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Morphometric variation in chromosomally polymorphic grasshoppers (Orthoptera: Acrididae) from South America: Bergmann and converse Bergmann patterns

Pablo César Colombo* and María Isabel Remis

Abstract

Leptysma argentina Bruner, *Trimerotropis pallidipennis* (Burmeister), and *Cornops aquaticum* Bruner are South-American grasshoppers (Orthoptera: Acrididae) whose chromosome polymorphisms were intensively studied. *Leptysma argentina* lives in central-east Argentina and in Uruguay and was polymorphic for a centric fusion whose presence is significantly correlated with a larger body size; this parameter was shown to be associated with sexual selection and longevity selection; this species exhibited a marked latitudinal Bergmann pattern. In contrast, *Trimerotropis pallidipennis* followed a converse altitudinal Bergmann cline; males from higher altitudes were significantly smaller. This species supported an extended polymorphism for several inversions, which are correlated intrapopulationally with larger body size. Finally, *C. aquaticum* showed an evident example of Bergmann's rule for tegmen length; this species was polymorphic for 3 centric fusions, whose frequency increased southward, as in *L. argentina*. One of the fusions was associated with increased body size. We noticed that in all cases the rearrangement that was related to body size increased in the direction in which this variable was adaptive, thus suggesting a possible involvement of chromosome polymorphism in body size selection.

Key Words: *Leptysma argentina*; *Trimerotropis pallidipennis*; *Cornops aquaticum*; chromosome polymorphisms; Bergmann rule; morphometrical studies

Resumen

Leptysma argentina, *Trimerotropis pallidipennis* y *Cornops aquaticum* son saltamontes sudamericanos cuyos polimorfismos cromosómicos fueron intensamente estudiados. *L. argentina* vive en Argentina central-oriental y en Uruguay, y es polimórfica para una fusión céntrica cuya presencia está asociada significativamente con un mayor tamaño corporal; se ha demostrado que este parámetro está asociado con la selección sexual y con selección para la longevidad; además, esta especie posee un patrón de Bergmann latitudinal marcado. En cambio, *T. pallidipennis* sigue una clina de Bergmann altitudinal inversa: los machos de latitudes más altas son significativamente más pequeños. Esta especie presenta un extendido polimorfismo para varias inversiones que están correlacionadas intrapoblacionalmente con un mayor tamaño corporal. Finalmente, *C. aquaticum* es un ejemplo evidente de regla de Bergmann para longitud de tegmina; esta especie es polimórfica para tres fusiones céntricas, cuya frecuencia se incrementa hacia el sur, como en *L. argentina*. Una de las fusiones está asociada con un mayor tamaño corporal. Notamos que en los tres casos el rearrreglo relacionado con el aumento en la longitud total o de tegmina incrementa su frecuencia en la dirección en la que esta variable es adaptativa, sugiriendo por lo tanto un posible involucramiento de los polimorfismos cromosómicos en la selección del tamaño corporal.

Palabras Clave: *Leptysma argentina*; *Trimerotropis pallidipennis*; *Cornops aquaticum*; polimorfismos del cromosoma; regla de Bergmann; estudios morfométricos

According to Bergmann (1847), individuals of an endothermic animal species coming from higher latitudes or altitudes have larger body size than those coming from lower ones. This makes sense, because an increased body size is adaptive for endotherms in that it exposes a lower surface area relative to its volume, thus reducing heat loss. Remarkably, for some ectotherms the same rule applies, too, but in others a converse pattern (called a converse Bergmann's rule) is observed. In arthropods, both patterns (Bergmann's and its converse) have been found. Moreover, several studies have found no pattern in some species within a group (e.g., Orthoptera), thus suggesting that there may be a continuum of patterns for ectotherms (Blanckenhorn & Demont 2004; Shelomi 2012).

In insects, chromosome polymorphisms can be frequent, and in several cases a marked association has been reported between body size variation and karyotype (White & Andrew 1960; White et al. 1963; Butlin et al. 1982; Hasson et al. 1992; Colombo et al. 2001, 2004; Werle & Klekowski 2004). In these cases, additional phenotypic differentiation is present on which selection may be acting and which represents valuable examples to relate chromosome and phenotype evolution.

