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Geographic and climatic factors related to a body-size cline in *Dichroplus pratensis* Bruner, 1900 (Acrididae, Melanoplinae)*

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*This paper is for Rocío Hassan and Lili Castagno, our dear wives. Without them our work would have been impossible.

Abstract

We studied geographic body-size variation in males and females of 25 populations of the South American melanopline grasshopper *Dichroplus pratensis* Bruner, 1900, along more than 22 degrees of latitude (S) and between 0 and almost 2500 m of altitude. Using mean body length of each sex and factors obtained from PCA analyses of six morphometric linear characters, it was shown that *D. pratensis* follows the converse to Bergmann's rule, becoming smaller at higher latitudes and altitudes. Variability of body size increased with latitude and altitude in males and females. Body-size trends were statistically significantly correlated with ambient temperature (annual mean, minimum and maximum), precipitation (annual mean, minimum and maximum), and two estimators of seasonality, the difference between the maximum and minimum temperatures, and the difference between maximum and minimum precipitation for each locality; both nonparametric correlations were positive. Body size was also positively and significantly correlated with Actual Evapotranspiration (AET), a measure of primary productivity, and with Potential Evapotranspiration (PET), a measure of ambient energy, but not with water balance (WB). Some allometric relationships also showed geographic variation. We suggest that the observed decrease in size with latitude and the increase in morphological variability, are joint consequences of the shortening of the growing season towards the south, the increasing seasonality and climatic unpredictability, lower primary productivity (as represented by AET); and that the species exhibits protandry, which contributes in the south, to smaller and more variably sized males, and smaller but more constant body size in females.

Key words

body size, converse Bergmann's rule, *Dichroplus pratensis*, evapotranspiration, grasshopper, latitudinal gradient, precipitation, temperature

Introduction

In its classical sense, Bergmann's rule (Bergmann 1847) proposed that homeothermic animals display size clines; species within a genus are larger in cooler climates and smaller in warmer climates because of selection on the ability to thermoregulate (Bergmann 1847, James 1970, Blackburn *et al.* 1999, Ashton *et al.* 2000). Rensch (1938, 1959) and Mayr (1956, 1963) reformulated this ecogeographical rule for an empirical pattern independent of ecophysiological interpretations and applicable to intraspecific variation, and James (1970) stressed the importance of climatic factors in determining size clines. Most of the available literature deals with intraspecific body-size variation and many different hypotheses other than the original thermoregulation explanation, have been proposed to explain Bergmannian (and converse Bergmannian) body-size clines (Atkinson & Sibly 1997; Ashton *et al.* 2000; Ashton 2001, 2002a,b; Ashton & Feldman 2003; Meiri & Dayan 2003; Blanckenhorn & Demont 2004).

Although Bergmann's rule was originally proposed for homeotherms, Bergmannian (and converse Bergmannian) clines occur in invertebrate and vertebrate ectotherms (Ray 1960; Masaki 1967, 1978; Honek 1993; Atkinson 1994; Mousseau 1997; Arnett & Gotelli 1999; Brisola Marcondes *et al.* 1999; Byers 2000; Huey *et al.* 2000; Smith *et al.* 2000; Trussell 2000; Roy & Martien 2001; Ashton 2001, 2002a; Belk & Houston 2002, Angilletta & Dunham 2003, Ashton & Feldman 2003; Heinze *et al.* 2003; Johansson 2003; Laugen *et al.* 2003, 2005; Blanckenhorn & Demont 2004; Hausdorf 2003; Litzgus *et al.* 2004; Schäuble 2004; Bidau & Martí 2007b; Peat *et al.* 2005; Cruz *et al.* 2005).

Converse Bergmannian clines are much more frequent in ectotherms than in endotherms, especially in insects (Brennan & Fairbairn 1995, Mousseau 1997, Fischer & Fiedler 2002, Blanckenhorn & Demont 2004, Bidau & Martí 2007b). Body sizes in insects probably respond to different ecophysiological factors and evolutionary pressures than those in endotherms. Several authors have proposed that size clines result from climatic selection on the duration of egg and nymphal development, which indirectly affects body size and can produce different geographic patterns according to the nature of the life cycle (Masaki 1967, 1978; Roff 1980; Blanckenhorn & Demont 2004).

Species with ample latitudinal and/or altitudinal geographic ranges are useful models for the analysis of body-size distribution at the intraspecific level, as is the case for a number of South American grasshopper species of the melanopline genus *Dichroplus* (Cigliano & Otte 2003, Bidau & Martí 2007a,b). Large distributions expose species to very different climatic conditions. Thus factors such as temperature and rainfall (Masaki 1967, 1978; Bidau & Martí 2007a,b), but also seasonality (Murphy 1985, Chown & Klok 2003), evapotranspiration (Rosenzweig 1968), primary productivity (Ashton *et al.* 2000), predation and competition pressure (Medina *et al.* 2007), *etc.*, may combine to produce different kinds of size clines.

