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Bergmann's rule in the ant lion *M; ele i ac la*

Lawton & Manly, 1993; Hawkins & Lawton, 1995). However, these patterns are difficult to interpret because species may not be statistically independent of one another (Felsenstein, 1985), and there may be confounding influences of speciation history

width and pigmentation patterns (Stange, 1980). Larvae live up to 2 years, construct silk cocoons, and emerge as adults after approximately 1 month (Furunishi & Masaki, 1981, 1982). Adults are weak fliers and live for approximately 1 month

reasoned that if individuals were distributed homogenously in a population, the slope of this line would be relatively shallow. If individuals were clumped in space, the slope would be much steeper (see also Lewontin & Levins, 1989).

Climatic and geographic variables

To examine correlations of body size, heterozygosity, and climate, we obtained maximum and minimum temperature (°C) and precipitation (mm) from the National Climatic Data Center (1992). Each variable represents a 30-year average of annual means (1961–1990) from the weather station closest to each population. Maximum and minimum temperature variance was obtained by calculating standard deviation and variance of the 30-year averages. Distance from weather stations to population sites ranged from approximately 5 to 100 km. Latitude and longitude (min) of each collection site were measured from detailed state maps. Latitudes ranged from 33°43′ N to 41°53′ N. Longitudes ranged from 71°43′ W to 97°05′ W. Elevation (m) was measured with USGS topographic maps, and ranged from 0 to 457.3 m above sea level.

Allozyme survey

Protein electrophoresis was used to measure genetic differentiation among *M. immaculatus* populations. During the summer of 1994, we collected a minimum of thirty third-instar larvae from each of seventeen collecting sites for genetic analyses. These larvae were mailed overnight in individual cryotubes to the University of Vermont, Burlington, where they were stored at −80°C. To ensure that we collected *M. immaculatus*, larvae were identified to species using the key of Lucas & Stange (1981).

To create extractions, we homogenized frozen larvae in chilled, distilled water. This homogenate was analysed using standard starch-gel electrophoretic techniques (May, 1991). Initially we surveyed twenty-four enzymes knownlly twenty-four.teryo2.edT705.6(ay3sdt,uherences)27 -0ucf.5(D10111n2(using)]TJ2mogeniz

Figure 1 Locations of thirty-four *M. immaculatus* populations used for larval body size analyses. ●, Populations samples; ○, sites with no or few ant lions.

Fig. 1). Between 36 and 40°N latitude (Virginia through New Jersey) we found no populations with enough third-instar larvae for inclusion in analyses (Fig. 1). Body size measurements of adults and larvae were natural log-transformed prior to analysis. Relationships among body size, observed heterozygosity, five climatic variables, three geographic variables, and density and patchiness were analysed with simple correlations. Stepwise forward multiple regression was also performed using all variables, except density and patchiness, due to differences in sample size. For multiple regression analyses, we used $P<0.25$ to enter variables into the model, and $P<0.05$ to retain them. For each dependent variable (larval body size, adult body size, heterozygosity), we conducted two regression analyses: (1) using the five climatic variables (maximum and minimum temperature, precipitation, and

Table 1 Simple correlation coefficients (r) for larval body size and observed heterozygosity with all predictor variables. (NS = P>0.05; * = P<0.05; ** = P<0.01; *** = P<0.001).

	Body size	Heterozygosity
Latitude	0.46*	0.84***
Longitude	−0.44*	−0.80***
Elevation	−0.46*	NS
Precipitation	−0.43*	−0.59**
Maximum temperature	−0.43*	−0.82***
Minimum temperature	NS	−0.77***
Density	NS	NS
Patchiness	NS	0.87***
Heterozygosity	NS	
Maximum temperature variance	0.41*	0.64**
Minimum temperature variance	0.46*	0.77***

Table 2 Multiple regression coefficients for larval body size and

body size was positively correlated with latitude (Fig. 2a), but negatively correlated with elevation (Fig. 2b). There was no significant correlation between latitude and elevation of the collection sites ($r = 0.07$; $P = 0.74$). In a regression model with climatic variables, minimum temperature variance was the only predictor of larval body size (Table 2).

