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Morphometric Variation Affecting Sexual Size Dimorphism in *Neopedies brunneri* (Orthoptera: Acrididae)

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ABSTRACT *Neopedies brunneri* (Giglio-Tos, 1894) is a grasshopper belonging to the family Acrididae. This group of insects usually has economic importance in Argentina because of their ability to experience outbreaks, but little is known about them. Insect populations usually differ at the phenotypic level, often according to geographical and environmental variables, which may be a good indicator of some other factors with adaptive significance (such as developmental rate, seasonal resource disposal, and growing seasonal length). The aim of this article is to report the first preliminary analysis of phenotypic variation in natural populations of *N. brunneri* from central Argentina to study the amount of intra- and interpopulation variation in morphometric traits and their probable association with geographic and climatic variables. We found the existence of morphometrical differences among populations and a pattern of geographical variation, with males and females from eastern populations being larger than the ones from the west. Sexual size dimorphism was also detected and found to be correlated to geographical and climatic variation. Moreover, geographic patterns of sexual size dimorphism were determined, helping to clarify differential susceptibility of both sexes to environmental conditions.

KEY WORDS morphometric trait, phenotypic variation, Orthoptera

Intraspecific body size differentiation is a component of variation with recognized ecological and evolutionary importance (Roff and Mousseau 2005, Matthews et al. 2011, Hausch et al. 2013). Body size-related traits are associated with growth, survival, and reproductive success across environments, and they frequently underlie the functional role of organisms in ecosystems (Hausch et al. 2013). Morphometric traits are complex traits, and their variation is attributed to many proximate and ultimate causes, including both biotic and abiotic factors (Whitman 2008, Hernández et al. 2009, Bidau et al. 2012).

There is extensive evidence in insect populations that morphometric variation is often correlated with geographical and environmental variables. Climatic conditions may be good indicator variables of some factors with adaptive significance (such as developmental rate, seasonal resource disposal, and growing seasonal length) affecting population differentiation in nature (Blanckenhorn and Demont 2004, Roff and Mousseau 2005). Species distributed across a range of altitudes and latitudes may exhibit phenotypic clinal variation associated with a diversity of climatic conditions as a result of local adaptation or phenotypic plasticity (change in phenotype in response to a change in the environment; Berner et al. 2004).

Another source of phenotypic variation within species is related with the amount of morphological differences between males and females. Sexual size dimorphism (SSD), a difference in body size between females and males (Stillwell et al. 2010), is a widespread phenomenon in animals, and this variation was mainly explained in terms of adaptive and phenotypic plasticity hypotheses (Fairbairn 2007, Stillwell et al. 2007).

There are many examples in Orthoptera showing intraspecific body size variation, and some of them efficiently analyzed the relative importance of plasticity and local adaptation in the detected patterns (Mousseau and Roff 1989, Berner et al. 2004). In a widely accepted adaptive scenario, the differential equilibrium hypothesis proposes that SSD is a result of opposing selective pressures on body size (Blanckenhorn et al. 2007, Stillwell et al. 2007, Hochkirch and Groning 2008). In insects, fecundity selection on females and sexual selection on males are likely the major sources of selection favoring larger size, whereas small-sized individuals avoid several presumed viability costs (because of long development, predation, and reduced agility). However, current approaches have also demonstrated that plasticity in body size can differ between sexes, thereby producing variation in SSD among populations of the same species (Stillwell et al. 2010). The direction and degree of

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Table 1. Locations of five populations of *N. brunneri* sampled in central Argentina

Population	Altitude (m)	Latitude	Longitude	T _{MAX} (°C)	T _{MIN} (°C)	PET (mm)	Sun (Hs)	Abbreviation
Villa del Rosario	249	31°34'S	63°31'W	24.03	10.7	106.97	7.52	VRosario
Villa Allende	497	31°18'S	64°18'W	24.17	11.03	113.05	6.3	VAllende
Rio Ceballos	790	31°10'S	64°20'W	24.17	11.03	113.05	6.3	RCeballos
Rio Cuarto	445	33°08'S	64°20'W	22.98	10.97	87.02	5.01	RCuarto
General Belgrano	720	31°58'S	64°39'W	24.17	11.03	113.05	6.3	GBelgrano

Geographical coordinates, climatic variables, and abbreviations used throughout this article are indicated for each location. PET, Potential of Evapotranspiration; Sun Hs, no. of hours with sun.

