Dichroplus vittatus (Orthoptera: Acrididae) follows the converse to Bergmann's rule although male morphological variability increases with latitude

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Abstract

Geographic body size variation was analysed in males and females of 19 populations of the South American grasshopper *Dichroplus vittatus* Bruner spanning 20 degrees of latitude and 2700 m of altitude. Using mean and maximum body length of each sex and factors obtained from principal components analyses of six morphometric linear characters it was shown that *D. vittatus* followed the converse to Bergmann's rule latitudinally but not altitudinally where no significant trends were observed. For males, variability of body size increased with latitude but not with altitude. Both types of trends were significantly correlated with mean annual temperature and minimum annual temperature (positive correlations), and two estimators of seasonality, the coefficients of variation of mean annual temperature (negative) and mean annual precipitation (positive). Some allometric relationships also showed geographic variation. It is suggested that the observed decrease in size with latitude together with the increase in morphological variability is a consequence of a number of factors: the shortening of the growing season southwards; the increasing seasonality and climatic unpredictability; and the fact that the species exhibits protandry which contributes to smaller and more variable size in males and smaller but more constant body size in females.

Keywords: converse Bergmann's rule, *Dichroplus vittatus*, grasshopper, latitudinal gradient, precipitation, temperature

Introduction

Bergmann's rule (Bergmann, 1847) postulates that, for any given genus of homeothermic animals, large-sized species rather than small-sized species will occur in cooler climates. Although Bergmann (1847) considered thermoregulation as the main factor accounting for size clines (James, 1970; Blackburn *et al.*, 1999; Ashton *et al.*, 2000), this hypothesis was later reviewed by Rensch (1938, 1959) and Mayr (1956, 1963) with respect to empirical patterns, independently of ecophysiological interpretations and pertinent to intraspecific variation. James (1970) supported the intraspecific considerations although stressing the importance of climatic factors in determining size clines. Recently, Blackburn *et al.* (1999), reviewing the current principles of Bergmann's rule, readdressed the conceptual basis of interspecific variation. However, most of the presently available literature deals with intraspecific body size variation, and many different hypotheses from the original thermoregulation postulate have been put forward for

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explaining Bergmannian (and converse Bergmannian) body-size clines (Atkinson & Sibly, 1997; Ashton *et al.*, 2000; Ashton, 2001a,b; 2002a,b; Ashton & Feldman, 2003; Meiri & Dayan, 2003; Blanckenhorn & Demont, 2004).

Although Bergmann's rule was originally proposed for homeotherms, it was later shown that Bergmannian (and converse Bergmannian) clines could also be found among ectothermic organisms (Ray, 1960; Masaki, 1967, 1978; Honek, 1993; Atkinson, 1994; Mousseau, 1997; Angilletta & Dunham, 2003), either invertebrate (Arnett & Gotelli, 1999; Brisola Marcondes *et al.*, 1999; Byers, 2000; Huey *et al.*, 2000; Smith *et al.*, 2000; Trussell, 2000; Roy & Martien, 2001; Hausdorf, 2003; Heinze *et al.*, 2003; Johansson, 2003; Blanckenhorn & Demont, 2004; Peat *et al.*, 2005; Bidau & Martí, 2006) or vertebrate (Ashton, 2001a, 2002a; Belk & Houston, 2002; Ashton & Feldman, 2003; Laugen *et al.*, 2003, 2005; Litzgus *et al.*, 2004; Schäuble, 2004; Cruz *et al.*, 2005).

The presence of Bergmannian patterns in ectotherms requires a different explanation from the one accounting for their presence in endotherms. Furthermore, converse Bergmannian clines are much more frequent in ectotherms, mainly in insects (Brennan & Fairbairn, 1995; Mousseau, 1997; Fischer & Fiedler, 2002; Blanckenhorn & Demont, 2004; Bidau & Martí, 2006), than in endotherms (Ochocinska & Taylor, 2003; Medina *et al.*, 2006). Body size clines in insects probably result from climatic selection on duration of egg and nymphal development combined with different life cycle types (univoltine, bivoltine, multivoltine), which may result in a variety of body-size distribution patterns, including some actually converse to Bergmann's rule (Masaki, 1967; Roff, 1980; Blanckenhorn & Demont, 2004).

Species with widespread, latitudinal and/or altitudinal geographic ranges are useful models for analysing body size distribution at intraspecific levels, as is the case of some South American grasshopper species of the melanopline genus *Dichroplus* (Cigliano & Otte, 2003; Bidau & Martí, 2006).

In this paper, we analyse the geographic (latitudinal and altitudinal) distribution of body size in populations of *Dichroplus vittatus* Bruner (Orthoptera: Acrididae), a species belonging to the *Maculipennis* group of *Dichroplus* (Cigliano & Otte, 2003) with respect to climatic variables, to contribute to the understanding of acridoid body size clines in nature, which are largely unknown, especially in widely distributed Neotropical species and also, considering the extensive size and allometric variations occurring within this species and among *Dichroplus* species in general, to help resolve the systematics, ecological constraints and evolutionary dynamics of this genus.