Adult body size

Adult females were significantly larger than adult males for both inter-eye distance (females [$n = 53$]: mean $\pm$ 1 SD = 3.7 ± 0.2; males [$n = 29$]: 3.5 ± 0.3; $F_{1,80} = 17.96$, P<0.0001) and average front-wing length (females: mean $\pm$ 1 SD = 35.0 ± 2.0; males: 32.5 ± 2.1; $F_{1,80} = 20.92$, P<0.0001). For this reason, we used sex as a categorical variable in our multiple regression models.

For the simple correlations, the only significant relationship was a negative correlation between female body size and elevation (Fig. 2d). The correlation between body size of both sexes and latitude was positive, but50(was)-femal-311.284.7565TD2u* 75 (

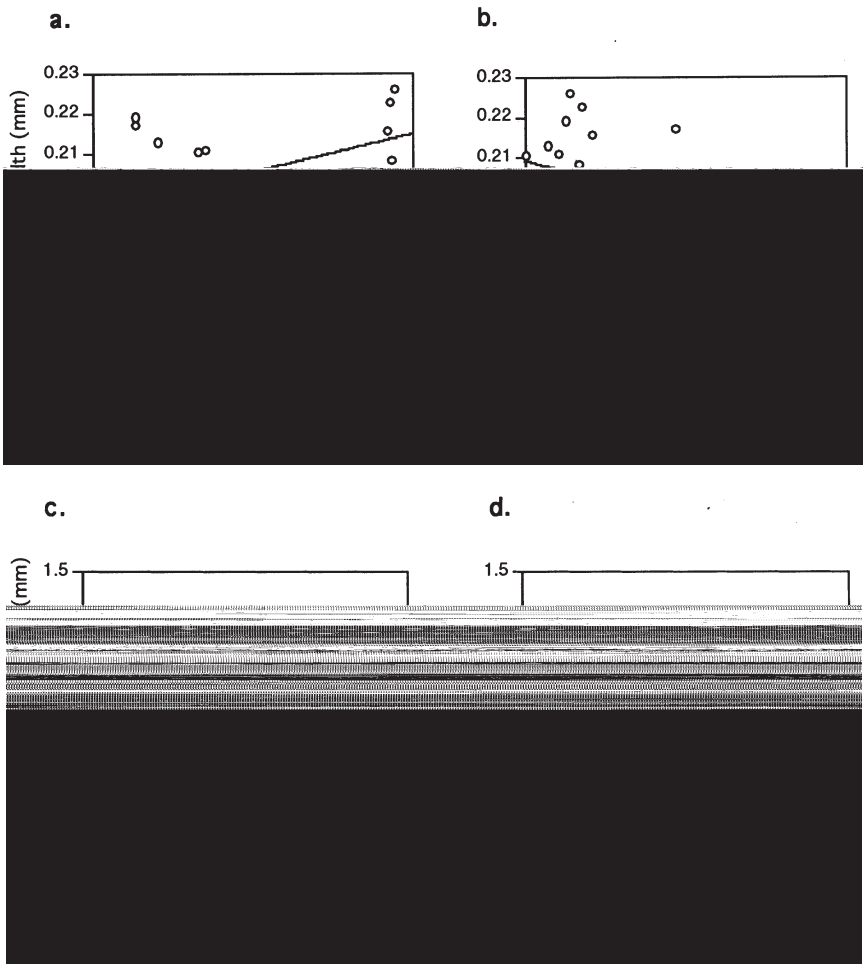

Figure 2 Average larval body size (a) increases with latitude and (b) decreases with elevation. Each point represents the average head-width of third-instar larvae from a population (N>5 larvae per population). Average adult body size, shown for females, (c) increases non-significantly with latitude, but (d) decreases significantly with elevation. Each point represents the inter-eye distance measured for a single adult female.

was less than one migrant per generation among all populations, but varied from 0.74 to 8.4 migrants per generation among populations within a region (Table 4).