SSD can vary with latitude, altitude (Blanckenhorn and Demont 2004, Blanckenhorn et al. 2007, Stillwell et al. 2007), and even with body size (Rensch 1950).

Acrididae is recognized as a group of Orthoptera with great biotic potential in Argentina because of the ability to dramatically increase their population sizes (outbreaks) (Cigliano et al. 2010, Mariottini et al. 2011). However, patterns of morphometric variation in South American grasshoppers belonging to the family Acrididae had been only documented in about seven species (Colombo 2001; Colombo et al. 2004; Bidau and Marti 2007a,b; Adis et al. 2008; Remis 2008; Sesarini and Remis 2008; Rosetti and Remis 2013). New approaches analyzing the morphometric variation in South American acridids may be helpful in understanding the phenotypic evolution in this group.

Neopedies brunneri (Giglio-Tos, 1894) (Orthoptera: Acrididae) is a South American acridid that inhabits natural prairies and is considered as a minor pest (Carbonell et al. 2006). There is currently no information available about intraspecific variation of this grasshopper species. In this article, we presented a preliminary assessment of phenotypic variation of *N. brunneri* from central Argentina to study the amount of intra- and interpopulation variation in morphometric traits and their probable association with geographic and climatic variables.

Materials and Methods

Population Sampling and Morphometric Trait Measurements. Adult males and females of *N. brunneri* were collected from the field during February 2005 from five natural populations located in the Córdoba Province in central Argentina: Villa del Rosario, Rio Cuarto, Villa General Belgrano, Villa Allende, and Rio Ceballos (Table 1). Villa del Rosario population, placed at a low altitude, is located in a semiarid zone, that is, with dry winters and humid summer periods; Rio Cuarto is located in the west of the humid Pampas, in the east of the Córdoba Hills; whereas Rio Ceballos, Villa Allende, and Villa General Belgrano are located in the foothills of the Córdoba Hills. In total, 86 individuals were measured for four morphometric traits: femur length (FL, length of third femur), tibia length (TiL, length of third tibia), thorax length (TxL, length of prothorax), and tegmen length (TegL, length of tegmen). Measurements were achieved on the right side of the grasshopper using a stereoscopic micro-

scope and an ocular micrometer (1 mm = 48 ocular units) (Carl Zeiss, Oberkochen, Germany).

Morphometric Data Analysis. We tested for statistical significance among populations through multivariate analysis of variance (MANOVA) and conventional one-way ANOVAs, considering the population as the independent factor and each morphometric trait as dependent variables. To analyze population variation on a reduced set of independent variables, principal component analyses (PCA) of morphometric variables were also performed. We tested for variation in principal components (PCs) by means of one-way ANOVAs, considering the population as the independent factor and PCs as dependent factors. All these analyses were performed using STATISTICA (StatSoft Inc., 1996; version 5.0, StatSoft Inc., Tulsa, OK). PCA graphics were performed using PAST 2.16 software (Hammer et al. 2001).

To evaluate the presence of sexual dimorphism for size in each population, we estimated a SSD index as the ratio between the arithmetic mean of each morphometric trait in females and the corresponding to males (Smith 1999).

In addition, Rensch (1950) found out that the magnitude of SSD tends to covary with body size. According to Fairbairn (1997), allometric relations can be quantified using the function $y = ax^b$, where x and y are body size, and a and b are constants. If x and y are measured in the same scale, y/x will be constant when $b = 1$. This defines isometry or no allometry. Alternatively, allometry occurs when $b \neq 1$. The presence of allometry for SSD can be estimated by regressing $\log(\text{male size})$ on $\log(\text{female size})$, as suggested by Fairbairn (1997). The slope of the regression is thus, an estimate of the parameter b . Because both variables are measured in the same way and with the same error, the most appropriate regression is reduced major regression (RMA) (Fairbairn 1997). RMA was estimated using 'lmodel2' package of R software (Legendre 2012). We tested the hypotheses of $b = 1$ (no allometry for SSD) with Clarke's T statistic with adjusted degrees of freedom (Clarke 1980).