We studied the geographic distribution of body size in natural populations of *Dichroplus pratensis* Bruner, 1900 (Figs 2, 3; Plate IV), which has a very large latitudinal, longitudinal and altitudinal distribution in Argentina (Cigliano & Otte 2003, Bidau & Martí 2007a,b), and is thus an excellent model for the analysis of body-size distribution at the intraspecific level. We relate body-size clines to climatic variables in order to understand acridoid body-size distribution in nature, and the relationship of these variables to development and sexual size dimorphism, which, until recently, were largely unknown for Neotropical species.

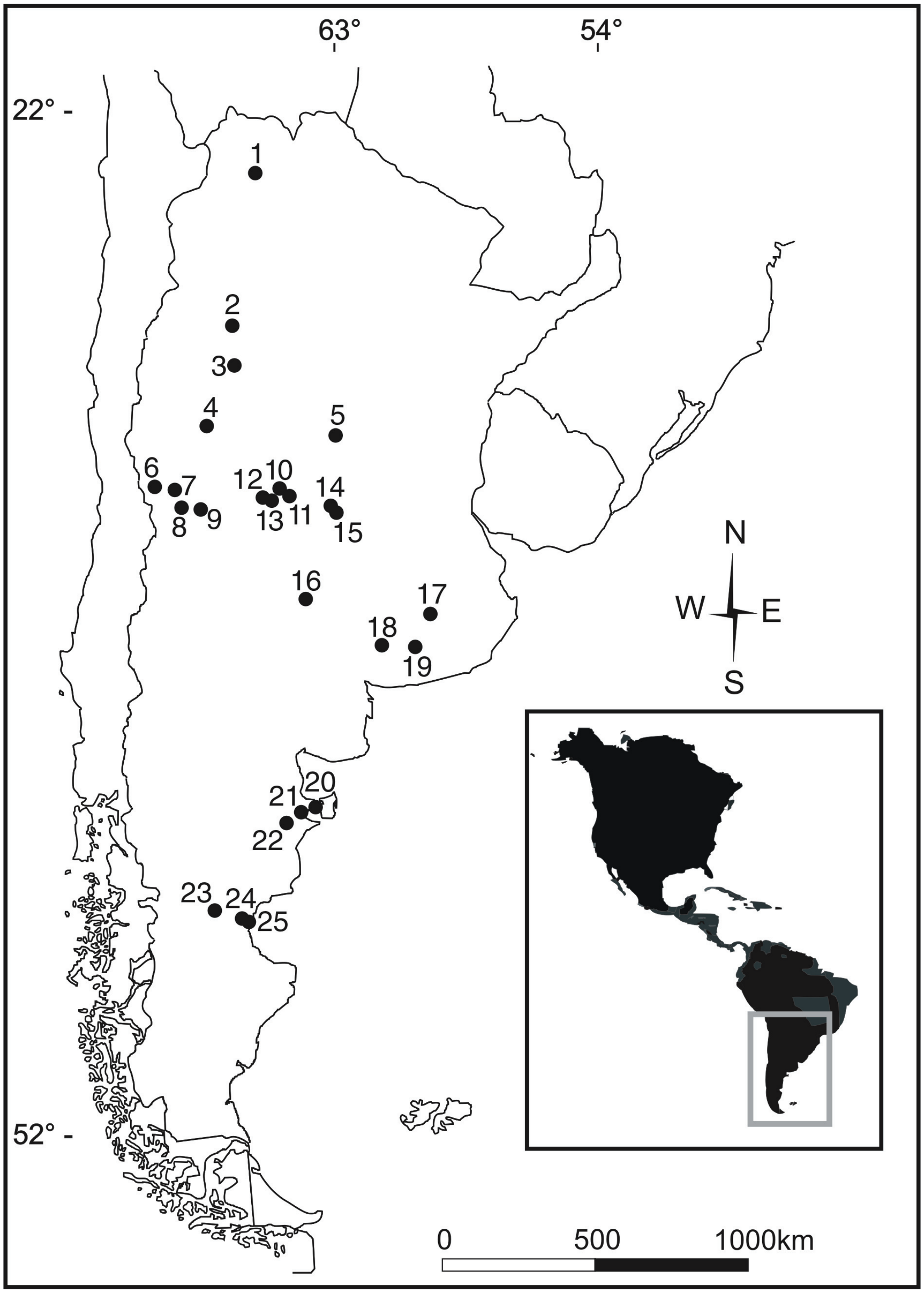

Fig. 1. Geographic distribution of 25 Argentine populations of *D. pratensis* analysed in this study.