DISCUSSION

We found two consistent geographic patterns in ant lion body size: a weak positive correlation between body size and latitude (Fig. 2a,c) and a strong negative correlation between body size and elevation (Fig. 2b,d). The latitudinal correlation for adults is weak (both sexes: $P=0.10$; females only: $P=0.32$), but the combined probability for the adult and larval pattern is significant (both sexes: Fisher's combined probability value $\chi^2_4=11.8$, $P=0.02$; females only: $\chi^2_4=9.57$, $P=0.048$). The disparity between larvae and adults in the strength of the latitudinal correlation is most likely due to sample size differences, and sampling differences in space and time. This correlation with latitude appears to be the first documented ce[(cea/F6 1()-331.2/ph5 1()-331.2/F6 1 Tf515n5&tingl81ehe)3' to.491 Tf1.000

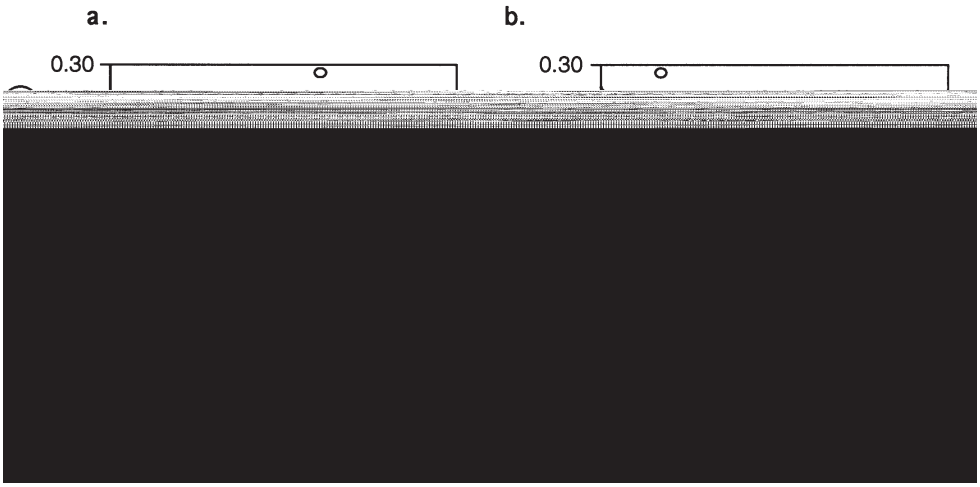

Figure 4 (a) Average observed heterozygosity increases significantly with maximum temperature variance. (b) Average observed heterozygosity decreases with increasing maximum temperature.

Table 3 Average expected and observed heterozygosities ± one standard deviation for seventeen

conservation (Bergmann, 1847; Kendeigh, 1969), and ecological

Table 4 *F*-statistics (Wright, 1978) for each variable locus of *M. immaculatus* from populations within specific regions and among all populations. Gene flow (number of migrants per generation) is shown in parentheses for each region and among all populations. Significance of the F_{st} is indicated by the G-value. Locus names are given in Methods. (* $P<0.05$; ** $P<0.01$; *** $P<0.001$)

