

## Body-Size Variation across Environmental Gradients in an Ectothermic Organism: An Intraspecific Approach to Ecogeographic Patterns

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**ABSTRACT:** Bergmann's rule states that endothermic species from cool areas tend to have larger body sizes than those from warm areas. Allen's rule maintains that endothermic species from cool environments should have shorter extremities than their counterparts from warm areas. Although a number of studies have supported both rules, the validity of these trends remains controversial, especially for ectothermic organisms. Here, we studied intraspecific morphological variation in Four-Eyed Frogs (*Pleurodema thaul*) to determine if these rules are valid in an ecogeographic context. Specifically, we analyzed how morphology varies across nine traits in males of *P. thaul* collected from nine localities in Chile. A discriminant analysis of all measured traits indicated differentiation between localities, and the first two canonical variables explained ~80% of the total variation in morphometric features. Additionally, these two canonical variables were correlated with precipitation and monthly minimum temperature. To determine the validity of Allen's rule, a stepwise discriminant analysis was performed incorporating three morphological variables measured on the extremities of the individuals. This analysis indicated no variation in the traits between populations. The first canonical variable of the discriminant analysis explained 90% of the total variation in extremity morphology and was not correlated with environmental variables. We did, however, detect a correlation between the canonical variables of the stepwise discriminant analysis, and both minimum temperature and precipitation. Overall, our results indicate that the populations of *P. thaul* in Chile comply with Bergmann's rule.

**Key words:** Allen's rule; Anura; Bergmann's rule; Ectotherms; Latitudinal variation; Leptodactylidae

ECOGEOGRAPHIC patterns (or rules) are spatial patterns of covariation between diverse biological traits and spatial or environmental variables (Gaston et al. 2008). Diverse ecogeographic patterns have been recognized, including latitudinal variation in body size (Bergmann 1847), variation in length of extremities (Allen 1877), and species distributions (Rapoport 1982). Because of their relevance to macroecological and macroevolutionary processes, Bergmann's and Allen's rules are the ecogeographic patterns that have been most frequently studied in a variety of organisms, and notably so in mammals (Lindsey 1966; Angilletta and Dunham 2003). Bergmann's rule states that endothermic species from cool climates tend to have larger body sizes relative to organisms from warm areas. Bergmann (1847) suggested that this pattern could be explained as a method to conserve heat because animals with larger body sizes have lower surface area to volume ratios, and thus maintain body temperature more efficiently than smaller organisms (Mayr 1956). Furthermore, Allen's rule states that endothermic organisms living in cool climates have appendages (e.g., limbs, ears, or tails) that are shorter than the appendages of individuals inhabiting warmer areas. Allen (1877) argued that having short extremities in cool areas reduces heat loss by decreasing the surface area to volume ratio of the extremities (Ray 1960). Both of these biogeographic rules were originally applied to interspecific comparisons and were subsequently extended to intraspecific comparisons where phylogenetic effects are not relevant.

The evidence supporting the validity of Bergmann's rule in endothermic organisms is extensive (e.g., Brown and Lee 1969; Murphy 1985; Ashton et al. 2000; Ashton 2002a; Meiri and Dayan 2003; Blackburn and Hawkins 2004; Meiri et al. 2004); however, Allen's rule has been validated for only a limited number of taxa (e.g., Griffing 1974; Cartar and

Morrison 2005; Yom-Tov et al. 2006). In contrast with endotherms, studies on the occurrence of these patterns in ectothermic vertebrates and invertebrates are few and remain controversial (Ashton 2002b; Laugen et al. 2005; Adams and Church 2008). Body size has been related to oxygen availability in water, habitat availability, predation avoidance, and seasonality in invertebrate ectotherms (e.g., Atkinson 1995). Furthermore, other mechanisms have been invoked to explain size differences among animal populations. These phenomena include character displacement, cell size variation, and density-dependent mortality (e.g., Arnett and Gotelli 1999). Notwithstanding the multiple mechanisms implied in the origin of differences in the body size among populations, the existence of ecogeographic patterns has been verified in a number of ectotherms (Lindsey 1966; Arnett and Gotelli 1999; Ashton 2002b; Ashton and Feldman 2003; Cruz et al. 2005; Olalla-Tárraga and Rodríguez 2007). However, there are also instances in which these rules have not been confirmed (Bidau and Martí 2007; Olalla-Tárraga and Rodríguez 2007; Adams and Church 2008; Bidau and Martí 2008; Cvetkovic et al. 2009; Feldman and Meiri 2014). As such, the extent to which the rules can explain such spatial patterns remains uncertain.