Materials and methods

D. pratensis is a species belonging to the *maculipennis* group of *Dichroplus* grasshoppers (Cigliano & Otte 2003). It is univoltine, shows obligatory egg diapause (Turk & Barrera 1979), and is a nonselective polyphagous feeder (Cigliano & Otte 2003, Bidau & Martí 2006). We studied 621 adult specimens (343 males and 278 females) from 25 Argentine localities, spanning from lat 23.92° S to lat 45.95° S, and 0 to 2474 m above sea level (Fig. 1, Table 1). Six morphometric external characters were measured in dried specimens: a) total body length (BL) (Table 1; in order to avoid error resulting from the shrinking of the abdomen in dried specimens, this measurement was taken from the tip of the head to the distal end of the left hind femur when aligned parallel to the longitudinal axis of the body, as in Martí 2002), b) length of left hind femur (F3L), c) length of left hind tibia (T3L), d) length of tegmina (TeL), e) mid-dorsal length of pronotum (PL) and f) height of pronotum (PH). Coefficients of variation for all characters were calculated as CV= $s \times 100/\bar{x}$ (Zar 1999). All size measurements were made in mm, using high-precision calipers (0.01 mm).

Climatic data for all samples were obtained from Leemans & Cramer (1991) (Table 1), and included: TMEA, Mean Annual Temperature; TMAX, Mean Maximum Monthly Temperature; TMIN, Mean Minimum Monthly Temperature (all in °C); PANN, Total An-

Table 1. Geographic coordinates, altitude, climatic parameters and mean adult body length of *D. pratensis* males and females from 25 Argentine localities. LAT: latitiude; LON: longitude; ALT: altitude. See Materials and Methods for other variable abbreviations and units.

Independent variables																		
	Geographic variables			Climatic variables													Body length	
Locality	LAT	LON	ALT	TMEA	TMIN	TMAX	CVT	TM-m	PANN	PMIN	PMAX	CVP	PM-m	AET	PET	WB	MBL	FBL
1. Volcán	23.92	65.45	2474	12.3	6.2	16.6	31.85	10.4	566	0	138	110.4	138	661	1218	-1263	22.4	24.3
2. E. Mazán	28.73	66.48	646	16.5	8.1	23.7	34.8	15.6	246	0	63	104.7	63	339	948	-925	23.8	26.5
3. Carrizal	28.90	67.55	522	13.3	6.1	20.2	38.7	14.1	164	0	44	110.6	44	293	1013	-960	24.0	28.2
4. Las Juntas	30.68	67.58	203	17.8	9.3	26.0	34.3	16.7	181	0	41	98.8	41	221	949	-926	21.8	25.7
5. C. Machado	31.46	63.58	314	18.0	11.0	24.9	28.0	13.9	742	14	109	63.7	95	794	821	-56	25.6	27.7
6. Guido	32.86	69.25	2099	15.1	6.9	22.8	38.7	15.9	384	10	86	85.3	76	297	1007	-691	25.1	26.9
7. Potrerillos	32.93	69.18	1469	15.1	6.9	22.8	38.7	15.9	225	9	30	35.0	21	297	1007	-691	23.8	23.8
8. Cacheuta	33.03	69.12	1310	15.1	6.9	22.8	38.7	15.9	225	9	30	35.0	21	329	1105	-758	23.5	24.9
9. Compuertas	33.05	69.07	1063	15.1	6.9	22.8	38.7	15.9	225	9	30	35.0	21	329	1105	-758	26.4	27.2
10. La Punilla	33.13	65.08	942	14.7	6.9	22.1	38.1	15.2	630	9	107	68.3	98	694	833	-123	24.2	25.8
11. Achiras	33.15	65.00	838	14.7	6.9	22.1	38.1	15.2	630	9	107	68.3	98	694	833	-123	23.8	26.7
12. Saladillo	33.21	65.87	840	14.6	6.7	22.1	38.9	15.4	604	8	108	71.7	100	595	829	-179	25.0	25.7
13. El Morro	33.22	65.48	993	15.7	7.9	23.3	35.9	15.4	604	8	108	71.7	100	645	842	-179	24.7	24.5
14. La Granja	33.50	63.28	125	16.8	9.2	24.4	33.1	15.2	774	16	111	56.8	95	856	1043	-171	26.0	26.8
15. Manantiales	33.53	63.33	134	16.8	9.2	24.4	33.1	15.2	774	16	111	56.8	95	856	1043	-171	26.1	26.9
16. Don Tomás	36.68	64.33	175	15.6	7.5	24.2	39.8	16.7	599	15	80	52.1	65	570	754	-106	24.2	25.4
17. Olavarría	36.92	60.12	162	14.0	7.2	21.8	38.2	14.6	831	38	115	29.2	77	793	892	-88	22.6	24.3
18. C. Pringles	37.97	61.37	251	14.0	7.0	22.1	39.4	15.1	683	22	98	36.6	76	695	882	-52	23.4	25.3
19. C. Ceferino	38.10	61.80	456	13.8	6.6	21.9	41.0	15.3	643	19	91	38.7	72	617	894	-125	23.3	25.2
20. I.Ameghino	42.50	64.53	55	13.2	6.6	19.4	35.9	12.8	204	9	27	36.4	18	226	567	-344	22.2	24.1
21. P .Madryn	42.81	65.05	18	13.3	6.4	19.8	37.4	13.4	180	8	23	28.9	15	200	567	-373	22.6	25.2
22. Km 1430	43.06	65.20	36	13.1	6.4	9.4	36.8	13.0	180	8	23	28.9	15	210	553	-354	22.5	22.7
23. L. Musters	45.50	69.13	261	10.3	3.5	16.6	48.6	13.1	110	5	18	47.2	13	203	477	-289	19.5	23.5
24. D.Argentina	45.78	67.67	326	11.1	5.1	17.1	41.1	12.0	181	0	41	98.8	41	216	468	-210	19.3	22.2
25. V.Rada Tilly	45.95	67.53	0	10.7	4.9	16.4	40.3	11.5	144	5	26	50.3	21	216	468	-210	18.9	23.2