Here, we present the available results for 3 cases of grasshoppers, *Leptysma argentina* Bruner, *Trimerotropis pallidipennis* (Burmeister), and *Cornops aquaticum* Bruner (Orthoptera: Acrididae), which have been studied for body size clines, altitudinal and/or latitudinal. All of these species are polymorphic for different chromosome rearrange-

ments, and, interestingly, in all cases these structural changes have been found to be intrapopulationally associated to body size-related variables. *Leptysma argentina* and *C. aquaticum* follow Bergmann's rule, but *T. pallidipennis*, as most grasshoppers (Bidau & Marti 2007a,b; Whitman 2008), follows its converse.

Materials and Methods

Body size variation was studied in chromosomally polymorphic populations of 3 South American grasshopper species. However, in *L. argentina* and *T. pallidipennis*, we have only body measurements of males because only males were collected. This was done because male meiosis is easier to study than female meiosis, given that in these 2 species only chromosome studies were performed. Morphometric variables were body length (BL) (from the phastigium to the articulation of the 3rd femur), 3rd femur length (FL), 3rd tibia length (TiL), pronotum length (TxL), prothorax height (TxH), and tegmen length (TgL). Measurements were taken on the left side of the specimens and done by the same observer (PCC) using a graded binocular microscope.

Trimerotropis pallidipennis

Three hundred and fifty-one males from 7 populations of *T. pallidipennis* sited along an altitudinal gradient in the province of Mendoza (central Andean Argentina) were examined for inversion frequencies and morphometric traits simultaneously (Colombo 2002).

Leptysma argentina

Four hundred and forty-nine individuals from 9 populations of *L. argentina* located in central-eastern Argentina assessed for Robertsonian translocation and body size-related traits were considered in order to analyze simultaneous patterns of chromosome and body length variation (Colombo 1989, 1997).

Cornops aquaticum

The data are those published by Romero et al. (2014). However, in that work and in this presentation, the results were compared with those of the morphometric study by Adis et al. (2007) in a wider study on a South American scale. These results were not aimed at dealing with Bergmann's or Rensch's rules (Adis et al. 2007) (according to Rensch's rule, sexual dimorphism decreases when body size increases). Therefore, in Romero et al. (2014) we added these results to ours and compared them in order to ascertain whether they were in keeping with Rensch's rule. In the present paper, we deal with Bergmann's rule. As in Romero et al. (2014), only tegmen length was measured in the same way as in Adis et al. (2007). Therefore, we chose only this variable for this study.

Results and Discussion

Trimerotropis pallidipennis

According to the data shown in Table 1 and Figure 1, body size was strongly and negatively correlated with altitude ($r = 0.9782$, $P = 0.0001$). This result suggests that chromosome inversions may be associated with adaptation to different environments not only at population levels (Colombo 2002) but also in a broader geographical scope. We think that in this case, body size-related variables may point in the direction of season length limitation due to a slower rate of growth caused by lower temperatures, along with the shortening of the time available for development (Berner et al. 2004; Blanckenhorn & De-

mont 2004; Berner & Blanckenhorn 2006). An altitudinal cline related with body size, temperature, and development rate was studied in the European grasshopper *Omocestus viridulus* (L.) (Berner et al. 2004; Berner & Blanckenhorn 2006); however, this species was revealed to be univoltine all along the gradient. *Trimerotropis pallidipennis* was shown to be bivoltine instead, at least in the high-mountain population of Uspallata (C. Lange, personal communication). We do not know whether there are variations in voltinism along the gradient.

One of the chromosome inversions affects a morphometric variable; in fact, inversion 6M in the population of Uspallata significantly increases tegmen length (Table 2, from Colombo 2002). We think that the effect on a morphometric variable at a location may be related to the pattern of distribution on a broader geographical scope.

Colombo & Confalonieri (1996) found that inversion frequencies were negatively correlated with minimum temperature; we think now that this correlation may be masking several other variables, which in time are covariate with it. Chromosome inversions may be related with the adaptation to such variables.

Leptysma argentina

Leptysma argentina bears a polymorphism for a Robertsonian translocation called "fusion 3/6" in most of its analyzed populations. In a low-ranging cytogeographical analysis covering latitudes 31°S to 34°S in mid-eastern Argentina, this rearrangement was observed to be correlated with latitude (frequency zero in the northernmost population and frequency one in the southernmost, with all the intermediate frequencies in between these latitudes) (Table 3; Fig. 1B). Moreover, in this species, body size-related variables were larger in fusion homozygotes than in unfused homozygotes; the effect over heterozygotes was variable (Table 4). This trend is clear both in males (Colombo 1989; 1997) and in females (Colombo et al. 2001; 2004) all over the geographical gradient.

