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Altitudinal size clines, species richness and population density: case studies in Orthoptera

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Abstract

We examined size clines for various external body structures in two grasshopper species (*Chorthippus vagans* and *Oedipoda miniata*) and one katydid species (*Poecilimon birandi*), along an altitudinal gradient ranging from sea level to 1,980 m in southwest Anatolia (Turkey). In *O. miniata* and *P. birandi* all measured structures (body, tegmina, pronotum, and hind femur) were smallest at the highest altitude for both sexes. Hence, in these species, different structures covaried in the same direction, with increasing altitude. In contrast, there was no clear relationship between altitude and size in *C. vagans*, and different structures covaried in different directions in males and females (*i.e.*, some structures became larger at higher elevations, whereas others became smaller, and this differed with sex). For some other *C. vagans* traits, there was no significant intraspecific variation. Hence, *O. miniata* and *P. birandi* followed the converse Bergmann's Rule, whereas there was no consistent pattern for *C. vagans*. For *C. vagans*, small body size was not associated with either local population density (measured as relative abundance) or local species richness, suggesting that neither intranor interspecific competition determined body size for this species. For *O. miniata*, the smallest individuals were found at the site with the highest grasshopper diversity, suggesting that interspecific competition could have influenced *O. miniata* body sizes at this altitude. However, the largest *O. miniata* individuals generally occurred at the sites with the highest relative abundance of *O. miniata*. Hence, in this species, body sizes were generally larger at sites with high population densities — consistent with sites that were most favorable and so able to support high densities of *O. miniata* also producing the largest individuals of this species. Observational data on *P. birandi* similarly suggested that, for this katydid, there is little relationship between local diversity/abundance and altitudinal size-clines.

Key words

body size, Bergmann's Rule, altitudinal gradient, population density, species richness, *Chorthippus vagans*, *Oedipoda miniata*, *Poecilimon birandi*

Introduction

Body size is an important feature of organisms, because it strongly correlates with numerous ecological, physiological and life-history traits (Peters 1983), and influences fecundity, fitness, and speciation (Masaki 1996, Merilä *et al.* 2000, Blackburn & Gaston 2001, McKay *et al.* 2001, Bégin & Roff 2004, Roff & Mousseau 2005). Relative sizes of various structures and overall body size also constitute essential characters for systematics and taxonomy, leading to considerable interest by ecologists, evolutionary biologists and taxonomists in determining how and why size-related characters vary through time and space (Arnett & Gotelli 1999, Merilä *et al.* 2000, Hausdorf 2003, Blanckenhorn & Demont 2004, Brehm & Fiedler 2004, Olalla-Tárraga *et al.* 2006, Meiri *et al.* 2007).

An important aspect of body size and size-related characters is their variation in relation to geography such as latitudinal or altitudinal gradients (Blackburn *et al.* 1999, Blanckenhorn & Demont 2004). Although geographic size clines have been mostly studied in relation to latitudes, similar patterns are expected altitudinally, because climatic gradients are similar in both cases (Chown & Klok 2003, Angilleta *et al.* 2004, Blanckenhorn & Demont 2004, Dillon *et al.* 2006). Scientists have identified two general patterns related to geographic size clines (Blackburn & Gaston 2001, Blanckenhorn & Demont 2004). Bergmann's Rule assumes an increase in body size with increasing latitudes/altitudes and was originally defined for endotherms, though later observed in many vertebrate and invertebrate ectotherms (Blackburn *et al.* 1999). The second pattern, the converse Bergmann's Rule, assumes a negative correlation between body size and latitudes/altitudes and is common among terrestrial arthropods. For example, in a review of size-related studies on insects, Blanckenhorn and Demont (2004) reported that 29 of the 47 species (59%) showed a negative clinal variation (the converse Bergmann's Rule) while the remaining 18 showed the reverse state (Bergmann's Rule).

The same size-related variation patterns are expected to be observed in interspecific comparisons among related species. However, inconsistent or mixed patterns are often reported. For example, lizard body size and latitudes showed a positive correlation in Europe, but a negative correlation in North America; for snakes, this correlation is negative in both continents (Olalla-Tárraga *et al.* 2006). Similarly, Brehm and Fiedler (2004) observed a mixed pattern in Andean geometrid moths. Thus, the generality of these patterns remains unknown, both within and among species, for diverse taxa.

In some size-cline studies, only a single reference parameter for body size is considered. For example, many size-cline studies in insects examine a single structure, such as a femur or overall body size (Blanckenhorn & Demont 2004, Dillon *et al.* 2006). However there are often complex allometric relationships among different body parts and these relationships are strongly influenced by both genes and environment. Some morphological traits covary in the same direction across different overall body sizes, whereas others do not (Masaki 1996, Bégin & Roff 2004, Bégin *et al.* 2004). Thus, conclusions about size clines can vary, depending on which structure is measured. Allometric relations may also vary with sex. For this reason, it is important to examine numerous structures and both sexes when conducting size-cline studies. In addition, examining multiple structures across multiple sites is an important first step toward determining if population size differences are gene- or environment-based.