Materials and methods

Adult male and female *D. vittatus* were collected at 19 Argentine localities spanning across 20° latitude, and at altitudes ranging from 36 to 2758 m above sea level during the summer months of 2001, except for a sample from Villa del Rosario which was collected during the summer of 1991 (fig. 1, table 1). Six morphometric external characters were measured in preserved specimens: (i) total body length (BL) (from the tip of the head to the distal end of the left third femur when aligned parallel to the longitudinal axis of the body following Martí (2002), for avoiding errors resulting from shrinking of the abdomen in dried specimens);

(ii) length of left hind femur (F3L); (iii) length of left hind tibia (T3L); (iv) length of tegmina (TeL); (v) mid-dorsal length of pronotum (PL); and (vi) height of pronotum (PH). The maximum total body length (MBL) for each sex (body length of the largest male and female in each sample) was also used as a dependent variable. The coefficient of variation of all characters was calculated as $CV = s*100/\bar{x}$. Measurements were taken with high precision calipers (0.01 mm).

Climatic data for all samples were obtained from Leemans & Cramer (1991) (table 2), and included: TMEA, mean annual temperature; TMAX, mean maximum monthly temperature; TMIN, mean minimum monthly temperature; PANN, total annual precipitation; PMAX, mean maximum monthly precipitation, and PMIN, mean minimum monthly precipitation. To estimate seasonality, the annual variability of climatic factors was calculated. Annual variability of temperature was estimated through the coefficient of variation of TMEA (CVT) and the difference between TMAX and TMIN (TM-m). Variability of precipitation was assessed by the CV of mean annual precipitation (CVP), and the difference between maximum and minimum monthly precipitation (PM-m). Actual evapotranspiration (AET), potential evapotranspiration (PET) and water balance (WB) were obtained for each locality. We used vectors, databases and maps for AET, PET and WB from Ahn & Tateishi (1994a,b) (table 2). Data analysis was performed with the Geomatica FreeView V. 10.0 software (PCI Geomatics, Ontario, Canada. www.pcigeomatics.com). All data are expressed in mm per year.

The normality of data was estimated through the Kolmogorov-Smirnov (with Liliefors correction) test. The Durbin-Watson statistic was employed for estimating serial autocorrelation. All measurements were log-transformed except for proportions between morphological measurements, for which the arcsine (angular) transformation was applied. Latitude (LAT) and longitude (LON) were converted to decimal units.

Principal components analysis (PCA) was employed for analysing the relationship between body size and geographic and climatic variables. Factors extracted in each analysis were rotated with the VARIMAX procedure with Kaiser normalization and used as dependent variables in correlation/regression tests.

Results

Geographic variation of body size in D. vittatus

As shown in table 1, body size varied widely between localities. The smallest and largest females showed body lengths of 17.30 mm (Playa Unión) and 29.59 mm (La Viña) respectively, while the smallest sampled male showed a body length of 14.40 mm (Playa Unión), contrary to the largest, with 22.02 mm (La Viña). This species shows a marked sex dimorphism in body size, with females being considerably larger than males across their geographic distribution (C.J. Bidau & D.A. Martí, unpublished). We studied the geographic variation of body size separately, in each sex, using BL and MBL as dependent variables against latitude or altitude in regression analyses. Initially, LAT was used as an independent variable because this parameter can be easily obtained and because of its likely correlation with several factors influencing body size clines (Blackburn *et al.*,
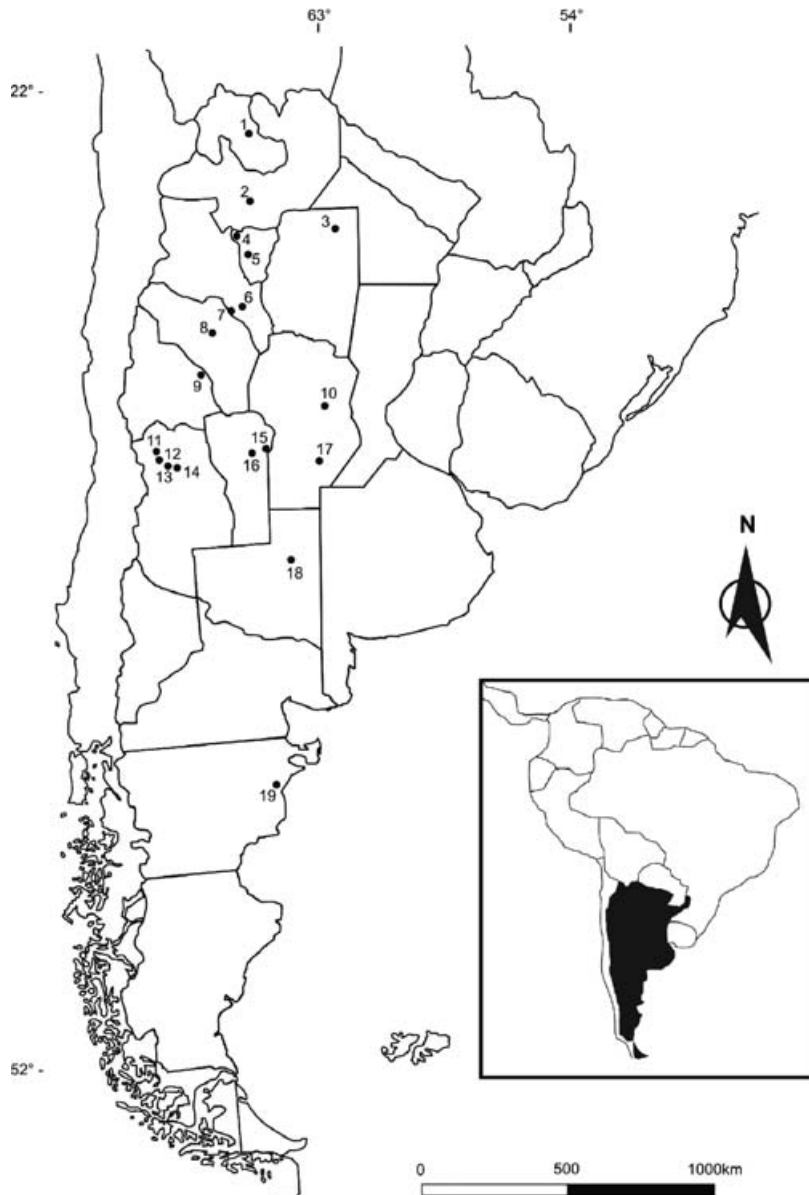
Fig. 1. Geographic distribution of the Argentine populations of *Dichroplus vittatus* analysed in this study.