The associations between morphometric traits with respect to geographic and some climatic conditions were analyzed by means of Spearman nonparametric correlation analysis using STATISTICA (StatSoft Inc. 1996). Climatic data were obtained through the Local Climate Estimator from www.fao.org/SD/dim_en3/en3_051002_en.

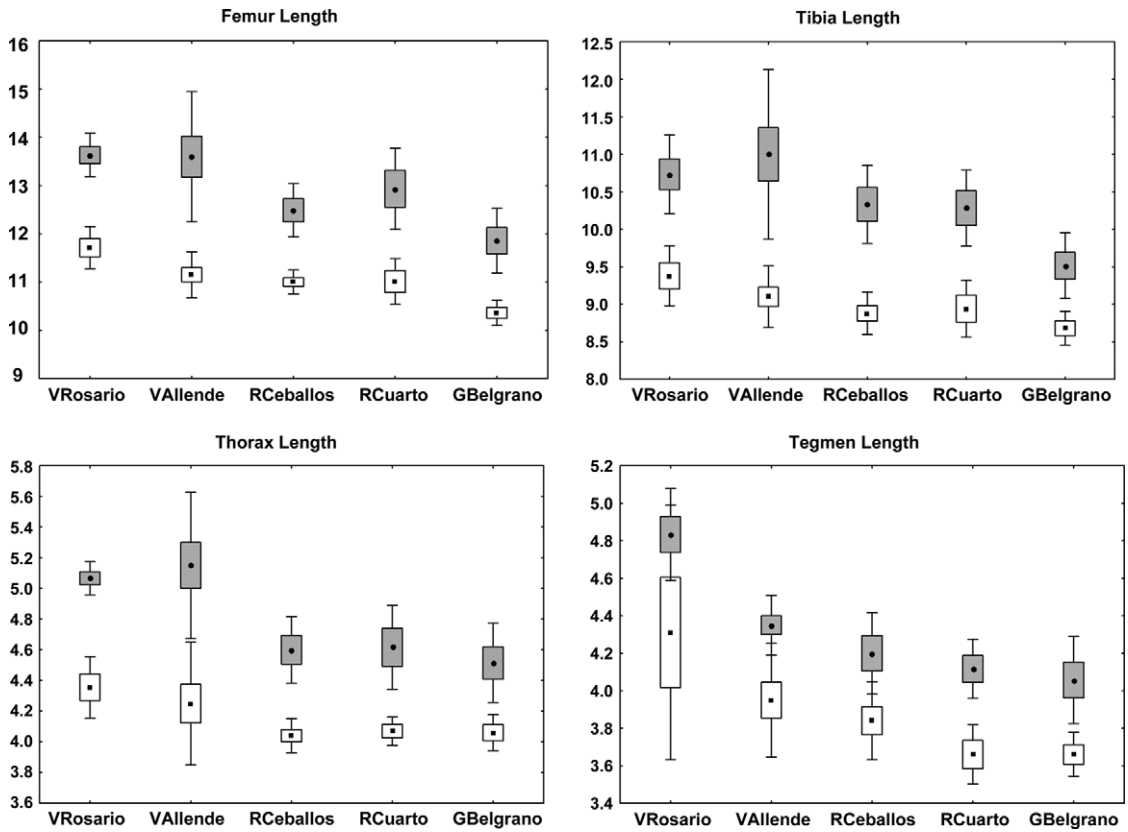


Fig. 1. Mean value (in millimeters; primary symbol), SE (boxes), and CI (bars) for morphometric traits in males (squares) and females (circles) from populations of *N. brunneri* (according to Table 1).

Results

Adult individuals of *N. brunneri* sampled in five populations from central Argentina were studied to analyze morphometric variation patterns. Four body size-related traits were scored in the grasshoppers, revealing a high level of phenotypic variation in the wild populations of *N. brunneri* (Fig. 1).