Indeed, numerous environmental factors can influence size clines (Whitman & Ananthakrishnan 2008). Among the most important

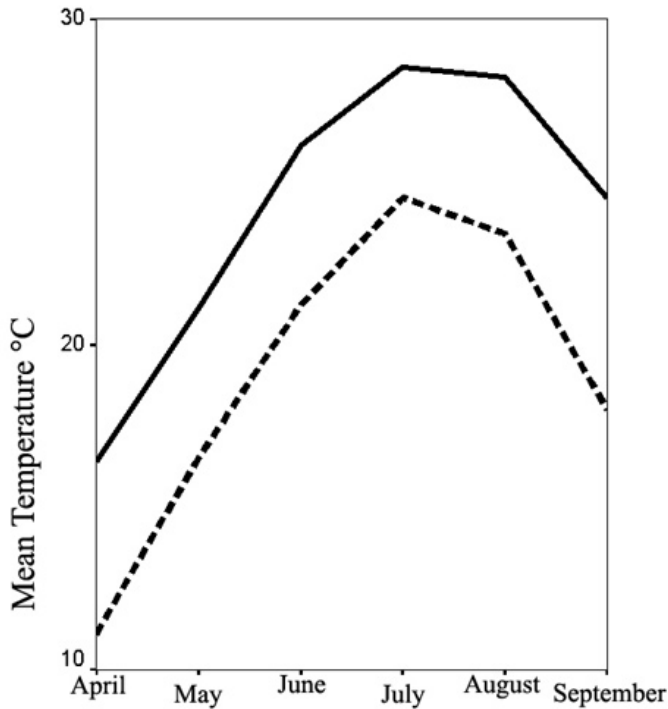


Fig. 1. Monthly mean air temperature at 92 m (black line) and 1095 m elevations (dashed line), for 2002 and 2003 combined.

are temperature, photoperiod, and energy use (or food availability) (Masaki 1996, Hodkinson 2003, Angilleta *et al.* 2004, Bégin *et al.* 2004, Bégin & Roff 2004, Blanckenhorn & Demont 2004). The energy use of a population, itself constitutes a set of constraints, consisting of different factors such as habitat quality (*e.g.*, for phytophagous vegetation type, abundance, and quality), other insects, and degree of both inter- and intraspecific competition, which competition can be estimated from local species richness or local population density respectively (Blackburn & Gaston 2001). However, the influence of population density and local diversity in determining size clines has not been widely tested in natural populations.

In the current study we examine size relationships for four different morphological parameters in both sexes of three species of sympatric Orthoptera, along an altitudinal gradient in southwest Anatolia (Turkey). We studied two Acrididae (*Chorthippus vagans* and *Oedipoda miniata*) and one Tettigoniidae (*Poecilimon birandi*) from various sites in the Akdağlar Mountain Range. Data obtained on diversity and abundance of Caelifera species at each site allowed us to test for possible correlations between size clines and population density or species richness (competitor abundance). Because vegetation varies altitudinally, we also discuss the possibility that food type influenced altitudinal size clines.

Material and Methods

The study area is in the Akdağlar Mts., part of the West Anatolian Taurus Mts in southwestern Turkey (lat 36° 16' N, long 29° 25' E). Elevations in this range go from sea level to 3,024 m at the highest summit, Mt. Uyluk Tepe. In this area, climate varies greatly with elevation (see <http://www.meteoroloji.gov.tr/2006/zirai/zirai-ayliksicaklik.aspx> for weather data). The lowlands have a warm Mediterranean climate with no snow throughout the year, and mean monthly temperatures during the sampling period range from 16.4°C (in April) to a hot 28.5°C (in July) (Fig. 1). The highlands are cold, and the summits are snow-covered from late autumn to early spring. At around 1,000 m elevation, mean monthly temperatures during the sampling period vary from 11°C (in April) to 24.5°C (in July) (Fig. 1). There are three main types of vegetation in the area: 1) pine forest (*Pinus brutia*) and macchia (based on abundance of *Quercus coccifera*) up to 500 to 700 m, 2) degenerated macchia and grass meadow up to around 1,800 m and 3) thorn-cushion or alpine meadows up to around 2,100 m (Paroly 2003). Summits higher than 2,100 m usually lack suitable vegetation for the presence of Orthoptera.

Specimens used in this study were obtained during a project on Orthoptera diversity and distribution in relation to vegetation and elevation. We regularly sampled at six stations, each separated by ~ 500 m altitude, and containing different vegetation (Table 1). Sites (stations) were sampled during spring, summer and autumn from April to September in 2002 and 2003 on a monthly basis. For each sampling period and each site, we sampled for 1 h, between 10:00 and 18:00 h under sunny skies and light winds, using a sweep net with a 35-cm diameter. This method can produce an accurate estimate of relative abundance (see Gardiner *et al.* 2005). All sampling was done by the same person to minimize error. After the 1-h sampling at each site, all collected specimens were returned to the laboratory for identification, counting, and eventual deposition in the Zoological Museum, Department of Biology, Akdeniz University, Antalya, Turkey (AUZM).