1999). In all four analyses, body size significantly decreased with increasing latitude (fig. 2a,b; table 4). However, no statistically significant, altitudinal body size clines were observed despite that the population from Huacalera (the population of *D. vittatus* occurring at the highest known altitude, at 2758 m above sea level), showed some of the lowest means in body size. In fact, when this exceptional population was removed from analyses, latitudinal clines became more steep and statistically significant (MBL, r = −0.885, P = 0.000; MMBL, r = −0.835, P = 0.000; FBL, r = −0.841, P = 0.000; MFBL = −0.660, P = 0.003).

To test if general body size followed the same trend, factors extracted by principal components analyses (table 3) were regressed against LAT and ALT. As shown in table 4 and fig. 3a,b, statistically significant, negative correlations

between PCA factors and LAT (but not with ALT) were observed.

A further interesting finding indicated that variability of male body length, denoted by its coefficient of variation, showed a highly significant positive correlation with latitude, showing that male body size appeared to be more variable towards higher latitudes rather than to higher altitudes (table 4; fig. 3d). The CV of TeL and PH showed a comparable behaviour respective to latitude ($r^2 = 0.520$; a = −35.300; b = 1.497; P = 0.000, and $r^2 = 0.311$; a = −2.691; b = 0.263; P = 0.013), while similar positive but non-significant trends occurred for the other estimates. No significant correlations between the CVs of morphometric characters and latitude or altitude were observed for females.

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Table 1. Means and standard errors of six morphometric characters in 19 populations of *Dichroplus vittatus*.