The correlation of fusion 3/6 frequency with body size-related variables was stunning (Colombo 1989; 1997), but it should be recognized that, superimposed on the fusion 3/6 effect, there was a within-karyotype latitudinal effect (Colombo 1997). It could be affirmed, with considerable care given the limited extent of the gradient (latitude 31°S to 34°S), that *L. argentina* showed a positive Bergmann's effect ($r = 0.9297$, $P = 0.0221$) (Fig. 1B). Besides, it can be said that the polymorphic chromosome rearrangement, in this case more clearly than in *T. pallidipennis*, would have an adaptive effect, at least with respect to body size-related characters.

Cornops aquaticum

In *C. aquaticum*, the chromosomal polymorphism consisted of 3 Robertsonian rearrangements that increased in their frequency southwards (Colombo 2008). The chromosomally studied area was small compared with the continental distribution of the species (latitude 23°N to 35°S) but not negligible at all. Thus, it extended from Corrientes (27°S) in northeastern Argentina to Tigre (34°S) in central-eastern Argentina. The Corrientes population was monomorphic without fusions; Santa Fe had 0.12 fusions per individual (fpi); in Rosario, this value remained small (0.11) and then it rose southwards (San Pedro: 1.25 fpi; Zarate: 3.07 fpi; Tigre: 5.14 fpi). The maximum possible (6 fpi, i.e., complete fixation) was never attained, at least in the studied populations. In an isolated sample, sent from Trinidad and Tobago (10°N), this population was also monomorphic without fusions; moreover, a study of *C. aquaticum* that aimed to establish its karyotype (Rocha et al. 2004) failed to detect the centric fusions in a population from São Lourenço da Mata, Pernambuco, Brazil (latitude 8°S), so at the moment