nual Precipitation; PMAX, Mean Maximum Monthly Precipitation, and PMIN, Mean Minimum Monthly Precipitation (all in mm). Seasonality was estimated as the coefficients of variation of TMEA (CVT), the difference between TMAX and TMIN (TM-m), the CV of mean annual precipitation (CVP), and the difference between maximum and minimum monthly precipitation (PM-m). Actual Evapotranspiration (AET, an estimator of primary productivity), Potential Evapotranspiration (PET, a measure of ambient energy) and Water Balance (WB), were obtained for each locality (Table 1). We used vectors, databases and maps for AET, PET and WB from Ahn & Tateishi (1994a,b) (Table 2). Data analysis was performed with Geomatica FreeView V. 10.0 software by PCI Geomatics, Ontario, Canada. www.pcigeomatics.com.

Normality of data was estimated through the Kolmogorov-Smirnov test (Zar 1984). All measurements were log-transformed, except for proportions to which the *arsin* (angular) transformation (Steel & Torrie 1980) was applied. Latitude (LAT) and longitude (LON) were converted to decimal units. Principal Components Analysis (PCA) was employed to analyze the relationship between body size and the geographic and climatic variables considered. Factors extracted in each analysis were rotated with the VARIMAX procedure with Kaiser Normalization and used as dependent variables in correlation/regression tests.

Table 2. Principal Components Analysis of morphological data of populations of *D. pratensis* from Argentina. Three factors were extracted and rotated with the VARIMAX procedure with Kaiser Normalization for 12 morphometric variables of males and females (see Materials and Methods for explanation 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.

	Principal Component		
	1	2	3
LOGBLM	0.887*	0.353	0.253
LOGF3M	0.833*	0.285	0.445
LOGT3M	0.792*	0.224	0.486
LOGTEM	0.664*	-0.004	0.727*
LOGPLM	0.894*	0.377	0.197
LOGPHM	0.828*	0.433	0.007
LOGBLF	0.465	0.828*	0.189
LOGF3F	0.254	0.866*	0.388
LOGT3F	0.020	0.855*	0.444
LOGTEF	0.233	0.236	0.924*
LOGPLF	0.445	0.838*	-0.010
LOGPHF	0.492	0.795*	-0.242
%VE	68.78	15.29	10.18

Table 3. Results of multiple regression (stepwise backward) of five estimators of body size *vs* latitude, longitude, and altitude in 25 Argentine populations of *D. pratensis*. r^2: coefficient of determination; F(df): F-statistic (degrees of freedom); p: probability; Coefficients: regression coefficients; t: Student´s t-statistic; Partial correlations: partial correlation coefficients from the multiple regression analyses; MBL, FBL: mean male and female body lengths; PC1, PC2, PC3: the first three Principal Components of the PCA shown in Table 2.