Population	Lat (S)	Lon (W)	A				Characters										
						Males							Females					
				N	BL±SE	F3L±SE	T3L±SE	TeL±SE	PL±SE	PH±SE	N	BL±SE	F3L±SE	T3L±SE	TeL±SE	PL±SE	PH±SE
1. Huacalera	23°26′	65°21′	2758	25	17.30±0.14	9.61±0.10	7.95±0.08	5.98±0.13	3.73±0.04	2.75±0.03	18	21.66±0.31	12.37±0.11	10.39±0.12	7.73±0.19	5.33±0.08	3.76±0.06
2. La Viña	25°28′	65°35′	1265	2	21.62±0.28	11.86±0.35	9.87±0.23	7.68±0.02	4.69±0.29	3.41±0.08	11	28.13±0.31	15.55±0.18	13.47±0.22	10.99±0.58	6.67±0.20	4.92±0.21
3. S. del Estero	26°01′	62°22′	174	10	20.33±0.28	11.47±0.15	9.41±0.13	8.02±0.19	4.45±0.10	3.07±0.06	10	24.83±0.29	13.44±0.15	10.45±0.16	8.55±0.25	5.51±0.21	3.82±0.21
4. C. del Valle	26°22′	65°57′	1662	3	19.81±0.50	11.13±0.40	9.11±0.45	6.98±0.24	4.42±0.10	3.12±0.03	2	25.39±1.67	14.59±0.67	12.24±0.62	9.19±0.55	6.15±0.28	4.58±0.16
5. Tafí del Valle	26°52′	65°43′	2014	24	20.14±0.17	11.02±0.08	9.03±0.09	7.54±0.09	4.56±0.05	3.23±0.04	21	25.68±0.19	13.99±0.11	11.84±0.10	9.36±0.15	6.22±0.06	4.43±0.05
6. Miraflores	28°36′	65°41′	537	4	18.99±0.36	10.22±0.35	8.98±0.48	5.68±0.49	4.10±0.09	2.95±0.03	3	25.68±0.18	14.05±0.18	11.99±0.12	8.91±0.28	6.15±0.06	4.06±0.05
7. Chumbicha	28°52′	66°14′	376	10	19.95±0.29	10.33±0.15	8.56±0.12	6.80±0.20	4.11±0.11	3.05±0.05	5	23.74±0.62	13.09±0.25	11.35±0.28	8.28±0.58	5.68±0.40	4.15±0.13
8. La Rioja	29°05′	66°40′	521	4	20.27±0..19	10.86±0.05	9.04±0.08	7.30±0.25	4.29±0.07	3.13±0.04	9	27.38±0.25	14.60±0.33	12.38±0.26	10.29±0.26	6.32±0.06	4.56±0.06
9. Valle Fértil	30°38′	67°27′	828	14	18.55±0.23	10.15±0.16	8.26±0.13	6.08±0.14	3.93±0.05	2.87±0.04	4	24.68±0.29	13.56±0.14	11.20±0.09	8.14±0.29	5.76±0.09	3.92±0.10
10. V. Rosario	31°34′	63°32′	248	25	19.19±0.14	10.39±0.09	8.54±0.08	6.91±0.12	4.13±0.04	3.06±0.03	25	26.08±0.17	14.28±0.13	12.03±0.16	9.37±0.13	6.23±0.06	4.27±0.03
11. Guido	32°52′	69°15′	2099	8	19.47±0.29	10.46±0.14	8.52±0.11	6.56±0.18	4.13±0.09	2.98±0.04	10	23.48±0.25	12.77±0.28	10.27±0.25	7.07±0.25	5.39±0.07	3.94±0.07
12. Potrerillos	32°57′	69°11′	1469	2	17.87±0.55	9.93±0.17	7.97±0.36	5.94±0.41	3.90±0.07	3.02±0.10	5	22.84±0.67	12.24±0.39	10.29±0.31	6.83±0.39	5.42±0.23	3.77±0.16
13. Cacheuta	33°02′	69°07′	1310	3	18.57±0.47	9.93±0.24	8.27±0.15	6.78±0.12	4.02±0.08	2.89±0.03	5	21.73±0.71	11.56±0.38	9.65±0.31	6.63±0.43	5.25±0.25	3.72±0.19
14. Compuertas	33°03′	69°04′	1063	10	19.60±0.39	10.42±0.20	8.44±0.21	6.39±0.13	4.19±0.09	3.06±0.04	2	22.02±1.28	12.23±0.56	10.15±0.33	6.77±0.31	5.52±0.38	3.89±0.18
15. La Punilla	33°08′	65°29′	942	4	18.86±0.42	10.26±0.21	8.40±0.23	6.50±0.28	4.19±0.10	2.86±0.08	–	–	–	–	–	–	–
16. El Morro	33°13′	65°05′	993	6	18.37±0.39	10.13±0.11	8.29±0.16	7.16±0.24	4.09±0.11	2.89±0.08	4	23.21±0.49	13.25±0.29	10.82±0.25	8.14±0.50	5.53±0.13	3.87±0.12
17. Olmos	33°30′	63°10′	117	10	18.45±0.40	10.20±0.22	8.48±0.19	6.73±0.20	3.75±0.10	3.05±0.03	10	22.65±0.22	12.70±0.27	10.71±0.28	8.40±0.22	5.29±0.10	3.77±0.05
18. Toay	36°40′	64°21′	174	9	16.77±0.43	9.47±0.24	7.62±0.20	5.25±0.34	3.69±0.11	2.61±0.08	9	20.76±0.20	11.84±0.27	9.59±0.18	6.51±0.19	5.39±0.08	3.85±0.05
19. Playa Unión	43°04′	65°03′	36	17	16.43±0.23	9.11±0.16	7.64±0.13	5.58±0.57	2.80±0.06	3.62±0.06	16	20.26±0.42	11.31±0.20	9.56±0.16	6.21±0.18	4.81±0.09	3.38±0.08

Populations are those indicated in fig. 1. Lat (S): latitude; Lon (W): longitude; A: altitude (metres above seal level); N: number of individuals; BL: total body length; F3L: left femur 3 length; T3L: left tibia 3 length; TeL: tegmina length; PL: pronotum length; PH: pronotum height; SE: standard error of the mean.

Table 2. Temperature, precipitation, evapotranspiration and water balance parameters of 19 Argentine localities where samples of *Dichroplus vittatus* were obtained.

Population	TMEA	TMIN	TMAX	CVT	TM-m	PANN	PMIN	PMAX	CVP	PM-m	PET	AET	WB
1. Huacalera	14.59	8.50	18.90	26.85	10.40	390	0	101	120.4	101	455	1237	−1263
2. La Viña	17.13	10.60	22.00	24.56	11.40	506	2	135	111.72	133	435	1154	−1072
3. S. del Estero	21.62	15.30	27.40	20.46	12.10	704	8	117	77.07	109	678	985	−304
4. C. del Valle	14.55	7.70	20.00	31.56	12.30	444	2	118	110.65	116	435	1095	−1243
5. Tafi del Valle	12.07	5.20	17.70	38.45	12.50	725	6	148	88.39	142	661	965	−1271
6. Miraflores	19.28	10.80	26.50	29.60	15.70	325	3	70	93.51	67	571	946	−926
7. Chumbicha	19.09	10.40	26.60	30.80	16.20	326	2	66	91.17	64	386	940	−925
8. La Rioja	17.43	8.90	24.90	33.53	16.00	264	1	60	97.76	59	407	954	−936
9. Valle Fértil	17.80	9.30	26.00	34.31	16.70	181	0	41	98.76	41	305	975	−924
10. V. Rosario	17.96	11.00	24.90	27.99	13.90	742	14	109	63.73	95	749	821	−62
11. Guido	15.11	6.90	22.80	38.65	15.90	384	10	86	85.27	76	297	1007	−691
12. Potrerillos	15.11	6.90	22.80	38.65	15.90	225	9	30	35.02	21	297	1007	−691
13. Cacheuta	15.11	6.90	22.80	38.65	15.90	384	10	86	85.27	76	329	1105	−758
14. La Punilla	15.73	8.30	23.30	35.93	15.00	604	8	108	71.68	100	645	842	−179
15. El Morro	14.66	6.90	22.10	38.10	15.20	630	9	107	68.34	694	98	833	−123
16. Compuertas	16.50	7.90	24.50	36.96	16.60	384	9	99	92.94	90	329	1105	−758
17. Olmos	16.70	9.30	24.20	32.55	14.90	812	19	121	54.33	102	865	1046	−171
18. Toay	15.57	7.50	24.20	39.78	16.70	599	15	80	52.10	65	570	754	−106
19. Playa Unión	13.33	6.40	19.80	37.36	13.40	180	8	23	28.85	15	210	553	−354

All temperature parameters except CVT in °C; all precipitation parameters except CVP, in mm. AET, PET and WB in mm per year. See text for nomenclature of variables.