SSD was verified in all morphometric analyzed traits across the geographic sampled area, with females being larger than males. MANOVA showed highly significant differences in body size among populations (Wilks = 0.257; $P < 10^{-4}$) and between sexes (Wilks = 0.355; $P < 10^{-4}$), whereas no significant interaction (population \times sex) was detected ($P > 0.05$). The individual ANOVAs revealed highly significant differences between populations and between sexes in all analyzed body size-related traits (Table 2). No significant interactions were detected in any analyzed trait, thus demonstrating female-biased SSD across the studied area.

We also studied morphometric variation on a reduced set of independent variables with PCA, examining both sexes independently. The first three PCs for males and females accounted for ≈ 93 and 96% of the total variance, respectively (Table 3). The PC₁ was negatively related with all four body size-related traits, and may be considered as a measure of overall size.

The PC₂ was positively associated with some traits and negatively with others, and may reflect information with regards to the shape. The individual ANOVAs demonstrated highly significant differences among populations in both male and female datasets for PC₁ and in females for PC₂ (Table 3).

The size of wild adult *N. brunneri* seemed to decrease from east to west, and partial correlation analysis of body size-related traits on west longitude maintained this statement. In both sexes the FL and TiL correlated negatively with longitude ($r = -0.90$; $P = 0.037$ in both cases). Moreover, in males a significant negative correlation was also found between longitude and TxL ($r = -0.97$; $P = 0.0048$). Similar results

Table 2. F and P values from one-way ANOVAs attained to compare morphometric means among sampled populations

Source of Variation	Femur	Tibia	Thorax	Tegmen
Among populations				
F	7.50	5.38	8.88	9.44
P	$<10^{-4}$	$<10^{-4}$	$<10^{-4}$	$<10^{-4}$
Between sexes				
F	83.46	79.91	100.02	21.75
P	$<10^{-4}$	$<10^{-4}$	$<10^{-4}$	$<10^{-4}$
Interaction (pop \times sex)				
F	0.60	1.05	1.23	0.10
P	0.66	0.38	0.30	0.98

Table 3. Principal component analyses (PCA)

	Machos			Hembras		
	PC1	PC2	PC3	PC1	PC2	PC3
A						
Total	-0.3594	0.7868	0.4646	-0.6895	-0.6075	0.3916
Femur	-0.8058	-0.3826	0.3655	-0.8822	0.3659	0.0501
Tibia	-0.7629	-0.5246	-0.2278	-0.8935	0.3152	0.1305
Tegmen	-0.7229	0.5804	0.2844	-0.7994	-0.5381	0.2643
Thorax	-0.8072	0.3579	-0.4044	-0.8852	-0.1969	-0.4204
Eigenvalues	2.4056	0.8865	0.4299	2.9992	0.5616	0.2661
Cum % Var	60.1408	82.3041	93.0515	74.9789	89.0199	95.6736
B						
F	5.752	0.8196	0.659	6.467	4.0414	2.119
P	0.0008	0.519	0.623	<10 ⁻⁴	0.009	0.100

(A) Loadings, eigenvalues, and cumulative percentage of variance explained for the main PC extracted. (B) F-values from one-way ANOVAs achieved to analyze population differentiation.

were obtained comparing PCs with geographic variables. PC₁ is positively correlated with longitude both in males and females ($r = 0.90$; $P = 0.037$ in both sexes). Both for females and males, biplots based on the first two PCs showed that two populations were well separated (Vrosario and Gbelgrano). These populations are located in the edges in a longitudinal cline formed by the populations sampled. A third population, RCuarto, displayed higher phenotypic variance, occupying a wider area in the PC space (Fig. 2).

Body size also seemed to decline with the elevation of the populations. TegL correlated negatively with altitude in males ($r = -0.90$; $P = 0.037$).

We estimated SSD as the ratio of the male mean value to the female mean value to visualize the magnitude of SSD in different populations (Table 4). SSD appeared to change from north to south. The SSD for TegL as indicator variable of body size demonstrated positive significant correlation with latitude ($r = 0.90$; $P = 0.037$). Negative correlations between tegmen SSD and maximum temperature and potential evapotranspiration were also detected ($P < 0.05$ in both cases). Moreover SSD also seemed to vary from west to east. The SSD for TxL correlated negatively with longitude ($r = -0.90$; $P = 0.037$; Fig. 3).