During the study, a total of 45 Orthoptera species were recorded from the Akdağlar Range. Of these species, eight were taken from three or more of our six stations (*Poecilimon birandi*, *Platycleis intermedia*, *Calliptamus italicus*, *Chorthippus bornhalmi*, *Chorthippus vagans*, *Acrotylus insubricus*, *Oedipoda coeruleus* and *Oedipoda miniata*), while others were recorded from only one or two sites. However, only two grasshopper species (*Oedipoda miniata* — from three stations, and *Chorthippus vagans* — from four stations), and one katydid (*Poecilimon birandi* — from four stations) were abundant enough (~ 20 specimens of each sex, from each station) for statistical analyses. Thus, these species were taken under study.

For these three species, we measured four morphological structures that are widely used in definition/diagnosis of Orthoptera species: body length (BL), tegminal length (TL) (except females of *P. birandi*), pronotum length (PL), and hind femur length (HFL).

Table 1. The sampling stations and distribution of *C. vagans*, *O. miniata* and *P. birandi* in the Akdağlar range.

Station Number	Altitudes (m)	Vegetation types	<i>O. miniata</i>	<i>C. vagans</i>	<i>P. birandi</i>
1	0-500	macchia, pine forest	X	X	X
2	500-1000	pine forest, degenerated macchia	X	X	X
3	1000-1500	degenerated macchia, grass-meadow	X	X	X
4	1500-2000	grass meadow, alpine meadow		X	X
5	2000-2500	alpine meadow, thorn-cushion			
6	2500-3000	thorn-cushion			

Table 2. Lengths of various structures (range, $\bar{x} \pm s_x$) from males and females of *C. vagans*, *O. miniata*, and *P. birandi* taken at different altitudes. N = 20 in all instances, except where given.

Species	Elevation (m)	Characters (mm)								
		Body Length		Tegmina Length		Pronotum Length		Femur Length		Ovipositor Length
		Male	Female	Male	Female	Male	Female	Male	Female	Female
<i>C. vagans</i>	214	15.0 – 17.0 16.1 ± 0.49	21.6 – 24.0 22.4 ± 0.63	15.0 – 16.7 16.1 ± 0.43	18.2 – 21.0 19.3 ± 0.86	3.0 – 3.6 3.4 ± 0.16	4.0 – 4.7 4.3 ± 0.20	9.8 – 11.0 10.3 ± 0.32	12.2 – 14.1 13.2 ± 0.52	-
	726	16.8 – 19.0 17.5 ± 0.61	21.5 – 24.3 22.3 ± 0.65	16.1 – 17.0 16.7 ± 0.28	20.0 – 22.0 20.8 ± 0.70	3.3 – 3.6 3.4 ± 0.11	4.3 – 4.6 4.4 ± 0.11	9.5 – 10.6 10.1 ± 0.31	12.4 – 13.9 13.2 ± 0.37	-
	1460	16.0 – 17.2 16.4 ± 0.37	22.0 – 24.0 22.9 ± 0.53	16.0 – 17.0 16.2 ± 0.27	18.0 – 21.0 20.1 ± 0.75	3.0 – 3.4 3.3 ± 0.14	4.0 – 4.4 4.3 ± 0.13	9.3 – 10.9 10.1 ± 0.51	11.5 – 13.8 12.9 ± 0.62	-
	1680	15.0 – 17.0 16.4 ± 0.37	22.0 – 25.5 23.5 ± 0.86	15.0 – 16.9 15.9 ± 0.39	19.0 – 22.0 20.5 ± 0.75	3.2 – 3.8 3.4 ± 0.17	3.9 – 4.8 4.4 ± 0.24	9.7 – 10.9 10.2 ± 0.39	11.6 ± 14.1 13.0 ± 0.63	-
<i>O. miniata</i>	214	19.0 – 21.0 19.9 ± 0.68	23.0 – 27.0 24.6 ± 1.00	20.0 – 22.0 20.9 ± 0.54	24.0 – 28.0 25.3 ± 0.99	4.4 – 5.3 4.8 ± 0.22	5.8 – 6.8 6.2 ± 0.28	10.9 – 12.8 11.6 ± 0.50	13.0 – 15.3 14.2 ± 0.62	-
	726	18.0 – 21.0 20.0 ± 0.80	23.0 – 27.0 24.6 ± 1.11	19.0 – 22.0 20.4 ± 0.80	24.0 – 27.0 25.8 ± 0.96	4.5 – 5.3 4.9 ± 0.22	5.8 – 6.9 6.4 ± 0.27	10.3 – 12.2 11.5 ± 0.43	13.6 – 15.3 14.4 ± 0.51	-
	1460	17.3 – 19.4 18.6 ± 0.58	23.0 – 24.5 23.8 ± 0.47	18.5 – 20.5 19.6 ± 0.53	23.5 – 26.0 24.5 ± 0.58	4.3 – 4.7 4.5 ± 0.2	5.4 – 6.8 5.9 ± 0.41	10.2 ± 11.9 11.1 ± 0.46	13.0 – 14.8 13.7 ± 0.54	-
	1980	22.1 – 26.7 24.2 ± 1.34	23.2 – 28.0 25.1 ± 1.43	3.8 – 5.8 5.0 ± 0.45	-	5.2 – 6.6 5.7 ± 0.33	5.5 – 6.6 6.1 ± 0.26	15.0 – 18.1 16.4 ± 0.96	16.0 – 20.0 17.6 ± 1.01	6.5 – 8.3 7.3 ± 0.50
<i>P. birandi</i>	670	19.0 – 25.0 21.8 ± 1.70	19.8 – 25.6 23.1 ± 1.41	4.0 – 5.8 4.9 ± 0.47	-	4.8 – 5.9 5.4 ± 0.35	5.4 – 6.1 5.8 ± 0.24	12.6 – 16.5 14.5 ± 0.93	15.0 – 17.7 16.5 ± 0.79	5.7 – 7.5 6.8 ± 0.52
	1110	16.2 – 22.6 20.5 ± 1.87	-	4.0 – 5.0 4.4 ± 0.35	-	4.7 – 5.3 5.0 ± 0.18	-	13.0 – 16.1 14.9 ± 1.02	-	-
	1980	14.2 – 19.9 16.8 ± 1.35	17.0 – 22.3 19.6 ± 1.48	3.5 – 4.4 3.9 ± 0.29	-	3.7 – 5.0 4.3 ± 0.41	4.0 – 6.0 4.9 ± 0.63	9.0 – 14.5 11.9 ± 1.47	12.2 – 17.3 14.6 ± 1.76	5.0 – 7.0 5.8 ± 0.76
			N=18	-	-		N=18		N=18	N=18