Four-Eyed Frogs (Leptodactylidae: *Pleurodema thaul*) are anurans with a wide geographic distribution in Chile, encompassing ~2200 km from the Atacama Desert to the Patagonian region. Because of the extensive geographic distribution of *P. thaul*, populations of this species are exposed to different environmental conditions with contrasting temperatures and precipitation levels. Populations of *P. thaul* in northern Chile are subjected to high temperatures attenuated by the oceanic influence at coastal locations. In this region, rainfall is less than 140 mm annually. Those *P. thaul* individuals in central Chile experience a Mediterranean climate (i.e., hot, dry summers and cool, wet winters), with an annual precipitation of ~450 mm. In contrast,

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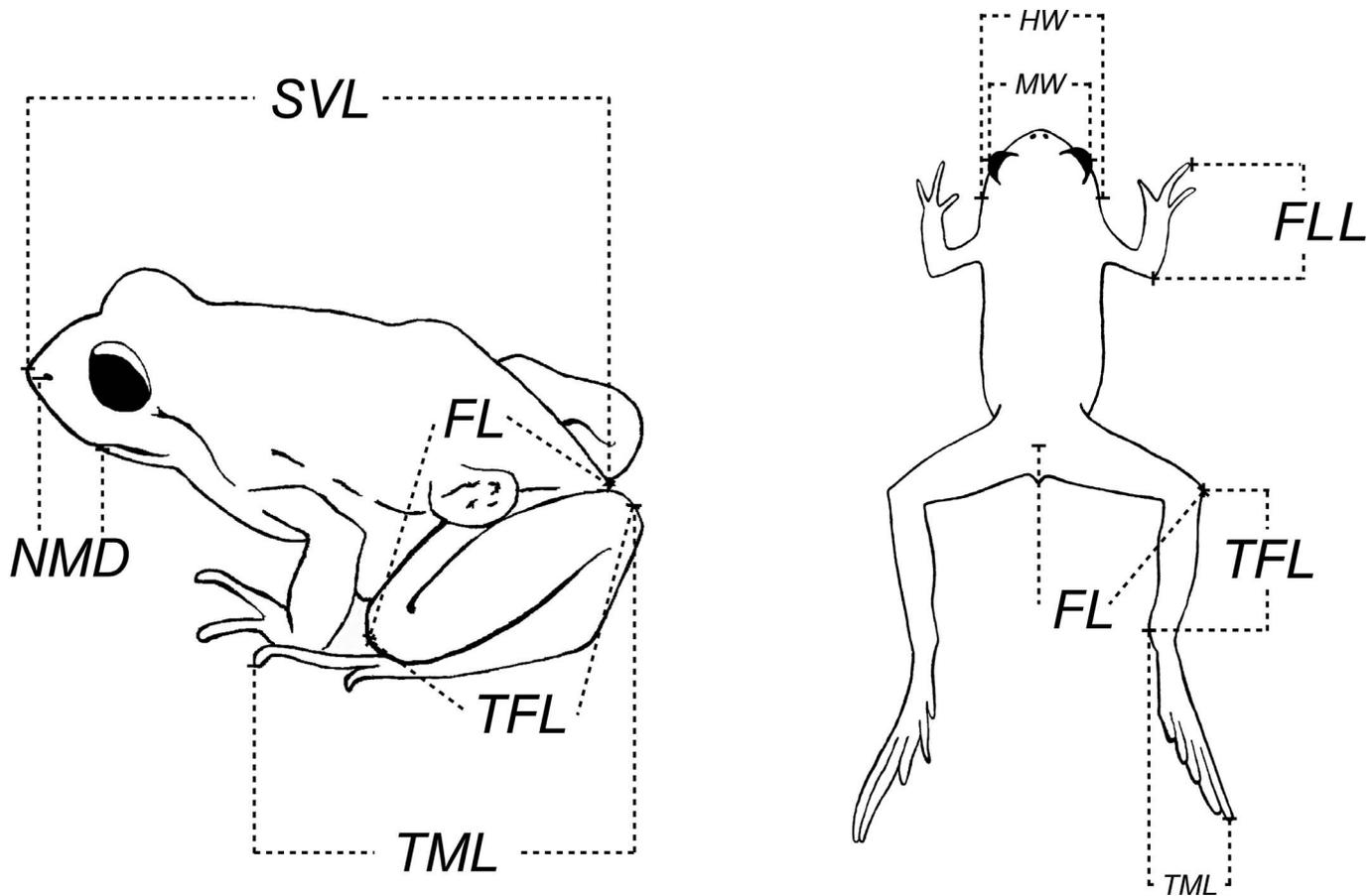


FIG. 1.—Lateral and dorsal view of a male *Pleurodema thaul* showing the morphological traits measured. Abbreviations: SVL = snout-vent length; NMD = nose-to-mouth distance; FL = femur length; TFL = tibia-fibula length; TML = tarsal-metatarsal length; HW = head width; MW = mandible width; FLL = forelimb length.