	Multiple regression							
Dependent variable	r^2	F (df)	p	Predictors	Coefficients	t	p	Partial correlations
LogMBL	0.51	11.50 (2,22)	<0.001	(constant)	1.599	30.19	<0.001	
				LAT	$-6.07*10^{-3}$	-4.58	<0.001	-0.70
				ALT	$-2.30*10^{-5}$	-1.97	0.062	-0.39
LogFBL	0.58	15.30 (2,22)	<0.001	(constant)	1.587	44.82	<0.001	
				LAT	$-4.79*10^{-3}$	-5.41	<0.001	-0.76
				ALT	$-2.16*10^{-5}$	-2.76	0.011	-0.51
PC1	0.36	12.69 (1,23)	0.002	(constant)	3.659	3.52	0.002	
				LAT	-0.103	-3.56	0.002	-0. 60
PC2	0.54	9.41 (1,23)	0.005	(constant)	3.307	3.03	0.006	
				LAT	-0.093	-3.07	0.005	-0.54
PC3	0.36	12.76 (1,23)	0.002	(constant)	0.606	2. 60	0.017	
				ALT	$-9.07*10^{-4}$	-3.57	0.002	-0.60

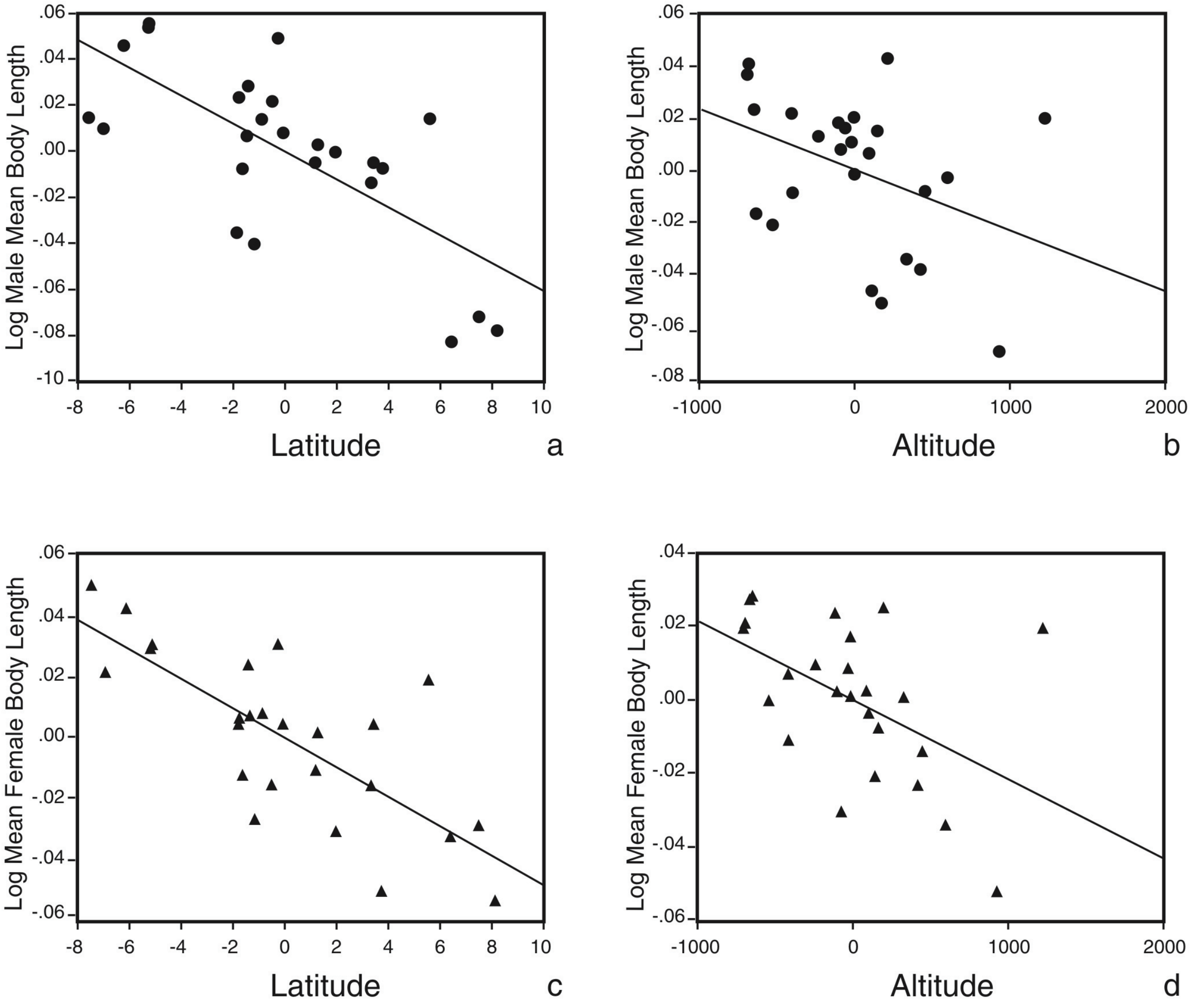

Fig. 2. Partial regression plots of male and female body length (mm) as a function of latitude (a, c) and altitude (b, d), in *D. pratensis*. X-axis scales resulted from the transformation of actual latitude and altitude values shown in Table 1.