For female *P. birandi*, we also measured ovipositor length (OL). Each of these structures was measured and analyzed in males and females separately to exclude possible bias of sexual dimorphism; thus eight parameters per species were used as reference to size variation (Table 2).

To test for possible correlations between altitudinal size variations and population density or species richness, only short-horned grasshopper (Caelifera) species were considered, because some katydids are semicarnivorous, and thus may not be competing with

other phytophagous insects (Whitman *et al.* 1994). Also, sweep-net collecting may be less accurate for katydids, which often hide during the day in the centers of bushes and trees.

Parametric or nonparametric nature of data was determined by applying Anderson-Darling (for normality) and Levene (homogeneity of variance) tests. As the data were parametric, ANOVA-GLM (General Linear Model) was carried out to test if there was significant intraspecific variation in each of the measured characters between populations from different altitudinal sites. Cor-

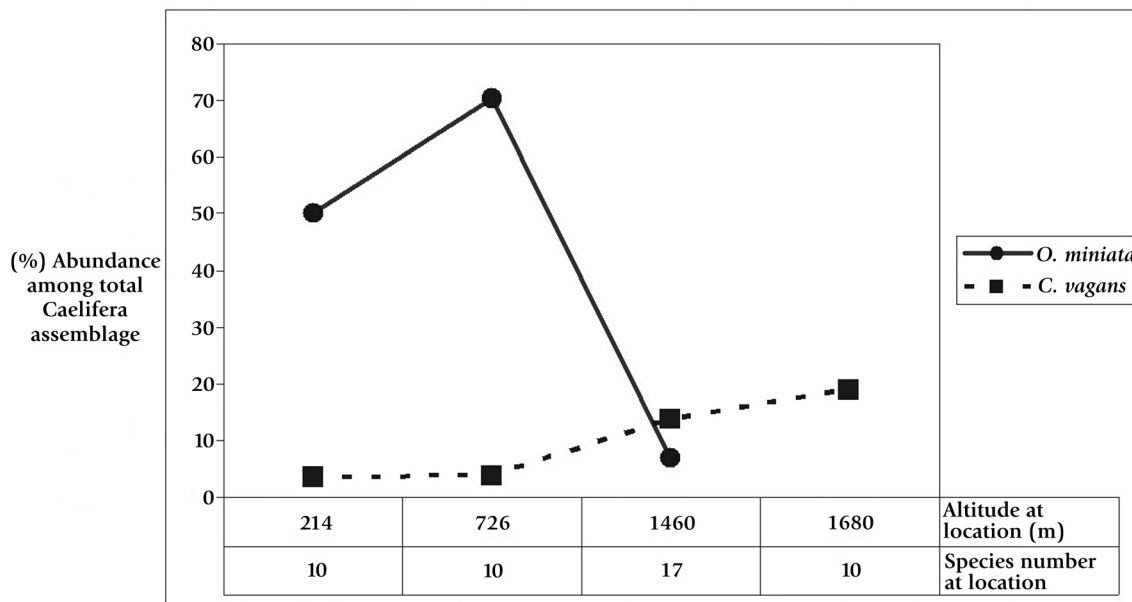


Fig. 2. Relative abundance of *O. miniata* and *C. vagans* in relation to altitude and Caelifera species diversity.