habitats in the southernmost portion of the *P. thaul* distribution are dominated by temperate forest where annual rainfall is ~2600 mm. Given these contrasting conditions, *P. thaul* is an appropriate model for studies of geographic variation in morphological (Cei 1958) and behavioral traits (Velásquez et al. 2013, 2014). Cei (1958) has reported differences in size and morphological traits related to size and head shape among distant populations of this species. Given that the extensive geographic distribution of this species covers a range of different environmental conditions, we investigated the morphological variation of *P. thaul* males to test the hypothesis that body size and the length of extremities covary with environmental variables. We expected that male body size would be negatively correlated with temperature and positively correlated with the amount of precipitation. Conversely, we expected that the length of appendages would be correlated positively with temperature and negatively with the amount of precipitation.

#### MATERIAL AND METHODS

##### Study Site

To explore the morphological variation of *P. thaul* along its latitudinal distribution, we captured 145 males from 9 localities encompassing a wide range of the geographic distribution of this species (65% of its latitudinal distribu-

tion). Specimens were collected in the following localities: Totoral (27°54'S, 70°57'W,  $n = 30$ ), Socos (30°43'S, 71°29'W,  $n = 15$ ), Los Maitenes (34°41'S, 71°25'W,  $n = 29$ ), Torca Lagoon (34°46'S, 72°2'W,  $n = 6$ ), Hualqui (36°55'S, 72°55'W,  $n = 12$ ), Elicura (37°55'S, 73°13'W,  $n = 15$ ), Coñaripe (39°32'S, 71°57'W,  $n = 10$ ), Mañil (39°41'S, 73°0'W,  $n = 7$ ), and Osorno (40°35'S, 73°3'W,  $n = 28$ ). The latitude and longitude of each sampling site were recorded using a handheld global positioning system unit (eTrex Vista® H, Garmin International, Inc.; datum = WGS84).

##### Morphological Measurements

To determine the variation among individuals from the nine sites, we measured eight linear morphometric traits in the collected *P. thaul* males (Fig. 1). All measurements were made following Márquez-García et al. (2009) using digital calipers ( $\pm 0.001$  mm; Traceable Products): snout-vent length (SVL), nose-mouth distance (NMD), mandible width (MW), head width (HW), forelimb length (FLL), femur length (FL), tibia-fibula length (TFL), and tarsal-metatarsal length (TML). The mass of each study subject was also recorded ( $\pm 0.01$  g; Pocket Pro Balance, Acculab). All measurements were recorded in the field and subjects were released immediately thereafter. Because previous studies in other anurans have shown that body size and length of extremities of postmetamorphic individuals and adults are

TABLE 1.—Canonical loadings, Eigenvalues, and explained variances for each canonical variable of two stepwise discriminant analyses (one including all morphometric variables and one including only the extremity variables) for nine populations of *Pleurodema thaul* individuals collected from nine localities spanning the distribution range of this species in Chile.

	CV1 <sup>a</sup>	CV2	CV3	CV4	CV5	CV6	CV7
All variables							
Weight	-0.589	-0.065	-1.018	1.426	-0.578	0.504	0.703
Snout-vent length	1.112	-0.490	0.351	-0.178	-0.916	-0.896	-0.550
Mandible width	-0.365	0.863	0.770	0.416	0.105	-0.350	-0.316
Head width	0.113	0.421	-0.591	-0.190	0.699	0.320	-1.010
Forelimb length	0.187	0.422	-0.491	-0.365	0.961	-0.402	0.891
Femur length	-0.309	0.528	0.296	-1.341	-0.687	0.635	0.250
Tibia-fibula length	0.685	-0.870	0.789	0.419	0.465	0.540	0.077
Eigenvalues	4.542	1.902	1.053	0.450	0.284	0.049	0.001
Explained %	54.8	23.0	12.7	5.4	3.4	0.6	0.0
Extremity variables							
Forelimb length	0.344	-0.700	0.746				
Femur length	1.098	0.488	-0.259				
Tibia-fibula length	-0.892	0.661	0.592				
Eigenvalues	1.223	0.359	0.185				
Explained %	69.2	20.3	10.5				

<sup>a</sup> CV = canonical variable.

related with temperature, precipitation, or pool desiccation time (e.g., Lonsdale and Levinton 1985; Laugen et al. 2003), we compared our morphological measurements with environmental features that vary along the geographical distribution of the species.

