the Brazilian coast. The observed deviation sheds light on the role of other selection pressures, such as small-scale oceanographic processes, in shaping body size along a broad latitudinal gradient in the marine realm. Therefore, studies on phenotypic diversity and conformance with Bergmann's rule in seabirds (or even in other marine animals) should also consider oceanographic parameters as potential direct or indirect mechanisms of population differentiation, so these local conditions could be drivers for intraspecific phenotypic diversification, although additional pressures (e.g. founder effect, nest density, and behavioral aspects) could not be ruled out to explain phenotypic diversity. Finally, if phenotypes mirror genotypes in brown boobies from Brazil, we suggest the existence of three molecularly supported clusters (SPSP, Rocas/FN, and Abrolhos/Cagarras/Moleques), with the similarity between SPSP and Abrolhos/Cagarras/Moleques owing to a case of adaptive convergence driven by environmental pressures. Further testing will be required to elucidate gene flow between the brown boobies along the Brazilian coast.

Acknowledgements – We are grateful to A. P. P. Beck, F. Vasconcelos, F. M. Neves, F. P. Marques, L. R. Camillo, and L. S. T. Cunha for help with fieldwork. For further support with fieldwork, we also would like thank Associação dos Pescadores Artesanais da Armação do Pântano do Sul (Parque Estadual da Serra do Tabuleiro); Projeto Ilhas do Rio (Monumento Natural das Ilhas Cagarras); Z. B. Silva (Reserva Biológica do Atol das Rocas); R. Jerozolimski (Parque Nacional Marinho de Abrolhos); Corpo de Bombeiros de Pernambuco (Parque Nacional Marinho de Fernando de Noronha); Marinha do Brasil and Comissão Interministerial para os Recursos do Mar (Arquipélago de São Pedro e São Paulo). Data from Cagarras were provided by Projeto Ilhas do Rio (Inst. Mar Adentro), which is funded by Petrobras (Programa Petrobras Ambiental). We are also grateful to P. G. Kinas and F. R. G. Silveira for support on regression analysis and model fitting. The manuscript greatly benefited from comments and suggestions by E. R. Secchi and L. Dalla Rosa on a previous version. Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio) granted sampling permits no. 38723-4 and 22697-4, and Fundação do Meio Ambiente de Santa Catarina (FATMA/SC) sampling permit 019/2013; CEMAVE (ICMBio) provided bands and permits; and Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) granted funds (no. 557152/2009-7 and 405497/2012-1). GTN and PLM received scholarships granted from Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES). PLM is a postdoctoral fellow of the Fundação de Amparo à Pesquisa do Estado de São Paulo (Proc. no. 2014-00194-2). LB is a research fellow of the CNPq (Proc. no. 308697/2012-0).

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Supplementary material Appendix ECOG-02209 at <www.ecography.org/appendix/ecog-02209>). Appendix 1–2.