Results

Geographic variation of body size in D. pratensis.—Multiple stepwise backward regression analyses of mean body length of males and females, and the first three regression factors obtained by PCA (Table 2) against LAT, LON and ALT, showed that in both sexes BL decreases with increasing latitude and less significantly so with altitude (Table 3, Fig. 2). When the dependent variable was one of the principal components, LAT was the main predictor of body size for PC1 and PC2, while ALT was this for PC3 (Table 3). PC3 is basically a 'tegmina length component' (Table 2) thus, length of tegmina appears to be the main character underlying the altitudinal cline in *D. pratensis* (see below).

Correlations of body size with climatic factors.—Latitude or altitude *per se* have no explanatory power on the origin of size clines (Hawkins & Diniz Filho 2004); thus, geographic body size variation in *D. pratensis* was analyzed in relation to climatic parameters and estimators of climate variability (Table 4). Three estimators of body size (MBL, FBL and PC1) showed statistically significant positive correlations with temperature parameters and with TM-m (Table 4). However, all temperature parameters are colinear with latitude, and TM-m is significantly correlated with altitude (Table 5).

Except for PC2, all body-size estimators were positively correlated with annual precipitation, and some, with PMIN and PMAX (Table 4). The former three precipitation variables are not correlated with latitude or with altitude in the studied area (Table 5). Only PC2 was correlated with CVP, while male and female body size were significantly positively correlated with PM-m. Both measures of precipitation variability are negatively correlated with LAT, while CVP is also positively correlated with ALT. Both PET and AET were good predictors of body size in *D. pratensis* (Table 4). Of these, only AET is not correlated either with latitude or altitude in our sampling area (Table 5).

Geographic variation of allometric relationships—As the results from the correlation analyses between factors obtained by PCA and geographic variables showed, it appeared that not all the analyzed morphometric characters followed the same geographic trends as total body length. Since this could be a result of varying allometric relationships, we analyzed first the nature of allometries in *D. pratensis* and second, the relationships of these allometries with geographic parameters. Table 6a shows the slopes of linear regression lines between the means of five morphometric characters and body length in both sexes of *D. pratensis*. F3L and T3L exhibit negative allometry in both sexes, being more evident in females (Table 6a). Individually, these variables showed negative nonsignificant latitudinal clines, except for female F3L (r= -0.403, p= 0.046). Tegmina length was basically isometric with body length in males, but strongly negatively allometric in females (Table 6a). In males, TeL was negatively, but nonsignificantly correlated with either LAT or ALT; in females, positive (LAT) and negative (ALT) correlations were observed, although none of them were statistically significant. Pronotum measurements were positively allometric in males but basically isometric in females (Table 6a). Furthermore, PL and PH showed negative latitudinal clines in males and females.

We tested the proportions between F3L, T3L, TeL, PL and PH (both sexes) and BL, *vs* LAT, LON and ALT. As shown in Table 6b, males and females show comparable geographic trends. However, the proportions of F3L, T3L and TeL increase with LAT and decrease with ALT, while the opposite occurs with both pronotum measurements (Table 6b).

Discussion

The existence of intraspecific converse Bergmannian clines in insects has been cited for a number of different taxa, although few studies deal with Orthoptera (Blanckenhorn & Demont 2004). In

Table 4. Nonparametric (Spearman's *rho*) correlation coefficients between body-size estimators and climatic factors in 25 populations of *D. pratensis*. Probabilities just below. See Materials and Methods for variable abbreviations. NS: statistically nonsignificant.

	Independent Variables															
	LAT	LON	ALT	TMEA	TMIN	TMAX	CVT	TM-m	PANN	PMIN	PMAX	CVP	PM-m	PET	AET	WB
LogMBL	-0.46 0.021	NS	NS	0.71 <0.001	0.59 0.002	0.70 <0.001	NS	0.73 <0.001	0.56 0.004	0.43 0.031	0.48 0.014	NS	0.49 0.013	0.59 0.002	0.48 0.014	NS
LogFBL	-0.61 0.001	NS	NS	0.65 0.000	0.53 0.007	0.63 0.001	NS	0.44 0.029	0.40 0.046	NS	0.42 0.039	NS	0.42 0.039	0.48 0.016	0.50 0.011	NS
PC1	NS	NS	NS	0.56 0.004	0.45 0.026	0.56 0.004	NS	0.57 0.003	0.41 0.044	NS	NS	NS	NS	0.39 0.055	0.50 0.011	NS
PC2	-0.61 0.001	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	0.50 0.011	NS	NS	0.43 0.033	NS
PC3	NS	-0.46 0.020	NS	NS	NS	NS	NS	NS	0.54 0.005	0.66 <0.001	NS	NS	NS	0.49 0.012	NS	0.70 <0.001

Table 5. Nonparametric (Spearman's *rho*) correlation coefficients between climatic factors and geographical variables in 25 populations of *D. pratensis*. Probabilities just below. See Materials and Methods for variable abbreviations. NS: statistically nonsignificant.