#### Environmental Variables

We obtained values for the following environmental variables from meteorological stations nearest to each collection locality (Dirección Meteorológica de Chile): Minimum air temperature ( $T_{\min}$ ), Maximum air temperature ( $T_{\max}$ ), and Precipitation (Precip). The environmental data recorded during the year of capture and for the four preceding years were considered in the analyses, as this time frame is relevant to the development of extant subjects. Although the reproductive season of *P. thaul* occurs between July and January (also the period during which subjects were encountered in the field), we included environmental data from all 12 mo of each year. For precipitation at each locality, we calculated the monthly accumulated precipitation as the sum of all daily precipitation. Then, we calculated the mean precipitation at each locality for each of the same months over the 5 yr considered in the study. Finally, the mean values of monthly precipitation were used to calculate a grand precipitation mean over the 5 yr for each site. Minimum and maximum temperatures were calculated averaging the minimum and maximum temperatures of each month per locality. Thereafter we assessed mean monthly temperature for each locality for the 5 yr considered in the study. The mean values of monthly temperature were then used to calculate a grand temperature mean over the 5 yr for each locality. From this grand mean, the temperature and thermal oscillation of each site was calculated for the 5 yr (i.e., difference between maximum and minimum temperatures).

#### Statistical Analysis

To test the hypothesis that body size covaries with environmental variables, we conducted a stepwise discriminant analysis including all of the morphological variables considered. This analysis was used because it extracts the discriminant function(s) that maximize differences between groups (i.e., locality). Additionally, we determined which among the original traits best explained the variation among

localities. To evaluate the effectiveness of the analysis to correctly classify each sampled individual to its native locality we used jackknife subsampling. To test the hypothesis that measurements of *P. thaul* appendages covary with environmental variables, we used another stepwise discriminant analysis that incorporated the three extremity measurements of all individuals. Using Spearman correlations ( $P < 0.05$ ) we then tested the relationships between geographical distance and the environmental features of minimum temperature, maximum temperature, precipitation, and mean thermal oscillation. In addition, we performed Spearman correlations to explore relationships between morphological and environmental variables. These correlations included the first two canonical variables obtained in the stepwise discriminant analyses. All statistical analyses were performed with Statistica v.8.0 (Statsoft Inc., Tulsa, OK).

#### RESULTS

The measurements taken from the *P. thaul* specimens showed differences among the collection localities. The stepwise discriminant analyses that incorporated all length and mass measurements differentiated specimens representing the localities (Wilks'  $\lambda = 0.01$ ,  $F_{72,828} = 13.89$ ,  $P < 0.0001$ ; Fig. 2). Specifically, a clinal pattern was seen in the linear morphometrics of the studied individuals. Taken together, the first two discriminant axes explained nearly 80% of the total variation (canonical variable 1 (CV1) = 54.8% and CV2 = 23.0%; Table 1), and correct assignment of individuals to their locality decreased by <10% after applying jackknife subsampling (from 82.9% to 73.0%; Table 2). The structural matrix, which correlates the discriminant functions with the original variables, showed that SVL had the highest correlation with CV1 (SVL-CV1,  $r = 0.82$ ) and MW had the highest correlation with CV2 (MW-CV2,  $r = 0.78$ ).

The stepwise discriminant analyses performed on the appendage measurements also discriminated among the collection localities (Wilks'  $\lambda = 0.23$ ,  $F_{32,517} = 7.93$ ,  $P < 0.0001$ ), with the two first discrimination axes explaining nearly 90% of the total variation (CV1 = 69.2 % and CV2 = 20.3; Table 1). The structural matrix showed a significant correlation between CV1 and FL ( $r = 0.69$ ). The correct