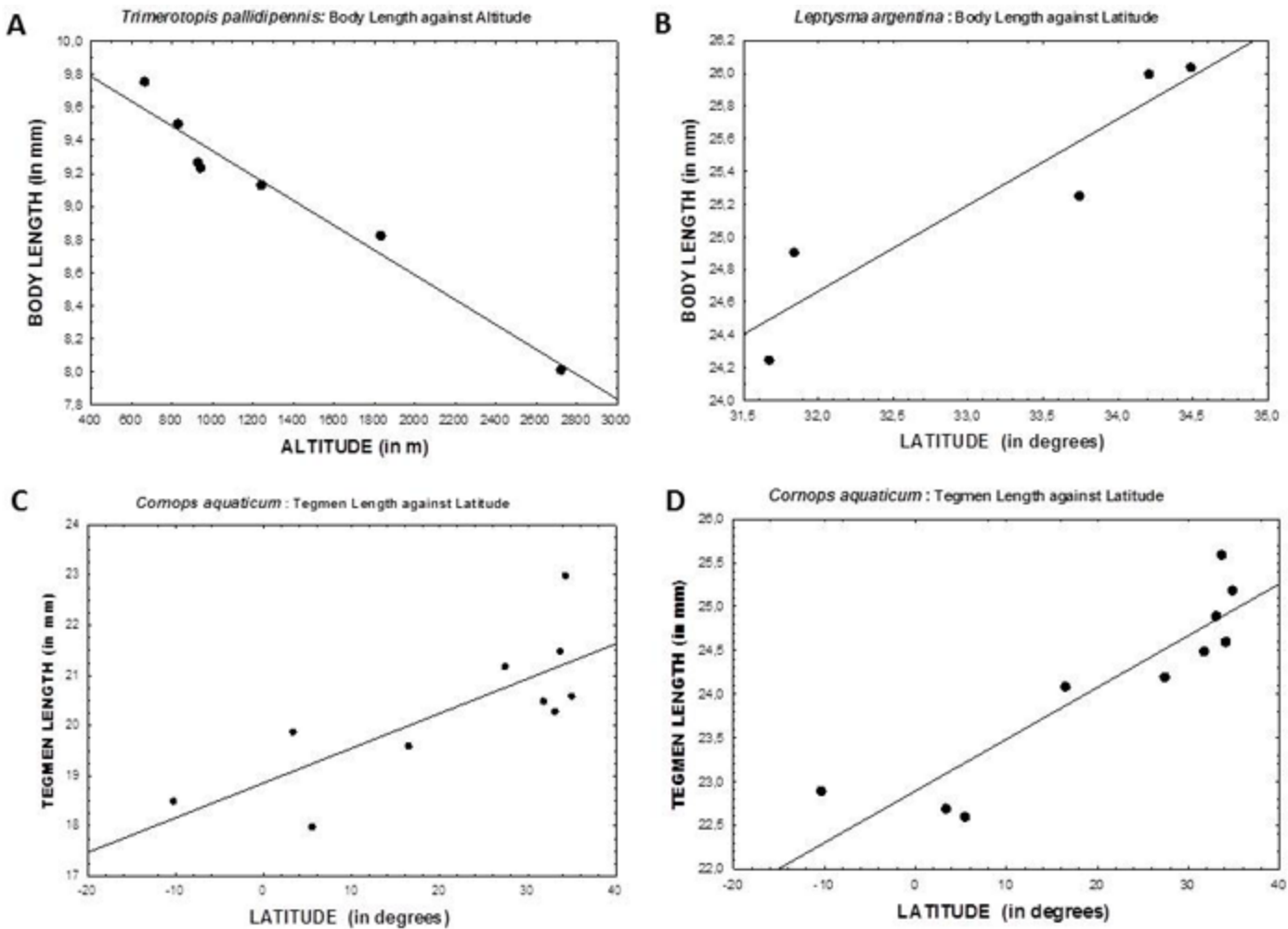


Fig. 1. A) *Trimerotropis pallidipennis*: Tegmen length (in mm) against altitude; B) *Leptysma argentina*: Total body length in mm against latitude; C) *Cornops aquaticum*: Tegmen length in mm against latitude in males; and D) *Cornops aquaticum*: Tegmen length in mm against latitude in females.

the only described chromosome rearrangements are those found in Argentina. Nevertheless, we know that these fusions were also present in Uruguay because there was a previous chromosome study mentioning them (Mesa 1956), and that was the first report ever of Robertsonian rearrangement polymorphisms in Orthoptera.

In Romero et al. (2014), we studied the relationship between morphometric variables and chromosomal constitution, and we found that body size–related variables positively correlated with the number of fused chromosomes from an intra-population point of view. Populations of *C. aquaticum* sited in the middle and lower course of the Paraná River were polymorphic for 3 centric fusions (1/6, 2/5, and 3/4). The relationship be-

tween the karyotype and the phenotype was analyzed in 2 populations (Zárate and San Pedro) where we found a representative number of individuals of each karyotypic class (Table 5). Males with fusion 1/6 were bigger than standard males. The Kruskal–Wallis analysis showed significant differences between the different numbers of fusion 1/6 for the tegmen length variable ($H = 7.280$, $P = 0.026^*$) (Table 5, as in Romero et al. 2014). Because fusion frequency is also correlated with latitude, southern populations would be expected to have a bigger size than northern ones.

With respect to a broader geographic point of view, we found no relationship between body size and geography in our own data, but we later merged them with those of the morphometric study by Adis

Table 1. Morphometric variables of *Trimerotropis pallidipennis* (mm) against altitude (m) from an altitudinal cline in the Andean province of Mendoza (central-western Argentina). SM = San Martín. ME = Mendoza. CH = Chacras de Coria. SC = San Carlos. CA = Cacheuta. US = Uspallata. PI = Puente del Inca. TL = Total length. FL = Femur length. TiL = Tibia length. TxL = Thorax length. TgL = Tegmen length. N = Number of individuals.

Population	N	Altitude	TL	FL	TiL	TxL	TgL	Inversion Frequency
SM	13	663	9.36	11.02	10.13	4.59	21.60	0.88
ME	11	827	9.50	10.63	9.70	4.67	20.33	1.00
CH	8	921	9.27	10.01	9.11	4.26	21.02	0.81
SC	16	940	9.24	10.06	9.03	4.14	20.93	0.44
CA	21	1,237	9.13	9.95	9.01	3.93	19.91	0.33
US	268	1,831	8.83	9.69	8.68	3.78	18.64	0.23
PI	14	2,729	8.02	8.99	7.88	3.42	16.83	0.00

Table 2. Tegmen length (TgL) (in mm) \pm standard error and *F*-statistic in an analysis of variance for the karyotypes of the 6M inversion in *Trimerotropis pallidipennis* from the population of Uspallata. *N* = number of individuals. A/A = standard acrocentric homozygote. M/A= inversion heterozygote. M/M = meta-centric inversion homozygote.