Table 3. Summary of ANOVA (GLM) on the morphometric data from males and females of *C. vagans*, *O. miniata*, and *P. birandi*.

Values of ANOVA GLM (General linear Model) Procedures							
Species	Gender		Body Length	Pronotum Length	Hind Femur Length	Tegmina Length	Ovipositor Length
<i>C. vagans</i>	Male	df_p :	3	3	3	3	-
		df_E :	76	76	76	76	-
		F:	28.63	2.97	0.91	19.85	-
		P:	<0.001	<0.05	0.438 n.s.	<0.001	-
	Female	df_p :	3	3	3	3	-
		df_E :	76	76	76	76	-
<i>O. miniata</i>	Male	F:	12.25	2.67	1.29	14.93	-
		P:	<0.001	0.053 n.s.	0.282 n.s.	<0.001	-
		df_p :	2	2	2	2	-
		df_E :	57	57	57	57	-
	Female	F:	26.13	13.91	7.38	22.15	-
		P:	<0.001	<0.001	<0.001	<0.001	-
<i>P. birandi</i>	Male	df_p :	2	2	2	2	-
		df_E :	57	57	57	57	-
		F:	4.90	13.54	7.98	11.85	-
		P:	<0.05	<0.001	<0.001	<0.001	-
	Female	df_p :	2	2	2	-	2
		df_E :	54	54	54	-	54
<i>P. birandi</i>	Male	F:	12.25	38.35	26.46	-	28.52
		P:	<0.001	<0.001	<0.001	<0.001	<0.001
		df_p :	3	3	3	3	-
		df_E :	65	65	65	65	-
	Female	F:	67.64	54.63	51.16	28.08	-
		P:	<0.001	<0.001	<0.001	<0.001	-

n.s. not significant, df_p : degrees of freedom for population number, df_E : degrees of freedom for error.

Table 4. Pearson correlation coefficients between altitudes and the characters measured from male and female of *C. vagans*, *O. miniata*, and *P. birandi*.

Species	Gender	Correlation values of characters with altitude					
		Body Length	Tegmina Length	Pronotum Length	Hind Femur Length	Ovipositor Length	
<i>C. vagans</i>	Male	r:	-0.10	-0.28*	-0.14	-	-
		P:	0.390	0.013	0.224	-	-
		n:	80	80	80	-	-
	Female	r:	0.52**	0.32**	-	-	-
		P:	<0.001	0.004	-	-	-
		n:	80	80	-	-	-
<i>O. miniata</i>	Male	r:	-0.58**	-0.66**	-0.40**	-0.43**	-
		P:	<0.001	<0.001	0.002	0.001	-
		n:	60	60	60	60	-
	Female	r:	-0.32*	-0.33*	-0.35**	-0.34**	-
		P:	0.013	0.011	0.007	0.008	-
		n:	60	60	60	60	-
<i>P. birandi</i>	Male	r:	-0.86**	-0.71**	-0.84**	-0.77**	-
		P:	<0.001	<0.001	<0.001	<0.001	-
		n:	69	69	69	69	-
	Female	r:	-0.84**	-	-0.73**	-0.70**	-0.70**
		P:	<0.001	-	<0.001	<0.001	<0.001
		n:	57	-	57	57	57

*Correlation is significant at the 0.05 level and ** correlation is significant at the 0.01 level

r: Pearson correlation coefficient

P: probability

n: number of studied samples

relation between character variation and changing altitude (for the characters exhibiting significant variation) was analyzed by Pearson Correlation Coefficient (PCC). Descriptive statistic (minimum and maximum values, means, standard deviation), error plots, graphs, ANOVA and PCC were prepared/performed using SPSS version 10.0 (SPSS Inc., Chicago, IL, USA).

Results

ANOVA analysis (Table 3) revealed that *O. miniata* and *P. birandi* exhibit significant intraspecific variation in both sexes in size for all structural traits measured (Table 2). This was not the case for *C. vagans*. According to ANOVA, this species exhibits a statistically significant intraspecific variation in five characters (BL, TL and PL in males; BL and TL in females). However, there was no significant variation for HFL ($F = 1.29, P = 0.28$) and PL ($F = 2.67, P = 0.053$) in females and HFL ($F = 0.91, P = 0.44$) in males (Table 3). Thus, we did not use these characters in subsequent correlation analyses.