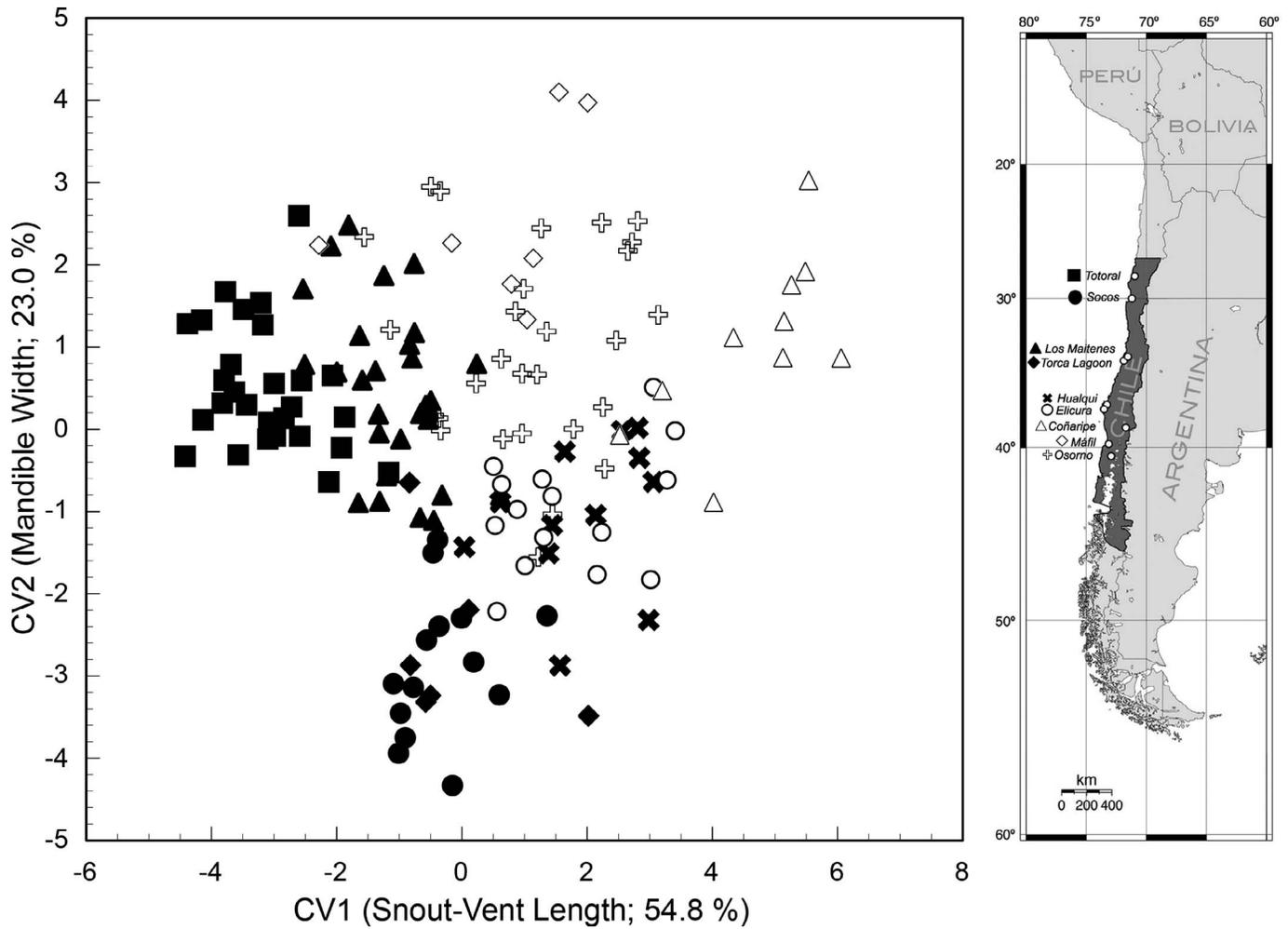


FIG. 2.—Left panel: Stepwise discriminant analysis (SDA) performed on all morphometric variables and weight measured for *Pleurodema thaul* males from different localities. The original variables to which each canonical variable is significantly correlated, and the explained percentages, are indicated on the axis labels. Right panel: Localities where males were collected are indicated with white circles. The symbols in the legend provide a representation of each locality on the SDA plot; the geographic distribution of *P. thaul* in Chile is shown in dark gray.

TABLE 2.—Classification matrix for two stepwise discriminant analyses (one including all morphometric variables and one including only the extremity variables) for nine populations of *Pleurodema thaul* individuals collected from nine localities spanning the distribution range of this species in Chile. Values are the number of individuals that the discriminant analysis correctly classified to each locality, whereas those in parentheses are the number of individuals that were classified to each locality using jackknife subsampling.

	Totoral	Socos	Los Maitenes	Torca Lagoon	Hualqui	Elicura	Coñaripe	Máfil	Osorno	Total
All variables										
Totoral	28 (25)	0 (0)	2 (5)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	30
Socos	0 (0)	12 (11)	0 (0)	1 (2)	0 (0)	1 (1)	0 (0)	0 (0)	1 (1)	15
Los Maitenes	3 (3)	1 (1)	23 (23)	1 (1)	0 (0)	1 (1)	0 (0)	0 (0)	0 (0)	29
Torca Lagoon	0 (0)	0 (1)	0 (0)	6 (4)	0 (0)	0 (0)	0 (0)	0 (0)	0 (1)	6
Hualqui	0 (0)	0 (1)	0 (1)	0 (0)	9 (5)	3 (5)	0 (0)	0 (0)	0 (0)	12
Elicura	0 (0)	1 (2)	0 (0)	0 (0)	1 (2)	12 (10)	1 (1)	0 (0)	0 (0)	15
Coñaripe	1 (0)	0 (0)	0 (0)	0 (0)	0 (1)	0 (1)	9 (8)	0 (0)	0 (0)	10
Máfil	1 (1)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	6 (5)	0 (1)	7
Osorno	0 (1)	0 (0)	0 (0)	0 (0)	3 (3)	2 (2)	1 (1)	1 (1)	21 (20)	28
Extremity variables										
Totoral	9 (9)	0 (0)	7 (7)	0 (0)	2 (2)	1 (1)	0 (0)	9 (9)	2 (2)	30
Socos	0 (0)	7 (6)	0 (0)	2 (3)	1 (1)	1 (1)	3 (3)	0 (0)	1 (1)	15
Los Maitenes	4 (5)	0 (0)	10 (9)	3 (3)	5 (5)	2 (2)	0 (0)	2 (2)	3 (3)	29
Torca Lagoon	0 (0)	1 (1)	1 (1)	0 (0)	1 (1)	1 (1)	2 (2)	0 (0)	0 (0)	6
Hualqui	1 (1)	1 (2)	2 (3)	0 (0)	3 (1)	3 (3)	2 (2)	0 (0)	0 (0)	12
Elicura	1 (1)	1 (1)	0 (0)	0 (0)	4 (4)	5 (5)	4 (4)	0 (0)	0 (0)	15
Coñaripe	0 (0)	2 (2)	0 (0)	0 (0)	0 (0)	1 (1)	7 (7)	0 (0)	0 (0)	10
Máfil	2 (2)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	2 (2)	3 (3)	7
Osorno	3 (4)	1 (1)	2 (3)	0 (0)	2 (2)	1 (0)	0 (1)	3 (3)	16 (14)	28