	Independent Variables												
	TMEA	TMIN	TMAX	CVT	TM-m	PANN	PMIN	PMAX	CVP	PM-m	PET	AET	WB
Lat	-0.57 0.003	-0.43 0.033	-0.52 0.008	0.47 0.017	0.47 0.019	NS	NS	-0.38 0.061	-0.54 0.006	-0.41 0.046	-0.71 <0.001	NS	0.43 0.032
Lon	NS	NS	NS	NS	NS	-0.70 <0.001	-0.63 0.001	-0.54 0.006	NS	-0.40 0.047	NS	-0.64 0.001	-0.72 <0.001
Alt	NS	NS	NS	NS	0.53 0.007	NS	NS	NS	0.45 0.026	NS	0.58 0.002	NS	-0.43 0.032

Table 6. Static allometric relationships of five morphometric characters in *D. pratensis*. a. Slopes of linear regression lines; b. Non-parametric correlation coefficients (Spearmn's *rho*) between male and female proportions between morphometric characters and body length (*arsin* transformation), and geographic parameters. See Materials and Methods for abbreviations of variables. NS: statistically non-significant; M: male; F: female.

a.	Slope of linear regression line	
Relationship	Males	Females
F3L/BL	0.84	0.62
T3L/BL	0.76	0.47
TeL/BL	1.01	0.62
PL/BL	1.21	0.99
PH/BL	1.14	1.07

b.	Spearman's correlation coefficient (probability)		
Arsin (proportion)	LAT	LON	ALT
MF3L	0.81 (<0.001)	NS	-0.59 (0.002)
FF3L	0.73 (<0.001)	NS	-0.41 (0.072)
MT3L	0.74 (<0.001)	NS	-0. 60 (0.002)
FT3L	0.72 (<0.001)	NS	-0.58 (0.008)
MTeL	0.64 (0.001)	NS	-0.68 (<0.001)
FTeL	0.78 (<0.001)	NS	-0.65 (<0.001)
MPL	-0.36 (0.079)	NS	NS
FPL	-055 (0.013)	NS	0.49 (0.029)
MPH	NS	NS	NS
FPH	-0.57 (0.009)	NS	0.44 (0.052)

the case of the Acrididae, only four species, *Chorthippus brunneus* and *Omocestus viridulus* in the Northern Hemisphere, and *D. pratensis* and *D. vittatus* in South America, have been analysed with respect to the relationship between body size, growth and external factors such as temperature (Telfer & Hassall 1999; Berner *et al*. 2004; Berner & Blanckenhorn 2006; Bidau & Martí 2007a,b; Walters & Hassall 2006). The problem of explaining size clines in insects (and in ectotherms in general) is directly related to the so-called temperature-size rule which was first analysed by Bergmann (1847) in endotherms. However, it was found that ectotherms, although they do not metabolically regulate their body temperature, frequently follow size-temperature rules, either Bergmannian or converse Bergmannian (Ray 1960, Atkinson 1994, Atkinson & Sibly 1997, Arnett & Gottelli 1999, Ashton 2002a, Bernardo & Reagan-Wallin 2002, Angilleta & Durham 2003, Ashton & Feldman 2003, Blanckenhorn & Demont 2004, Walters & Hassall 2006). While it has been repeatedly observed that ectotherms grow larger (although more slowly) when reared at low temperatures (reviewed by Atkinson 1994), most insects follow the converse of Bergmann's rule: body size is larger at higher, than at lower, temperatures (Masaki 1967, 1978; Blanckenhorn & Demont 2004; Bidau & Martí 2007a,b).

The positive growth-temperature relationship is the case with *D. pratensis* reported here and in a previous work (Bidau & Martí 2007a) and also, of a closely related species, *D. vittatus* (Bidau & Martí 2007b). The latitudinal decrease in size of *D. pratensis* parallels the corresponding decrease in mean, minimum and maximum ambient temperatures; however, temperature *per se* cannot explain the converse Bergmannian size cline unless temperature indirectly affects some other biological parameters independent of thermoregulation. In univoltine insects of wide latitudinal and altitudinal distribution such as *D. pratensis*, duration of the growing season (thus ambient temperature) can be a powerful limiting factor to body size (Masaki 1967, Roff 1980).

D. pratensis goes through an obligatory egg diapause, with only one generation per year, resulting in an arrest of embryogenesis at the end of anatrepsis, with eggs initiating diapause for several months. The number of months varies in different geographic regions (Turk & Barrera 1979). Obligatory diapause and one generation per year represent the normal condition of *D. pratensis* natural populations (Cigliano & Otte 2003, Bidau & Martí 2007b). The number of nymphal stages is five in males and six in females (with a further facultative stage), and the duration of the nymphal cycle varies negatively with temperature (Turk & Barrera 1979).