The regression of log (male size) on log (female size) to test allometry demonstrated that the RMA slopes for FL, TiL, and TegL did not contrast from 1.0, indicating that these traits scale isometrically, whereas slope for TxL was marginally significant lower than 1.0, suggesting SSD allometry for this trait (Table 4).

Discussion

Many studies in arthropods are dedicated to analyze the influence of biotic and abiotic variables over intraspecific variation. Compelling evidence supports that morphometric variation in this group is frequently correlated with environmental variables, even though these variables themselves might not be the causal agents of variation, but they might be good indicators of some factors with adaptive significance (Blanckenhorn and Demont 2004, Roff and Mousseau 2005). Therefore, analysis of body size-related pattern is relevant because it may suggest environmental con-

straints and may reveal local adaptations (Stearns 1992, Berner and Blanckenhorn 2006, Huizenga et al. 2008).

In *N. brunneri* from central Argentina, we found significant differences between populations in terms of body size, and this variation was reflected in a pattern of geographic variation: male and female body size varied longitudinally. In general, individuals from the eastern populations showed larger body size than those from the western populations, even when we considered the measured morphometric traits or the components extracted from PCA. Moreover a pattern of altitudinal variation was also detected in males being smaller at higher elevations. The longitudinal (≈ 100 km) and altitudinal range (≈ 470 m) analyzed in this study are moderate ranges, but include important differences in the landscape: a transition area between plain space, gentle slopes, and low hills. Our results suggest that the geographic effect on climatic conditions in this area rendered significant intraspecific variation, which may be associated with local adaptation.

Significant body size variation was detected for other species of South American acridid grasshoppers, such as *Dichroplus elongatus*, *Dichroplus vittatus*, *Dichroplus pratensis*, and *Sinipta dalmani*, and in all cases substantial heterogeneity for body size-related traits were found to correlate with geographic and climatic conditions (Bidau and Marti 2007a,b; Sesarini and Remis 2008; Rosetti and Remis 2013). The current study confirmed the existence of SSD in *N. brunneri*, as females are larger than males for all studied traits. It has been observed that SSD may vary among populations according to different geographical patterns and the relative importance of selective forces acting in phenotype evolution. In *N. Brunneri*, SSD for some body size-related traits showed geographical variation, as tegmen SSD correlated positively with latitude, and thorax SSD correlated negatively with longitude.

Rensch (1950) noticed that the magnitude of SSD may vary according to body size. When males are larger than females, then SSD increases with size; conversely, if females are larger than males, then SSD decrease with size (Rensch 1950, Fairbairn 1997).