Geographic variation of allometric relationships

We analysed the variation of the relative size of F3, T3, Te and pronotum with respect to BL, as well as other relevant morphometric relationships (T3L/F3L, PH/PL, PL/TeL, and PH/TeL) in males and females, by means of linear regression. All regressions indicated a strong negative allometry except for female T3L/F3L, which showed a slope not significantly different from 1.

We tested whether these allometrically significant proportions also showed a geographic variation. Five proportions showed statistically significant or marginally significant latitudinal clines: MPH/BL (r = 0.432, P = 0.065), FTeL/BL (r = −0.637, P = 0.003), FPL/TeL (r = 0.633, P = 0.004), MPH/TeL (r = 0.405, P = 0.086), and FPH/TeL (r = 0.553, P = 0.014).

Correlations of body size with climatic factors

Body size clines were tested against climatic parameters and measurements of climate variability (tables 2, 4). We found significant positive correlations between body size estimators and temperature means (TMEA and TMIN), but a negative, significant correlation with CVT. It is worth mentioning that neither TMEA nor TMIN were significantly correlated with latitude (Spearman's rho = −0.348, P = 0.144, and Spearman's rho = −0.415, P = 0.077, respectively), a reason why temperature clines could not be attributed to colinearity between latitude and temperature. CVT was also non-significantly correlated with latitude (r = 0.413, P = 0.079). Regarding precipitation, we found a negative correlation between PMIN and several body size estimators, and a consistent, positive correlation between body size and CVP (table 4). In both cases, strong correlations between PMIN, CVP and latitude occurred (r = 0.699, P = 0.001, and r = −0.725, P = 0.000, respectively). No significant correlations were found between temperature and the above mentioned precipitation parameters. With PMIN, the respective r estimates were: PMIN/TMEA = −0.017,

PMIN/TMIN = −0.027 and PMIN/CVT = 0.232. With CVP, r estimates were: CVP/TMEA = −0.081, CVP/TMIN = −0.017 and CVP/CVT = −0.371.

The CV of male TBL was highly significantly correlated with both CVT (r^2 = 0.306; a = 0.067; b = 0.132; P = 0.014) and CVP (r^2 = 0.247; a = 6.766; b = −0.028; P = 0.031). Female CVs for the same characters appeared to be independent of these seasonality factors.

Regarding estimators of water balance, no consistent results were obtained despite the finding of some significant correlations with body size estimators (table 4). Both PET and WB were highly significantly correlated with latitude (r = −0.740, P = 0.000, and r = 0.642, P = 0.003, respectively), while AET was not (r = −0.199, P = 0.414).

Discussion

In ectothermic species of widespread latitudinal/altitudinal distribution, several geographic body size patterns have been found: Bergmannian, converse Bergmannian and combined (Chown & Gaston, 1999; Chown & Klok, 2003; Johansson, 2003; Bidau & Martí, 2006). Blanckenhorn & Demont (2004) listed 46 insect species belonging to 11 orders with 17 (37%) species following Bergmann's rule, and 29 (63%) with a converse pattern, suggesting that these two clinal patterns might be part of a continuum of adaptive responses to ambient temperature (following Bergmann's rule) or growth duration (converse Bergmann's rule). These different effects, as well as counter gradient variation might be jointly operating to produce a variety of clines, from typically Bergmannian to converse Bergmannian (Blanckenhorn & Demont, 2004).

Ectotherms grow slower at lower temperatures but reach larger adult sizes than their counterparts from more temperate climates (Ray, 1960; Atkinson, 1994; Atkinson & Sibly, 1997; Angilletta & Dunham, 2003), thus supporting Bergmann's rule. However, this might not necessarily apply to univoltine insects of widespread distribution like
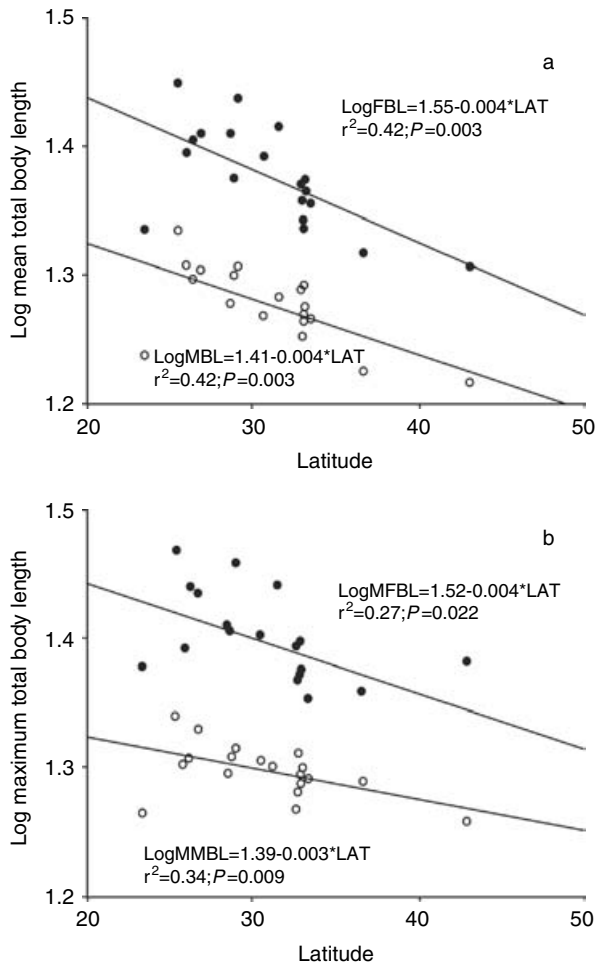
Fig. 2. Linear relationships between estimators of body size of female and male *Dichroplus vittatus*, and latitude. a. Log mean total body length vs. latitude. b. Log maximum body length vs. latitude. ●, females; ○, males.