Among *D. pratensis* populations, we observed significant positive correlations of body size with temperature (TMEA, TMIN and TMAX). These three parameters are significantly correlated with latitude in our sample (Table 5). Temperature *per se* may explain Bergmann's rule in ectotherms (Atkinson & Sibly 1997, Blanckenhorn & Demont 2004), but not its converse, except when temperature operates as an indirect selective factor on body size by limiting nymphal growth and development (Masaki 1967). Converse Bergmannian patterns are 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, Bidau & Martí 2007b). In *D. pratensis* (and *D. vittatus*, Bidau & Martí 2007b), the converse Bergmannian cline is probably, in part, a consequence of these constraints. However, although an altitudinal consistent but nonsignificant body-size pattern was found in *D. pratensis*, temperature parameters *were not* correlated with altitude (Table 5). Thus other climatic factors like precipitation may play an additional role in the latitudinal converse clines of *D. pratensis*.

In this study, body size and rainfall estimates tended to be positively correlated (Table 4), although only PMAX showed a significantly negative correlation with latitude (Table 5). Since *D. pratensis* is an ecological generalist occurring in both dry and relatively humid habitats, it is probable that larger individuals occur in areas of higher precipitation which coincide with ecologically central environments (Bidau & Martí, 2002). In fact, temperature parameters are positively correlated with rainfall parameters within the studied range. For example, TMEA and PANN showed a Spearman correlation coefficient of ρ= 0.525, p= 0.007. Thus, larger individuals are predicted, in principle, in areas of higher mean temperatures and higher total annual precipitation.

Furthermore, two noncorrelated seasonality estimates, TM-m and PM-m were positively correlated with body size (Table 4), although their relationship to LAT was opposite (Table 5). A multiple regression between male body size and TM-m and PM-m, produced the following results: r^2= 0.574, F= 14.844, p<0.001; partial correlations, TM-m (0.676, p= 0.000) and PM-m (0.539, p= 0.007). In the case of females, r^2= 0.401, F= 7.360, p= 0.004; partial correlations, TM-m (0.537, p= 0.007) and PM-m (0.421, p= 0.041). Accordingly, larger *D. pratensis* individuals should also occur in more seasonal environments that also show higher mean annual temperature and total rainfall in the studied area. Thus, although lower temperature and precipitation may produce smaller individuals in general, variability of these parameters probably favors larger body sizes.

Regarding evapotranspiration, body size was significantly correlated with AET and PET (Table 4). AET is an estimate of primary productivity (Rosenzweig 1968) and in our study it was not correlated with latitude (Table 5). It thus seems reasonable that larger body sizes occur at localities with higher AET values, which are also significantly positively correlated with TMEA, PANN and PM-m, although not with TM-m.

We conclude that converse latitudinal body-size clines in *D. pratensis* are probably influenced by a set of several climatic factors, some of which are correlated with latitude, and others, not. These factors are: annual mean temperature and rainfall, which probably limit the length of the growing season; seasonality, that possibly selects for larger body sizes in more heterogeneous and less-predictable environments, and primary productivity (as estimated by AET) that affects resources availability.

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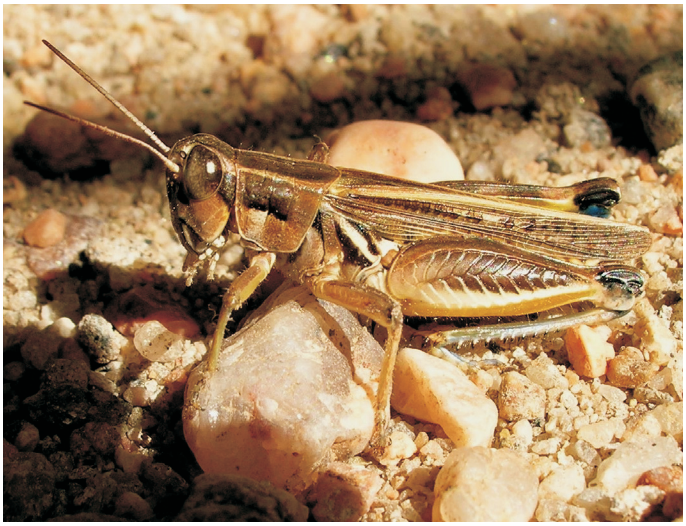

Fig. 2. *Dichroplus pratensis* male, natural population at Saladillo, San Luis, Argentina, summer 2006. Photo by Dardo A. Marti. See Plate IV.

Fig. 3. *Dichroplus pratensis* male, as Fig. 2. See Plate IV.