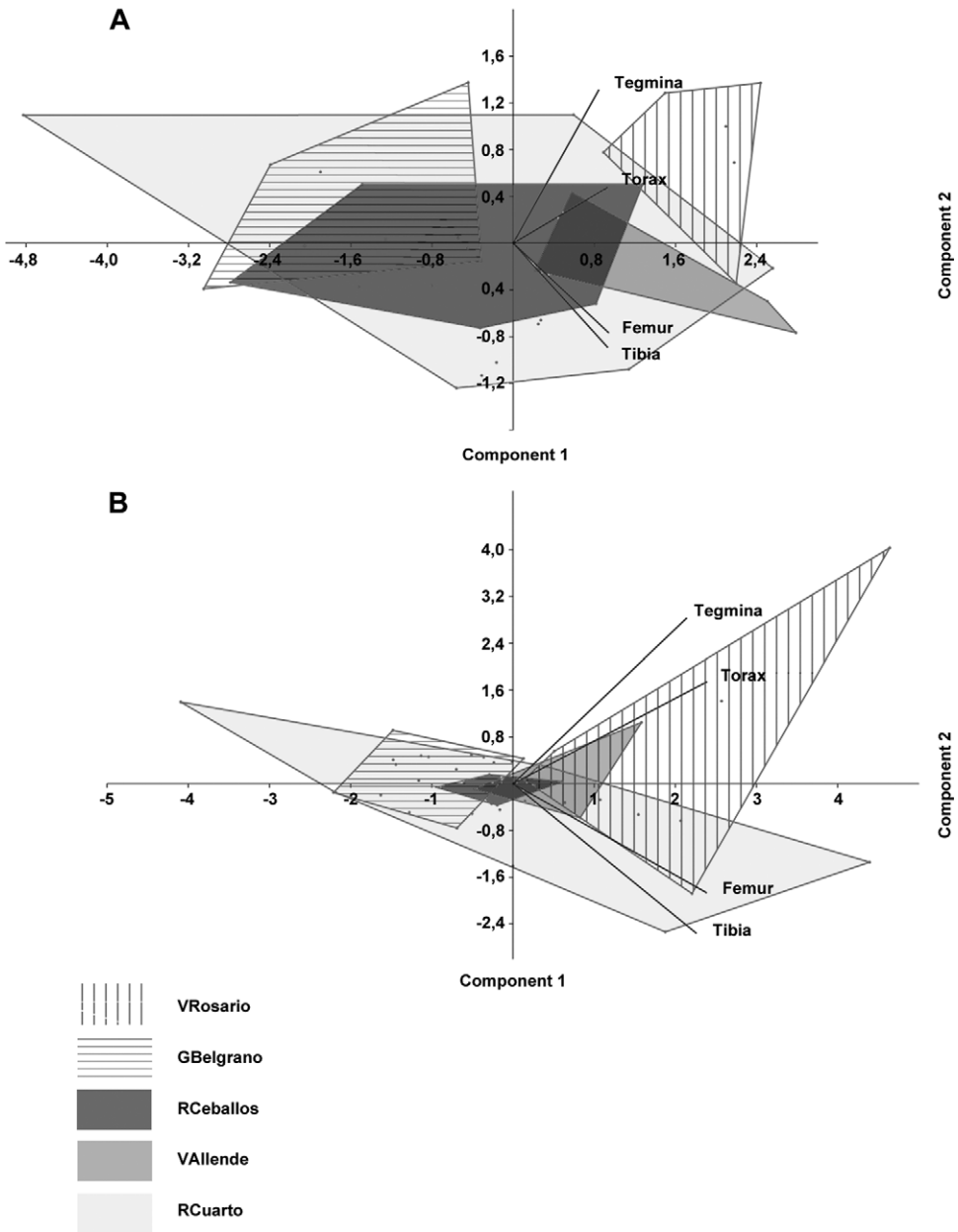


Fig. 2. Biplot from PCA on females (A) and males (B) of *N. brunneri* from different populations.

Table 4. SSD estimates for the analyzed populations

	Femur	Tibia	Thorax	Tegmen
VRosario	1.164	1.145	1.163	1.121
VAllende	1.219	1.209	1.121	1.101
RCeballos	1.135	1.164	1.121	1.093
RCuarto	1.175	1.164	1.134	1.125
GBelgrano	1.145	1.096	1.111	1.108
b	0.74	0.52	0.54	0.97
T	1.26	1.91	2.65	0.44
√	5.00	5.21	4.91	4.71
P	0.27	0.11	0.05	0.68

Clarke's *t*-statistic tests the null hypotheses that the RMA slope (b) = 1. (√ = degrees of freedom).

Most species in Orthoptera present female-biased SSD (Blanckenhorn et al. 2007, Stillwell et al. 2010), but the allometrical relationships are variable. For example, in the grasshoppers *D. vittatus* and *D. elongatus*, it was showed that SSD increases with an increase in body size, which is in contrast to Rensch's rule (Bidau and Martí 2008, Rosetti and Remis 2013). On the contrary, the bushcricket *Poecilimon thessalicus* and the grasshopper *D. pratensis* constitute examples of Rensch's rule where SSD decreases as body size increases (Bidau and Martí 2008, Lehman and Lehman 2008). In *N. brunneri*, the pattern of SSD varied among traits.