Table 3. Principal components analysis of morphological data of populations of *Dichroplus vittatus* from Argentina.

Variable	Components	
	1	2
LOGFBL	0.829*	0.509*
LOGFF3L	0.882*	0.437
LOGFT3L	0.922*	0.348
LOGFTEL	0.845*	0.443
LOGFPL	0.905*	0.353
LOGFPH	0.818*	0.443
LOGMBL	0.482	0.841*
LOGMF3L	0.489	0.848*
LOGMT3L	0.559*	0.785*
LOGMTEL	0.220	0.901*
LOGMPL	0.469	0.826*
LOGMPH	0.461	0.783*
% VE	82.58	9.27

Two factors were extracted and rotated with the VARIMAX procedure with Kaiser normalization for 12 morphometric variables of males and females (see Materials and methods and table 2 for nomenclature of variables). Values correspond to correlation coefficients between variables and factors. Relatively high loadings ($|r| > 0.5$) are marked with an asterisk. %VE, % total variance explained.

The number of nymphal stadia is five in males and six in females, and the duration of the nymphal cycle varies negatively with temperature, from 51 or 53 days (means for males and females, respectively) at 23.8°C in the field at *c*. 26°S/65°W and 577 m altitude, to 33 or 36 days at 27° in laboratory conditions (Turk & Barrera, 1979).

Dichroplus vittatus exhibits the converse patterns to Bergmann's rule with respect to latitude because the body size of this species decreases with increasing latitude. This is similar to a sister species, *D. pratensis* Bruner, whose body size decreases both with increasing latitude and altitude (Bidau & Martí, 2006). However, the underlying mechanisms may not be the same for these different taxa.

In *D. vittatus*, significant positive correlations with temperature (TMEA and TMIN) were observed, and these two parameters were not correlated with latitude. Temperature *per se* may explain Bergmann's rule in ectotherms (Atkinson & Sibly, 1997; Blanckenhorn & Demont, 2004) but not its converse pattern except when temperature operates as an indirect selective factor on body size by limiting nymphal growth and development (Masaki, 1967). Converse patterns are often genetic and probably adaptive (Masaki, 1967, 1978; Roff, 1980; Blanckenhorn & Fairbairn, 1995; Blanckenhorn & Demont, 2004), and essentially depend on constraints imposed by season length on growth and development (Masaki, 1967; Roff, 1980; Blanckenhorn & Demont, 2004). In *D. vittatus* (and *D. pratensis*; Bidau & Martí, 2006), the converse Bergmannian pattern is probably a consequence of these constraints. However, it is not clear why an altitudinal consistent pattern (as in *D. pratensis*) was not found in *D. vittatus*. Other climatic factors like precipitation, may play a role in the latitudinal converse cline of *D. vittatus* (table 4). However, the most consistent correlations were observed between body size and seasonality estimates (table 4) although it must be borne in mind that, while CVP is colinear with latitude, CVT is not. Furthermore, when partial correlations controlling for

D. vittatus, for which duration of growing season might represent a powerful limiting factor (Masaki, 1967; Roff, 1980).

Dichroplus vittatus goes through an obligatory egg diapause, with only one generation per year, resulting in a 7-month arrest of embryogenesis at the end of anatrepsis, with eggs initiating diapause for several months. The number of months in diapause varies in different geographic regions (Campodónico, 1968; Turk & Barrera, 1979). Obligatory diapause and one generation per year represents the normal condition of *D. vittatus* natural populations (Cigliano & Otte, 2003). However, Turk & Barrera (1979) observed that, under certain laboratory conditions, some eggs, in a population captured at low latitude, hatched without undergoing diapause and produced a second generation, although hatching rate was low (10–15%). *Dichroplus vittatus* eggs also showed high tolerance to external conditions. Turk & Barrera (1979) obtained some hatchlings from eggs that had been kept under uncontrolled room conditions for 2 years after collection. These features may be related to the arid habitat and seasonal conditions to which this species is exposed.

Table 4. Correlation coefficients and their statistical significance between estimators of body size of *Dichroplus vittatus* and geographic and climatic variables.