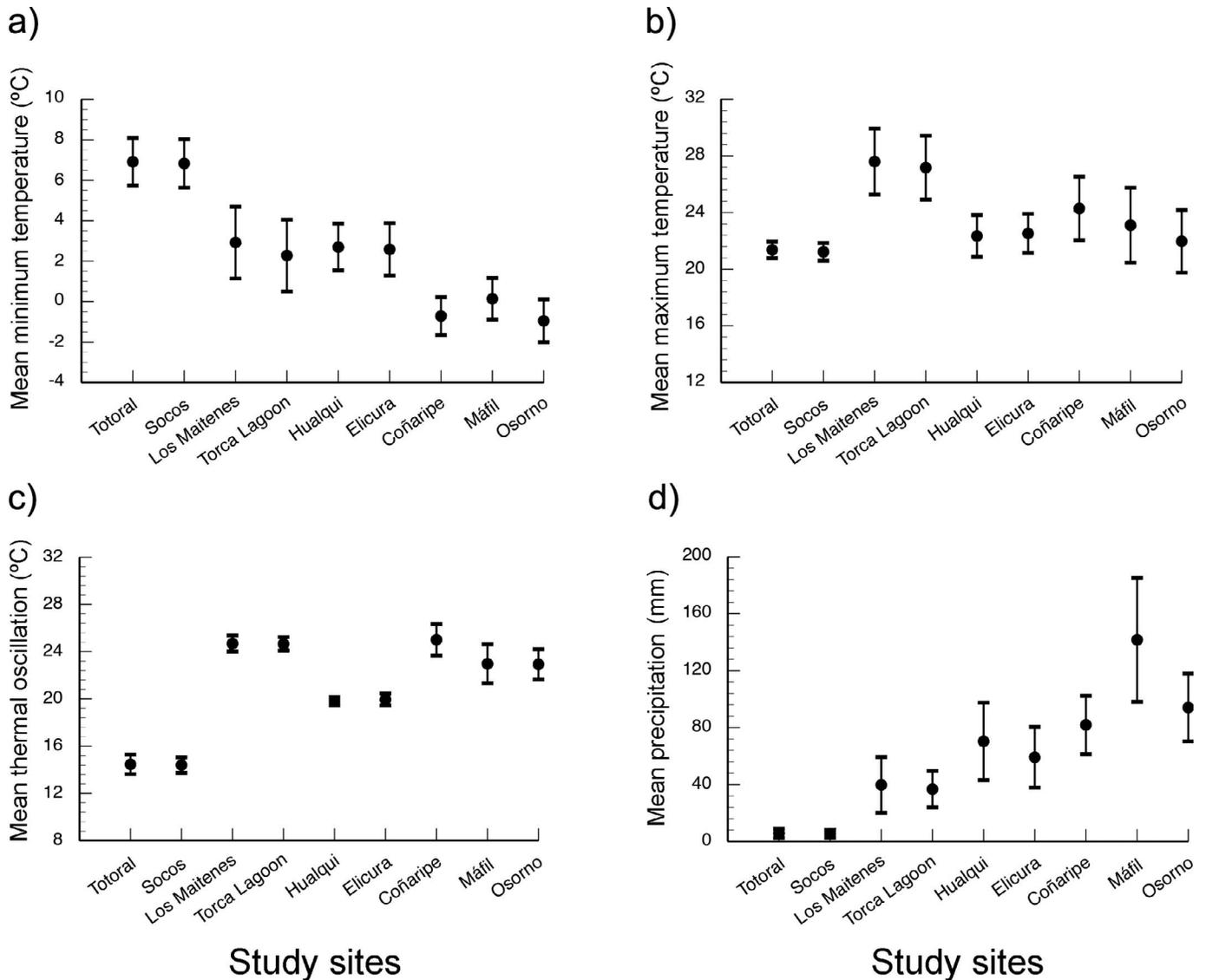


FIG. 3.—Variation in environmental variables of *Pleurodema thaul* locality in Chile considered in this study. (a) Mean minimum temperature; (b) mean maximum temperature; (c) mean thermal oscillation; (d) mean precipitation. Value labels along the x-axes are ordered in a north–south latitudinal axis (see right panel of Fig. 2).