In *C. vagans*, TL was negatively correlated with altitude in males ($r = -0.28, P = 0.013$), but positive in females ($r = 0.32, P = 0.004$). But, maximal TL in both sexes occurred at moderate altitudes (700 m) (Table 4). Female BL also exhibited a significant positive correlation with altitude ($r = 0.52, P < 0.001$). Remaining traits of this species, both in males (BL, PL and HFL), and in females (PL and HFL) did not show a consistent pattern with changing altitude (Table 4, Fig. 3).

Results of correlation analysis for both genders of *O. miniata* and *P. birandi* were largely identical. In these two species, four characters of both sexes showed a negative correlation in relation to altitude (Table 4, Fig. 3). In *O. miniata*, the correlation coefficients between trait values and increasing altitude in males (BL, $r = -0.58, P < 0.001$; TL, $r = -0.66, P < 0.001$; PL, $r = -0.40, P = 0.002$; HFL, $r = -0.43, P = 0.001$) were much higher than those of females (BL, $r = -0.32, P = 0.013$; TL, $r = -0.33, P = 0.011$; PL, $r = -0.35, P = 0.007$; HFL, $r = -0.34, P = 0.008$) (Table 4). All characters of females in this species displayed maximum values at moderate altitudes (~700 m) (Table 2), where the species is the dominant Caeliferan. However this was not the case in males, which exhibited the longest TL and FL at the lowest altitude, but longest BL and PL at moderate altitudes (Table 2). However the minimum values for each of these traits, for each sex, were found at around 1,500 m where Caeliferan species diversity is a maximum and the relative abundance of *O. miniata* is a minimum, indicating a partial correlation between sizes and abundance/species richness.

The strongest size-related clinal patterns were observed in *P. birandi*. All characters in both males and females of this species showed a significant negative correlation with increasing altitude (in males: BL, $r = -0.86, P < 0.001$; TL, $r = -0.71, P < 0.001$; PL, $r = -0.84, P < 0.001$; HFL, $r = -0.77, P < 0.001$ and for females: BL, $r = -0.84, P < 0.001$; PL, $r = -0.73, P < 0.001$; HFL, $r = -0.70, P < 0.001$; OL, $r = -0.70, P < 0.001$) (Table 4, Fig. 3). The maximum value of each character was found at lowest altitude and the minimum value at highest altitude (Table 2). Because members of Ensifera were not included in calculations for species number and relative abundance, no data relating to the relative abundance of this species are given.

During our 2-y field study, we collected 33 Caelifera species from six stations in the Akdağlar range. Most species were restricted to one or two sites. The Caelifera species diversity in three stations containing *O. miniata* and *C. vagans* was 10, but 17 at Station 3 (1,000 - 1,500 m) (Table 5, Fig. 2). Relative abundances of these two species varied from station to station. The maximum relative

Table 5. Caelifera species diversity and relative abundances of *C. vagans* and *O. miniata* per station.

Station Number	Caelifera Species richness	<i>C. vagans</i> Relative Abundance (%)*	<i>O. miniata</i> Relative Abundance (%)*
1	10	3.3	50.0
2	10	3.6	70.2
3	17	13.7	6.7
4	10	18.9	-

*Relative abundance is calculated as: number of individuals of the given species / total number of individuals of all Caelifera × 100.

abundance of *C. vagans* increased at the highest altitudes. In contrast, relative abundance of *O. miniata* was highest at middle altitudes (Table 5, Fig. 2).

Discussion

In this study, three Orthoptera species exhibited different size relationships with altitude. The tettigoniid *P. birandi* showed a strong clinal pattern with respect to size-related measures in an altitudinal gradient. The grasshopper *O. miniata* exhibited a moderate clinal pattern, and the grasshopper *C. vagans* exhibited no overall pattern. For the first two species, body length, pronotum length, tegmina length (except for female *P. birandi*, whose tegmina are concealed under the pronotum), and hind femur length, generally decreased with altitude in both sexes. Ovipositor length in female *P. birandi* also decreased with altitude. Hence, these two species follow the converse Bergmann's Rule, as is observed in many other terrestrial insects (Blanckenhorn & Demont 2004, Dillon *et al.* 2006).

However, the variation patterns in the third species, *C. vagans*, are complicated, since neither male nor female size showed a consistent pattern with changing altitude. In this species, 5 of 8 variables (BL, PL and HFL in males, and PL and HFL in females) showed no correlation with altitude. Of the remaining, male TL was negatively and female BL and TL positively, correlated with increasing altitude. Thus, female *C. vagans* follow Bergmann's Rule in respect to BL and TL, whereas male TL follows the Converse Bergmann's Rule.

Hence, our study found no general pattern among related species, since two acridid species (*C. vagans* and *O. miniata*) showed different clinal patterns, while two species belonging to different suborders (*O. miniata* and *P. birandi*) showed the same clinal patterns. Similar intraclade mixing patterns have been observed in other terrestrial ectotherms (Brehm & Fiedler 2004, Dillon *et al.* 2006, Olalla-Tárraga *et al.* 2006).