Karyotype	<i>N</i>	TgL	<i>F</i> -statistic	Wilk's lambda
6A/A	112	18.68 \pm 0.10		
6M/A	118	18.74 \pm 0.11	0.001**	0.030*
6MM	35	18.93 \pm 0.17		

et al. (2007) on a continental scale, going from Trinidad and Tobago (latitude 10°N) in the north to Montevideo (latitude 35°S) in the south. We had to limit the analysis to tegmen length, because it was the only variable that Adis et al. (2007) and we had measured in the same way. The results are shown in Table 6 and Figures 1C and 1D. It turns out that, at least for tegmen length, there is a clear positive Bergmann effect in both sexes ($r = 0.7790$, $P = 0.0079$ in males and $r = 0.9067$, $P = 0.0003$ in females). Hence, in this species the morphometric chromosome effects also are correlated with the geographic tendency.

COMMON PATTERNS AND DIFFERENCES

Previous reviews showed different species within a main group (e.g., Orthoptera) may exhibit various phenotypic variations with respect to latitude (Shelomi 2012). Moreover, in some species, such as *Dichroplus elongates* Giglio-Tos, contrasting patterns of body size variation with respect to latitude were observed generating Bergmann and converse Bergmann patterns along about 1,000 km (Rosetti & Remis 2013). With respect to Bergmann's rule, it is clear that *L. argentina* and *C. aquaticum* show a positive Bergmann effect, while *T. pallidipennis* follow a negative one. However, with respect to this rule, it is clear that its author devised it for endotherms, and that perhaps its extension to ectotherms produces these paradoxes. Perhaps the trends of ectotherms regarding latitude and/or altitude are governed by different needs, such as the length of breeding season (which would lead to a negative Bergmann effect) or the reduction in the number of genera-

Table 3. Mean total length (in mm) of male individuals of *Leptyisma argentina* \pm standard error against southern latitude (in degrees) from a latitudinal cline in central-eastern Argentina. SF = Santa Fe, EP = El Palmar, PT = Puerto Talavera, RL = Río Luján, P = Pilar. *N* = Number of males. Fusion 3/6 in each population (q) is also shown. UU = homozygous unfused males; UF = structural heterozygotes; FF = fusion homozygotes.

Population (q)	Karyotype	Total length	Latitude	<i>N</i>
SF (0.00)	UU	24.25 \pm 0.07	31.7	11
	UF	—	—	—
	FF	—	—	—
EP (0.40)	UU	24.50 \pm 0.06	31.9	76
	UF	25.02 \pm 0.05	31.9	111
	FF	25.36 \pm 0.11	31.9	41
PT (0.78)	UU	—	—	—
	UF	25.17 \pm 0.10	33.7	12
	FF	25.46 \pm 0.03	33.7	21
RL (0.89)	UU	—	—	—
	UF	26.07 \pm 0.04	34.2	9
	FF	25.99 \pm 0.02	34.2	42
P (1.00)	UU	—	—	—
	UF	—	—	—
	FF	26.04 \pm 0.07	34.5	13

Table 4. Mean body size (in mm) and analysis of variance (ANOVA) per fusion 3/6 karyotype in population El Palmar of *Leptyisma argentina* in years 1986–1988. Numbers of individuals are given in parentheses.

a) Frequencies Karyotype	Year of collection		
	1986	1987	1989
UU	24.88 \pm 0.07 (8)	24.33 \pm 0.13 (7)	25.72 \pm 0.10 (8)
UF	24.63 \pm 0.06 (16)	25.18 \pm 0.13 (7)	25.31 \pm 0.09 (12)
FF	25.50 \pm 0.14 (7)	26.20 \pm 0.52 (2)	26.27 \pm 0.23 (4)

b) ANOVA Source	df	SS	MS	VR	P
Between	8	8.3433	1.4287	2.118	0.200 NS
A-karyotype	2	5.8841	2.1151	14.017	0.015*
B-years	2	1.5230	2.6107	3.871	0.025*
A x B	4	0.9360	0.1509	0.224	0.92 NS
Within	68	49.7284	0.6745	—	—
Total	76	35.4725	—	—	—

tions in a year. Hence, we take the Bergmann's law in ectotherms with extreme care, treating each species as a special case.