assignment of individuals to their respective populations was very low before and after performing jackknife subsampling (38.8% and 34.9%, respectively; Table 2). Because the first canonical variable explained most of the total variation in extremity measurements, we considered this axis only for subsequent Spearman correlations.

The relative distances from the northernmost population (i.e., Totoral) to each of the eight other populations was correlated to minimum air temperature ( $r = -0.93$ ,  $P < 0.05$ ; Fig. 3a) and precipitation ( $r = 0.93$ ,  $P < 0.05$ ; Fig. 3d), but not to maximum air temperature ( $r = 0.20$ ,  $P > 0.05$ ; Fig. 3b) or thermal oscillation ( $r = 0.43$ ,  $P > 0.05$ ; Fig. 3c). There is a latitudinal gradient in both mean minimum temperature and mean precipitation levels. Relative to the southern collection sites, the northern localities are exposed to high mean minimum temperatures and low precipitation. In contrast, mean maximum temperature and mean thermal oscillation did not show clinal variation (Fig. 3).

The Spearman correlations using the first two canonical variables of the stepwise discriminant analysis performed for all morphometric variables and using the four environmental variables yielded a significant relationship between the first canonical variable and minimum air temperature ( $r = -0.67$ ,  $P < 0.05$ ), and between the second canonical variable and precipitation ( $r = 0.78$ ,  $P < 0.05$ ; Fig. 4). The relationships between the canonical variables and the other environmental variables were not significant ( $P > 0.05$  in all cases; CV1–Precip,  $r = 0.65$ ; CV1– $T_{\max}$ ,  $r = 0.13$ ; CV1–TO,  $r = 0.28$ ; CV2– $T_{\min}$ ,  $r = -0.57$ ; CV2– $T_{\max}$ ,  $r = 0.32$ ; CV2–TO,  $r = 0.57$ ). In addition, the Spearman correlations including the first canonical variable from the stepwise discriminant analysis performed on extremity measurements and using the four environmental variables did not yield significant values ( $P > 0.05$  in all cases; CV1–Precip,  $r = 0.33$ ; CV1– $T_{\min}$ ,  $r = 0.05$ ; CV1– $T_{\max}$ ,  $r = -0.12$ ; CV1–TO,  $r = -0.15$ ).