In *P. birandi*, all eight parameters were maximum at lowest altitudes and minimum at the highest altitude; hence, this species constitutes a perfect example of the converse Bergmann's Rule. *O. miniata* also shows a negative correlation between sizes and altitude, but this relationship is not straightforward. For example, of the eight variables measured for *O. miniata*, the maximum mean trait values for four structures of females and two of males were observed at moderate (not at the lowest) altitudes. For the third species, *C. vagans*, there was no overall relationship between size and increasing altitude.

Size was not perfectly correlated with altitude in two of the above species and this suggests that factors other than altitude influenced size. What could these other factors be? Body size is influenced by numerous factors, and the strengths of these factors can vary with altitude (Masaki 1996, Arnett & Gotelli 1999, Blackburn *et al.* 1999, Rourke 2000, Blackburn & Gaston 2001, Chown & Klok 2003, Hodkinson 2003, Angiletta *et al.* 2004, Bégin *et al.* 2004,

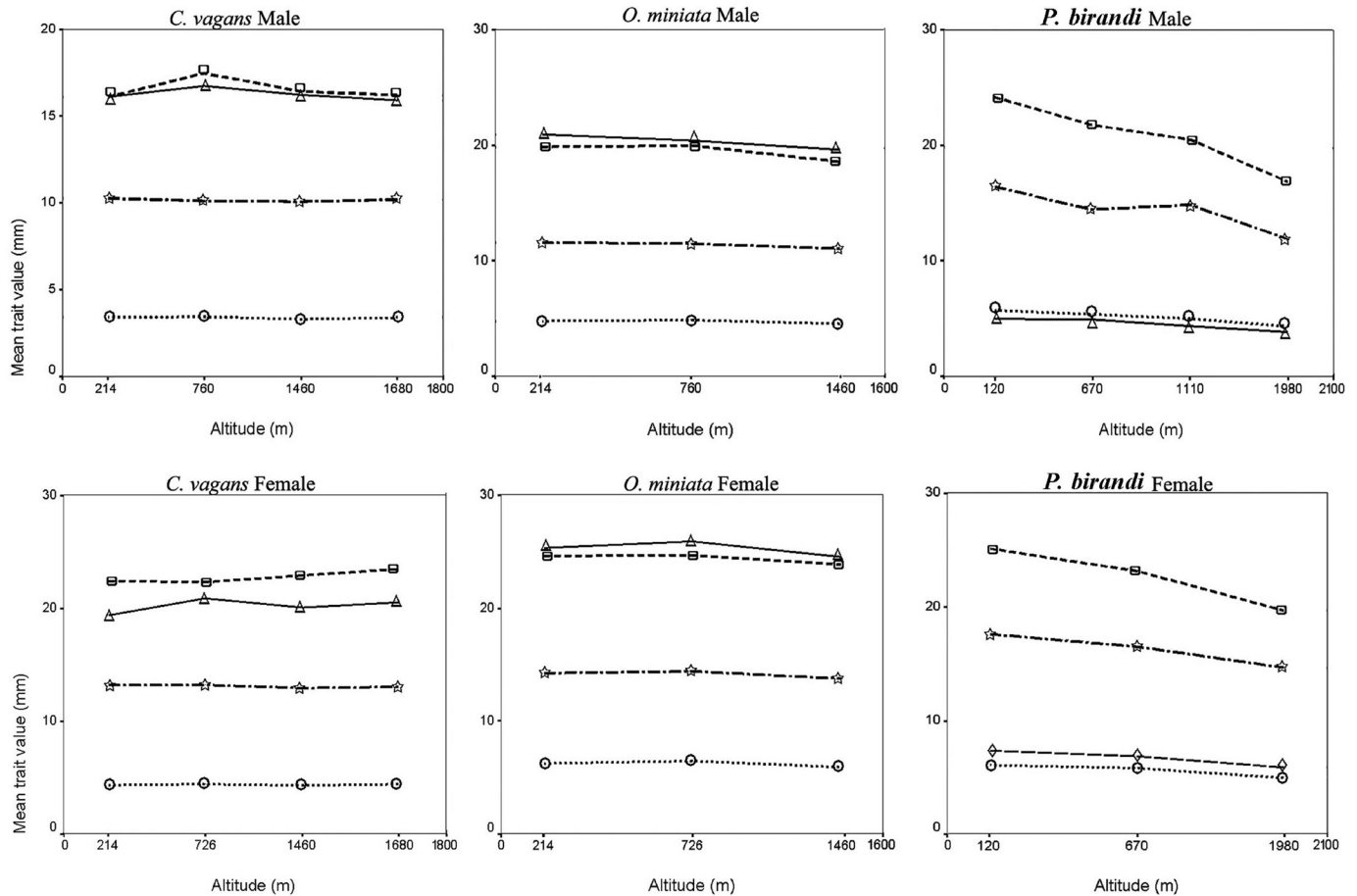


Fig. 3. Mean lengths for various structures in relation to altitude in males and females of *C. vagans*, *O. miniata*, and *P. birandi*. Square: body length; triangle: tegmina length; circle: pronotum length; star: hind femur length; diamond: ovipositor length (see Table 2, for details).