As for chromosome polymorphisms and their morphometric effects, we noticed a common pattern in all 3 species studied: they were coherent with their geographical distribution (Colombo 1989; 2008; Colombo & Confalonieri 1996). In fact, in all cases the chromosome polymorphisms were associated with body size enlargement (the chromosome rearrangement in question was associated with enlarged body size—related variables in all 3 species). Effectively, in *C. aquaticum* and *L. argentina* the Robertsonian rearrangement(s) were more frequent in southern populations (Colombo 2014), and these 2 species follow a Bergmann's pattern. Conversely, in *T. pallidipennis* populations sited at lower altitudes tend to support larger individuals, where pericentric inversions are more frequent (Colombo 2014). Apparently, this may be an adaptive effect of chromosome polymorphisms, which probably support genes that cause increased body size in the appropriate environments. This would be another evidence of adaptive effects associated with chromosome polymorphisms, of which abundant evidence has been provided in the past (Colombo 1993; Colombo & Confalonieri 1996; Norry & Colombo 1999; Colombo et al. 2004; Romero et al 2014). Current molecular studies may shed more light on these patterns.

Table 5. Mean values (in cm) and standard errors (in parentheses) for tegmen length (TgL) in males of *Cornops aquaticum* sampled in San Pedro and Zárate and their karyotype composition. UU: Unfused homozygotes; UF: heterozygotes; FF: fused homozygotes. *N*: number of individuals sampled.

	San Pedro TgL	Zárate TgL
Fusion 2/5		Fusion 2/5
UU (<i>N</i> = 7)	2.184(0.155)	UU (<i>N</i> = 5) 2.256(0.172)
UF (<i>N</i> = 2)	2.140(0.084)	UF (<i>N</i> = 11) 2.304(0.119)
FF (<i>N</i> = 0)	—	FF (<i>N</i> = 7) 2.314(0.106)
Fusion 1/6		Fusion 1/6
UU (<i>N</i> = 5)	2.125(0.095)	UU (<i>N</i> = 3) 2.333(0.103)
UF (<i>N</i> = 3)	2.250(0.240)	UF (<i>N</i> = 15) 2.245(0.114)
FF (<i>N</i> = 1)	2.200(0.000)	FF (<i>N</i> = 5) 2.428(0.030)
Fusion 3/4		Fusion 3/4
UU (<i>N</i> = 5)	2.200(0.156)	UU (<i>N</i> = 5) 2.212(0.122)
UF (<i>N</i> = 4)	2.133(0.115)	UF (<i>N</i> = 14) 2.299(0.114)
FF (<i>N</i> = 0)	—	FF (<i>N</i> = 4) 2.395(0.104)

Table 6. Tegmen length ± standard error (in cm) in South American populations of *Cornops aquaticum* (Romero et al. 2014). Data marked with * come from Adis et al. (2007). *N* = Number of individuals. Southern latitude is given in degrees. Fusion 1/6 frequency is also given.

Population	Tegmen length		Latitude S	Fusion 1/6
	males (N)	females (N)		
Trinidad*	1.85 ± 0.019 (26)	2.29 ± 0.025 (23)	−10.40	0
Manaus*	1.99 ± 0.017 (20)	2.27 ± 0.028 (26)	3.23	NA
Belém*	1.80 ± 0.018 (40)	2.26 ± 0.020 (40)	5.43	NA
Pantanal*	1.96 ± 0.014 (31)	2.41 ± 0.039 (17)	16.40	NA
Laguna Pampín	2.221 ± 0.017 (43)	2.494 ± 0.042 (43)	27.17	0
Santa Fe	2.234 ± 0.024 (21)	2.577 ± 0.050 (7)	31.65	0.015
Rosario	2.027 ± 0.030 (14)	2.489 ± 0.044 (9)	32.95	0.026
San Pedro	2.146 ± 0.042 (7)	2.560 ± 0.050 (7)	33.65	0.25
Zárate	2.297 ± 0.023 (23)	2.460 ± (0.047)	34.10	0.524
Piriápolis *	2.08 ± 0.035 (11)	2.52 ± 0.100 (8)	34.83	NA

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