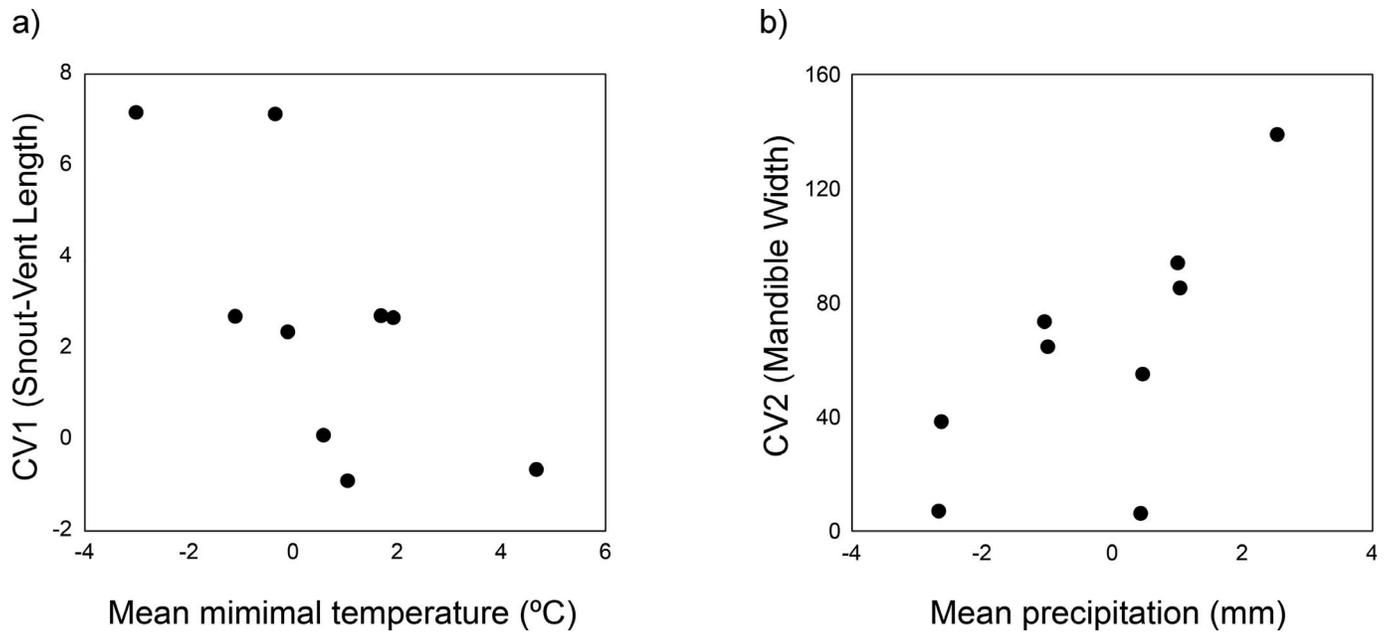


FIG. 4.—Significant Spearman correlations between canonical variables (CVs) and environmental variables for the nine sites where *Pleurodema thaul* were collected in Chile. (a) CV1 and mean minimum temperature; (b) CV2 and mean precipitation.

#### DISCUSSION

Our results indicate that there is geographic variation in morphological traits among males of *P. thaul* that represent different localities. The pattern of males from southern populations having larger morphological traits relative to those from northern populations follows Bergmann's rule. Cei (1958) reported that *P. thaul* subjects from northern localities have elongated heads and rounded noses, in contrast with subjects from southern localities that have wide heads and pointed noses. The geographic variation in morphological traits reported here mirrors geographic variation in behavioral and genetic traits reported for this species in previous studies (Velásquez et al. 2013, 2014). Our results are also in agreement with studies involving other anuran species that have reported similar trends of spatial variation in morphological traits (e.g., Ashton 2002a; Ashton and Feldman 2003; Olalla-Tárraga and Rodríguez 2007).

In contrast with the geographical trend of variation in body size, we found no geographic variation in the measurements of appendage length, indicating that the morphology of *P. thaul* does not comply with Allen's rule. The variation in temperature and precipitation to which *P. thaul* is exposed reflects the extent of the geographical distribution of this species throughout Chile (Hajek and Di Castri 1975). As such, individuals from southern localities, which are exposed to lower mean minimum temperatures and higher precipitation, had larger SVLs and mandible widths compared to individuals from northern localities (Figs. 3 and 4), indicating an association between these morphometric attributes and environmental variables.

Previous studies have demonstrated that Bergmann's rule holds at interspecific levels in some European and North American species of anurans. Among these anurans, the annual potential for evapotranspiration, a measure of energy available in the environment, has been documented as a reliable predictor of morphological variation (Olalla-Tárraga and

Rodríguez 2007). In addition, water deficit, a measure of water availability, has been shown to explain morphological variation in tropical South American anurans (Olalla-Tárraga et al. 2009). Such results are in agreement with heat balance and water availability hypotheses that state that anuran body size should increase with decreased thermal energy and water availability. In turn, this agrees with the tenet that the lower surface area to volume ratio of larger animals allows for more efficient control of heat and water balance (Mayr 1956). Our results differ from those from Olalla-Tárraga and Rodríguez (2007), however, because *P. thaul* males were larger in rainy temperate zones at high latitudes relative to individuals inhabiting desert zones with very low precipitation at low latitudes.

Intraspecific variation in the body size of *P. thaul* has also been shown to be related to variation in water availability for larval development because the duration of this resource affects the body size of postmetamorphic individuals (Denver et al. 1998; Richter-Boix et al. 2006). Márquez-García et al. (2009) found that tadpoles from ponds with high and medium levels of desiccation reach metamorphosis at earlier ages. Additionally, postmetamorphic subjects are larger when developing in conditions of less desiccation compared to individuals that develop in wetlands having fast desiccation rates (Márquez-García et al. 2009). Accordingly, differences in the SVL among *P. thaul* from different localities could be explained by water availability in pools during metamorphosis, as subjects from biogeographic zones with higher levels of precipitation and lower minimum temperatures had larger SVLs. In contrast, individuals from zones with low precipitation and higher minimum temperatures would have reduced hydroperiods, and therefore would likely have small postmetamorphic sizes. Studies have demonstrated that a negative relationship between the body size of juvenile frogs and ambient environmental temperature can be explained by a decoupling between growth and development rate (e.g., Atkinson 1994). Thus, lower ambient

temperatures likely decrease development rate but do not necessarily decrease maximum body size, allowing subjects to reach later developmental stages at more advanced ages or larger sizes (Van der Have and de Jong 1996).

Geographic variation in body size of anurans could result from either phenotypic plasticity or adaptation to particular environments. Further research that incorporates a common garden design could unveil the processes accounting for body size differences between populations of species that, like *P. thaul*, have extensive geographical distributions.

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