Region	Locus	F_{is}	F_{it}	F_{st}	G-value	d.f.
MS	GPI	0.356	0.361	0.008	5.498	4
(4.6)	MDH	0.884	0.888	0.030	28.816***	8
	DIA	0.916	0.922	0.079	40.416***	6
	PEP	0.388	0.423	0.057	10.801**	2
	SOD	1.000	1.000	0.069	14.002***	2
Mean		0.713	0.728	0.051	99.533***	22
AL	GPI	−0.064	−0.028	0.034	8.520	4
(5.7)	MDH	0.701	0.707	0.020	5.991	4
	DIA	0.865	0.876	0.077	25.653***	4
	PEP	0.510	0.523	0.027	7.537	4
	SOD	1.000	1.000	0.023	5.683	2
Mean		0.618	0.634	0.042	53.384***	18
GA	GPI	0.255	0.579	0.435	133.524***	4
(0.74)	MDH	0.712	0.760	0.167	77.386***	4
	DIA	0.844	0.868	0.155	65.201***	6
	PEP	0.566	0.572	0.013	2.476	2
	SOD	1.000	1.000	0.592	124.696***	2
Mean		0.674	0.756	0.252	403.283***	18
SC	GPI	0.080	0.161	0.089	22.272***	2
(4.1)	MDH	0.944	0.946	0.029	8.368*	2
	DIA	0.946	0.950	0.069	19.982***	2
	PEP	0.428	0.447	0.033	4.280*	1
	SOD	1.000	1.000	0.082	11.021***	1
Mean		0.708	0.725	0.057	65.924***	8
NC	GPI	0.102	0.110	0.008	8.724	4
(7.8)	MDH	0.822	0.825	0.016	12.703*	6
	DIA	0.885	0.894	0.077	52.180***	6
	PEP	0.316	0.321	0.007	8.762	4
	SOD	1.000	1.000	0.032	11.134**	2
Mean		0.613	0.625	0.031	93.502***	22
CT/RI	GPI	0.213	0.252	0.049	27.923***	6
(8.4)	MDH	−0.172	−0.105	0.058	30.361***	4
	DIA	0.625	0.626	0.003	1.167	4
	PEP	0.582	0.587	0.011	2.170	2
	SOD	1.000	1.000	0.007	1.364	2
Mean		0.362	0.380	0.029	62.984***	18
Overall Mean (0.73)		0.609	0.708	0.254	2422.774***	208

One such factor is photoperiod. Insect growth, metamorphosis, development, and body size are often tightly growth rate in all instars. They also found a high variance in instar and pupal weight that depended on the photoperiod in which larvae were raised. Thus, latitudinal differences in photoperiod may be responsible for reversing the negative correlation we found for ant lion body size and elevation. We suggest that photoperiod should be considered as a possible explanation for geographic gradients in body size of insects.

Our data cannot distinguish among a variety of other hypotheses that implicate variation in food or temperature as a cause of Bergmann's rule. These include geographic gradients in prey body size (McNab, 1971), starvation resistance of populations in seasonal enviroments (Kondoh, 1977; Lindstedt & Boyce, 1985), and effects of cooler temperatures (Berrigan & Charnov, 1994; Atkinson, 1994), reduced humidity (Aldrich & James, 1991; Bonato, Mapangoudivassa & Gutierrez, 1995), seasonality (Murphy, 1985), voltinism (Roff, 1992; Bradford & Roff, 1995) and food availability (Boyce, 1978; McNab, 1971) on survival and individual growth rates. Some of these hypotheses are also consistent with our finding that heterozygosity increases in the north (Fig. 3), and in populations that experience greater seasonal fluctuations in temperature (Fig. 4a).

Clines in body size may also result from geographic variation in juvenile or adult mortality (Rowe & Ludwig, 1991; Roff, 1992). We do not have data on this type of mortality in the field. However, local population density of ant lions did not vary with latitude ($r=0.09$; $P=0.80$) or elevation ($r=-0.18$, $P=0.61$), so mortality due to crowding is probably not important.

A complete understanding of Bergmann's rule requires information on the genetic and environmental components of body size (James, 1982). For our data, we cannot say how much of the geographic variation in body size is due to genetic differences between populations (Blanckenhorn & Fairbairn, 1995; Conover & Present, 1990), and how much is due to phenotypic plasticity of individuals growing in different environments (Via, 1985; Kodoh, Ishiguri & Kawano, 1995). However, our allozyme analyses (Table 4) do suggest that populations are relatively isolated and well-differentiated genetically from one another, and that heterozygosity increases in the north (Fig. 3). We are currently conducting common garden and reciprocal-transplant experiments (A. Arnett, unpublished data) to tease apart the environmental and genetic components of body size in larval ant lions and to directly test some of the hypotheses that have been proposed to account for Bergmann's rule.

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