Berner *et al.* 2004, Blanckenhorn & Demont 2004, Dillon *et al.* 2006, Olalla-Tárraga *et al.* 2006, Meiri *et al.* 2007).

One factor that is especially important in determining body size is nutrition (Whitman & Ananthkrishnan 2008). Available nutrition is influenced by both inter- and intraspecific competition. According to Blackburn and Gaston (2001) "size and number of the individuals necessarily trade off within the constraint imposed by the amount of energy", and thus, there should be a negative correlation between body size and population density. This assumption can also be extended to the community level, and a negative correlation might be expected between body size and species richness, which may correlate with interspecific competition.

Our data allowed us to evaluate size variations of *O. miniata* and *C. vagans* in respect to both local population density and Caelifera species richness. If increasing competition causes small body size, then minimum body-size values should be found in places with the highest diversity and the highest population density. However, as with clinal variation (above), our data show complex interactions between relative abundance, local diversity, and body size.

In *O. miniata* the smallest body sizes were observed at Station 3, the site with the highest grasshopper diversity and lowest relative abundance (Table 2, Figs 2, 3). The largest *O. miniata* generally occurred at Station 2, which had the highest *O. miniata* relative abundance (Tables 1, 2; Figs 2, 3). As such, there was no linear correlation between population density / species diversity and clinal variation in this species. Thus, we did not find a consistent

relationship between body size and density/species richness in *O. miniata*.

C. vagans exhibited little overall relationship between body size and either relative abundance or local grasshopper diversity (Tables 1, 2; Figs 2, 3). In fact, the largest female BL (a trait which showed a positive correlation with altitude) occurred at Station 4, the site with maximum population density (Tables 1, 2; Figs. 2, 3). Thus, there seems to be no relationship between size-clines and population density/species diversity for *C. vagans*.

Although we were not able to determine population density of the katydid *P. birandi* according to the standard method used for grasshoppers, our observations still support the same pattern for this species. *P. birandi* is univoltine and the adults occur from mid-April to the end of May at low elevations, and from the end of June to mid-August at high elevations. During its adult phase at both locations, *P. birandi* was the dominant species and experienced low Orthoptera diversity (only two other Orthoptera species were present at either site). Despite these similarities among sites, *P. birandi* exhibited a strong size cline with altitude, indicating no correlation between population density, species richness, and size-cline. As with the two grasshopper species (above), we did not find evidence that either inter- or intraspecific competition influenced the size cline in this species.

A plausible explanation for the failure of body size to correlate with density/diversity, is that perhaps in our system, local resources remained above a critical threshold at sites with high density and

high diversity. Hence, species richness and relative abundance may cause competition, and thus influence body size and clinal variation, but only when resources such as available forage, are poor. If there are sufficient amounts of resources in the habitat, and there are no constraints on availability, then there will be no direct correlation between these variables. For example, *C. vagans* prefer open meadows, and such habitats are abundant at high elevations with cold temperatures in the Akdağlar Range (Sirin *et al.* unpublished data). This habitat is relatively finite at low altitudes, but comparably infinite at higher altitudes. So, it is not surprising that the largest females of *C. vagans* were observed at the higher elevations (containing ample forage), despite the fact that population density and caeliferan species diversity were high at these sites. Similarly, *O. miniata* prefer warm arid habitats in Anatolia (Yalim & Ciplak 2002), and thus might be expected to exhibit higher population densities and larger body size at medium and low altitudes, where temperatures are higher.

In the above analysis, we failed to find an overall relationship between body size and level of competition, as measured by relative local abundance and grasshopper species diversity. However, perhaps not competition, but overall habitat quality, influences body size in this system. An especially important component of habitat quality in our system would be vegetation type and quality, because all the species examined are phytophagous (or largely so), and each probably prefers a specific plant composition. Vegetation at the lowest altitude is dominated by numerous tree plants (*Pinus brutia*, *Quercus coccifera*, *Olea europaea*, *Ceratonia siliqua*, *Styrax officinalis*, *Arbutus andrachne*, etc.) and is poor in herbaceous plants: hence it may not represent good food sources for Orthoptera. Moderate altitudes contain more diverse habitats and vegetation, from macchia to high-grass meadows, which may offer greater choices for feeding Orthoptera. If overall habitat quality is more important than population density/species richness in determining body size, then maximum body sizes should occur at elevations where the most optimum combination of different environmental factors occurs and deviation from the optimum conditions should reduce body size. We are currently preparing a paper that examines this hypothesis.

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