	Independent variables															
	LAT	LON	ALT	TMEA	TMIN	TMAX	CVT	TMAX-MIN	PANN	PMIN	PMAX	CVP	PMAX-MIN	PET	AET	WB
F1MF	−0.529 0.020	−NS	+NS	+NS	0.485 0.035	+NS	−0.514 0.024	−NS	−NS	−0.519 0.023	+NS	0.537 0.018	+NS	+NS	+NS	+NS
F2MF	−0.456 0.050	+NS	+NS	+NS	+NS	+NS	−0.480 0.038	−NS	+NS	−NS	+NS	+NS	+NS	0.414 0.078	+NS	−NS
F1M	−0.652 0.002	−NS	+NS	0.507 0.027	0.612 0.005	+NS	−0.751 0.000	−NS	+NS	−NS	0.442 0.058	0.402 0.088	0.508 0.027	0.434 0.063	+NS	−NS
F1F	−0.675 0.002	−NS	+NS	0.539 0.017	0.663 0.002	+NS	−0.749 0.000	−NS	+NS	−0.527 0.020	+NS	0.562 0.012	0.468 0.043	+NS	+NS	−0.406 0.085
LogMBL	−0.644 0.003	+NS	+NS	0.524 0.021	0.578 0.010	+NS	−0.673 0.002	−NS	−NS	−0.420 0.073	+NS	0.579 0.010	+NS	0.461 0.047	+NS	−NS
LogFBL	−0.645 0.003	−NS	+NS	0.603 0.006	0.697 0.001	+NS	−0.750 0.000	−NS	+NS	−0.504 0.028	+NS	0.517 0.024	+NS	+NS	+NS	−NS
LogMMBL	−0.585 0.009	−NS	+NS	0.481 0.037	0.551 0.015	+NS	−0.600 0.007	−NS	+NS	−NS	0.453 0.051	0.528 0.020	0.518 0.023	+NS	+NS	−NS
LogMFBL	−0.522 0.022	−NS	+NS	0.452 0.052	0.536 0.018	+NS	−0.678 0.001	−NS	−NS	−0.603 0.006	+NS	0.518 0.023	+NS	−NS	+NS	−0.491 0.033
CVMBL	0.656 0.002	+NS	−NS	−NS	−0.464 0.046	−NS	0.593 0.007	0.434 0.063	+NS	0.472 0.041	−NS	−0.497 0.031	−NS	−NS	−0.511 0.025	0.436 0.062
CVFBL	+NS	+NS	+NS	−NS	−NS	−NS	+NS	+NS	−NS	−NS	−NS	−NS	−NS	−NS	+NS	−NS

In the case of the temperature parameters (except CVT), Spearman non-parametric correlation was performed (see Materials and methods). See text for nomenclature of variables.
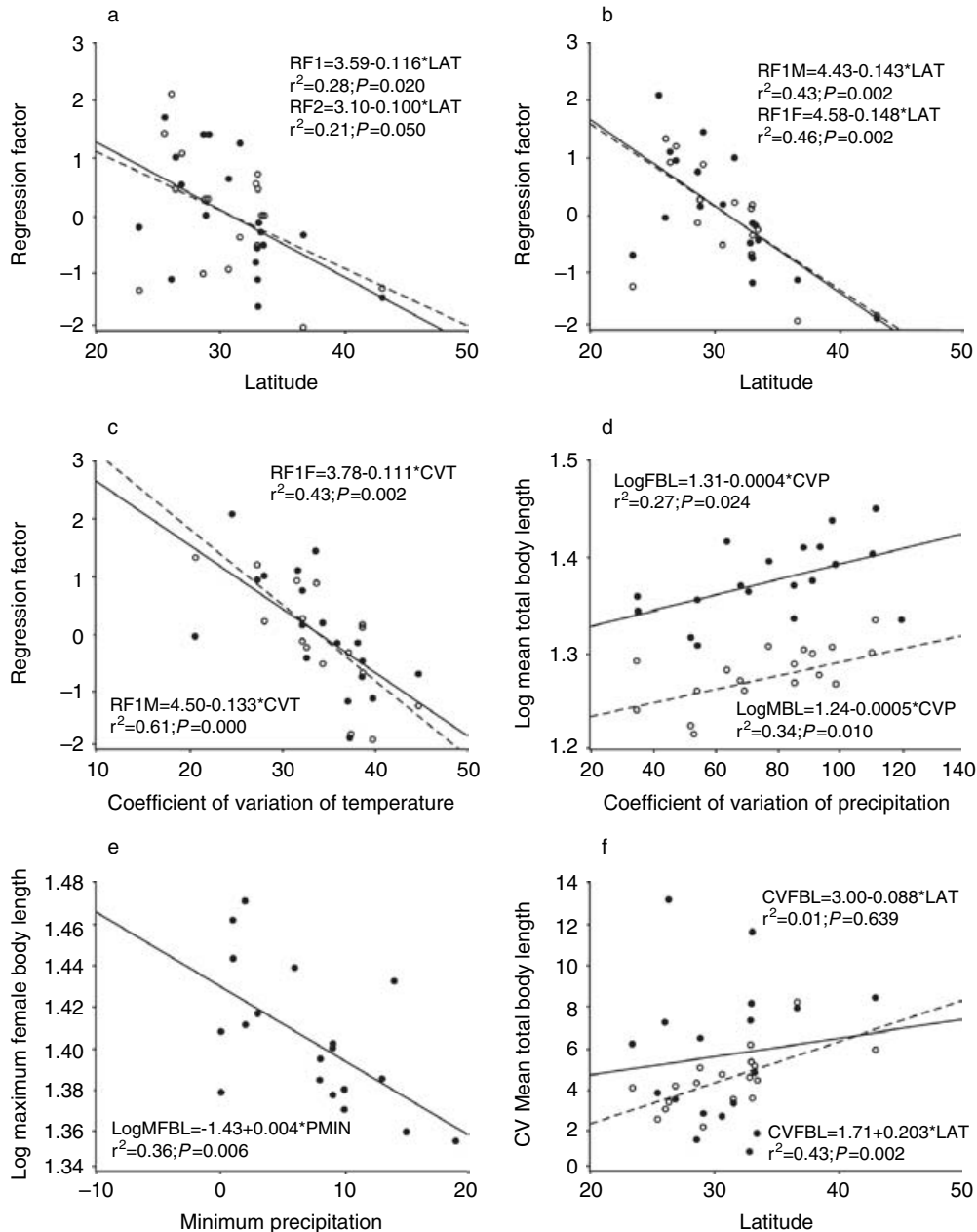
Fig. 3. Linear relationships between (a) the first (full line) and second (dashed line) principal components from the joint female-male PCA and latitude; (b) the first principal component of each individual PCA, and latitude (female: full line; male: dashed line); (c) the first principal component of each individual PCA (female: full line; male: dashed line), and the coefficient of variation of annual temperature; (d) female (●) and male (○) mean total body length, and the coefficient of variation of precipitation; (e) maximum female body length and minimum precipitation; (f) the coefficients of variation of female (●) and male (○) mean total body length and latitude.