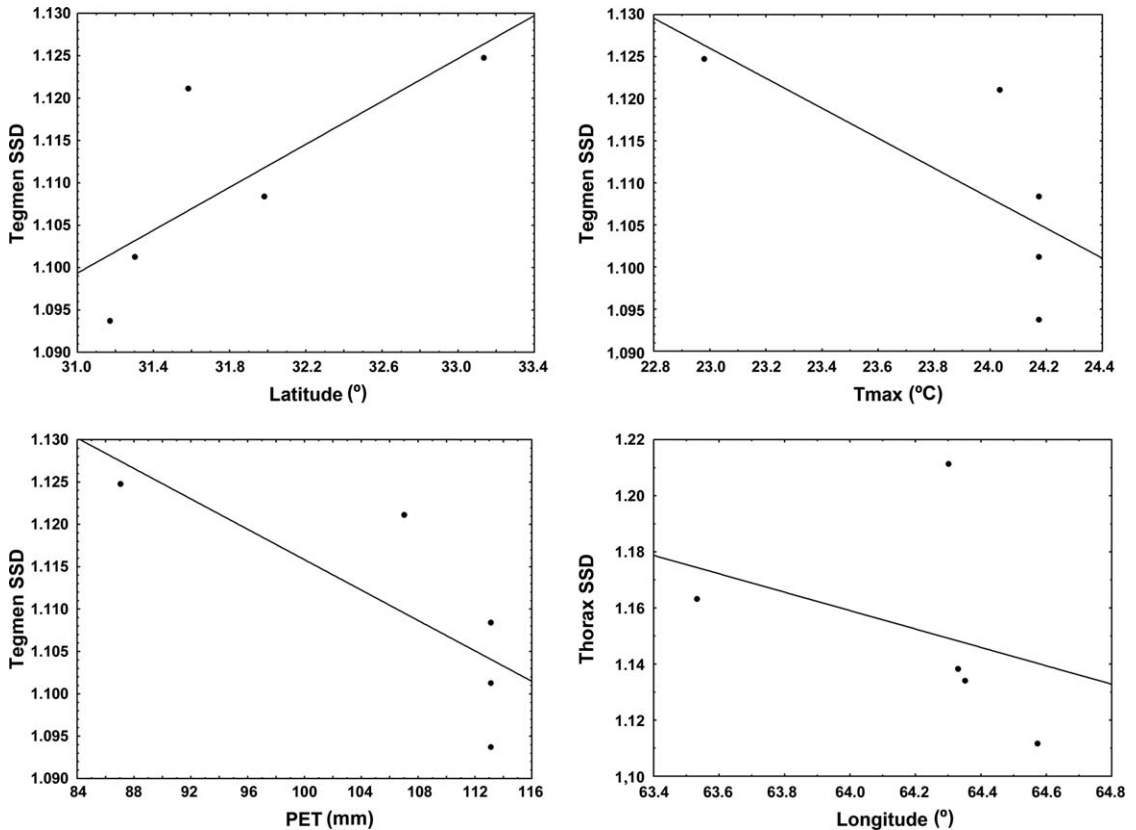


Fig. 3. Correlations between SSD for morphometric traits and geographic and climatic conditions in *N. brunneri* from central Argentina. T_{max} , temperature maximum; PET, Potential of Evapotranspiration.

The slope of RMA indicated that SSD for FL, TiL, and TegL scaled isometrically ($b \approx 1$) as body size evolved in similar fashion in males and females. Furthermore, SSD for TegL increased with latitude, and was also related with some climatic variables such as maximum temperature and potential of evapotranspiration, thereby demonstrating the relative importance of environment conditions acting on body size and local adaptation. On the contrary, SSD for TxL scaled allometrically (slope < 1), suggesting a larger phenotypic variation in females than males size according to the converse of Rensch's rule. When female-biased SSD establishes large difference between sexes, the possibility of female size revealing superior sensitivity to environmental conditions would be higher (Teder and Tammaru 2005). The pattern detected in this study could be explained through the higher vulnerability of females to reach their optimal body size. Here, all body size-related traits analyzed in *N. brunneri* showed significant variation between sexes and among populations, thus the patterns of SSD variation can differ significantly between males and females, possibly reflecting the greater susceptibility of females to environmental condition. Phenotypic variation is a fundamental component of biodiversity, and the evolution of body size-traits that influences interactions among species can result in changes in the community

dynamics affecting ecosystem functions (Matthews et al. 2011). Because of this, the amount and geographical distribution of morphometric differentiation detected in this study may provide useful information for future ecosystem dynamic studies.

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