latitude were performed between body size and CVT, their significance increased (e.g. MBL/CVT, $r = -0.630$, $P = 0.005$).

How can seasonality be related to body size geographic variation in *D. vittatus*? An important and seldomly assessed problem is how body size variability might be affected by latitude, altitude and related parameters. Male *D. vittatus* body length variability increases with latitude while mean and maximum TBL decrease. In the closely related

D. pratensis, a similar pattern occurs (Bidau & Martí, 2006). In the latter case, our proposed hypothesis postulates that smaller individuals occur in marginal habitats where genetic recombination indices are higher due to low chromosome polymorphisms and high chiasma frequencies (Bidau & Martí, 2002). Thus a higher genetic variability would be available for explaining the higher variation of body size dimensions despite an absolute decrease of body size (Bidau & Marti, 2005).

This hypothesis is not applicable to *D. vittatus* in which the frequency of recombination is uniformly low across the range (Bidau & Marti, 2000). However, the increasing body size, latitudinal variability may be related to the converse Bergmannian pattern if two factors were taken into account: seasonality and sexual size dimorphism.

Seasonality is a powerful determinant of body size variation (Chown & Gaston, 1999; Chown & Klok, 2003). At higher latitudes and altitudes, ambient temperatures are likely to be lower, reducing the duration of insect growing season (Masaki, 1967). As seasonality tends to increase at higher latitudes and altitudes (Chown & Gaston, 1999; Körner, 2000; Chown & Klok, 2003), the availability of resources is affected, constraining growth and development to a degree depending on length of generation time relative to length of season (Chown & Klok, 2003). With constant generation time across the geographic range of *D. vittatus*, resource limitations to development and growth will increase towards latitudes, with more seasonal climates producing smaller body sizes. This interpretation is supported by the plasticity in development observed under different laboratory conditions described above. The lack of altitudinal clines in this species is probably a consequence of the lack of correlation between altitude and seasonality within the study area.

Furthermore, *D. vittatus* is female-biased, size-dimorphic, although sexual size dimorphism varies across the geographic range following Rensch's rule (C.J. Bidau & D.A. Martí, unpublished). Part of this sexual size dimorphism occurs due to protandry (Morbey & Ydenberg, 2001) because males emerge and mature before females, a strategy for early access to females during the breeding season (Andersson, 1994; Morbey & Ydenberg, 2001; C.J. Bidau & D.A. Martí, 2006, unpublished). This leaves males with less time to grow than females in all parts of the range, although this constraint is more stringent at higher than at lower latitudes, contributing to the smaller size of males towards the South. Laboratory experiments have shown sex differences in the time of development in different controlled conditions (Turk & Barrera, 1979). Natural variability for development and maturing time also occurs among males, while females tend to be more homogeneous (Turk & Barrera, 1979; Cigliano & Otte, 2003; Bidau & Martí, 2006). Furthermore, with increasing latitude, populations occupy increasingly marginal, more seasonal, heterogeneous, changing and unpredictable habitats that simultaneously account for the latitudinal decrease in male body size and increase in body size variability. In low latitudes and less seasonal habitats, although protandry also occurs, the longer growing season and a greater availability of resources might have an homogenizing effect on body size, reducing variability among males although producing larger individuals of both sexes.

Several body dimensions also showed significant latitudinal clines, mainly involving the modification of pronotum morphology and a relative decrease of tegmina length. Since these insects are brachypterous and flightless, the significance of these variations are obscure.

Thus, converse Bergmannian clines may in principle result from climatic selection on the duration of the nymphal stage which indirectly brings about larger adult sizes at lower latitudes (Masaki, 1967, 1978; Roff, 1980; Blanckenhorn & Demont, 2004). We thus conclude that the converse Bergmannian clines of *D. vittatus* and the increase of body size variability in males result from a combination of a shorter growing season, increasing seasonality limiting available resources, and sexual size dimorphism resulting, partially, from protandry.

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