

Geographic Variation in Body Size and Sexual Size Dimorphism of a Seed-Feeding Beetle

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ABSTRACT: Body size of many animals varies with latitude: body size is either larger at higher latitudes (Bergmann's rule) or smaller at higher latitudes (converse Bergmann's rule). However, the causes underlying these patterns are poorly understood. Also, studies rarely explore how sexual size dimorphism varies with latitude. Here we investigate geographic variation in body size and sexual size dimorphism of the seed-feeding beetle *Stator limbatus*, collected from 95 locations along a 38° range in latitude. We examine 14 variables to test whether clines in environmental factors are adequate to explain geographic patterns of body size. We found that body size and sexual size dimorphism of *S. limbatus* varied considerably with latitude; beetles were smaller but more dimorphic at lower latitudes. Body size was not correlated with a gradient in mean temperature, contrary to the commonly accepted hypothesis that clines are produced by latitudinal gradients in temperature. Instead, we found that three factors were adequate to explain the cline in body size: clinal variation in host plant seed size, moisture (humidity), and seasonality (variance in humidity, precipitation, and temperature). We also found that the cline in sexual size dimorphism was partially explainable by a gradient in moisture, though moisture alone was not sufficient to explain the cline. Other ecological or environmental variables must necessarily contribute to differences in selection on male versus female body size. The main implications of our study are that the sexes differ in the magnitude of clinal variation in body size, creating latitudinal variation in sexual size dimorphism, and that clines in body size of seed beetles are likely influenced by variation in host seed size, water availability, and seasonality.

A central goal of ecology and evolutionary biology is to explain large-scale systematic patterns of variation in nature (MacArthur 1972; Gaston and Blackburn 2000). Consistent patterns of body size evolution are of particular interest because body size affects virtually all physiological and life-history traits of an organism (Brown et al. 2004). Many organisms show common broadscale patterns in body size. For example, body size tends to increase within taxa over geologic time within lineages (Cope's rule), sexual size dimorphism increases with increasing overall body size when males are the larger sex and decreases with body size when females are the larger sex (Rensch's rule; Fairbairn 1997), and body size shows latitudinal clines (Bergmann's rule/converse Bergmann's rule; Ashton 2004; Blanckenhorn and Demont 2004). However, the mechanisms producing these patterns are poorly understood.

Latitudinal clines in body size of animals are one of the most widely observed patterns in nature. Latitudinal clines take two general forms: animals are either larger at higher latitudes/colder temperatures (Bergmann clines; Bergmann 1847; Ashton 2004; Blanckenhorn and Demont 2004) or smaller at higher latitudes/colder temperatures (converse Bergmann clines; Mousseau 1997; Ashton and Feldman 2003; Blanckenhorn and Demont 2004). The cause underlying converse Bergmann clines is probably season length: the shorter length of the growing season at higher latitudes limits the time available for growth and reproduction and thus limits the body size that can be achieved (Blanckenhorn and Demont 2004). However, the explanation for Bergmann clines is less clear. Bergmann clines have been shown to be genetically based (Partridge and Coyne 1997; Gilchrist and Partridge 1999), to be repeatable across continents (Coyne and Beecham 1987; Capy et al. 1993; Imasheva et al. 1994; James et al. 1995; Van't Land et al. 1995), and to evolve very rapidly following colonization of new continents (Huey et al. 2000; Gilchrist et al. 2001, 2004). They are thus likely produced by natural selection, but the sources of selection remain

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poorly understood (Partridge and Coyne 1997; Angilletta and Dunham 2003).

Because temperature co-varies consistently with latitude, temperature is often assumed to be the selective agent producing Bergmann clines in animals. This was the original explanation proposed by Carl Bergmann himself, who suggested that in endotherms a reduction in the surface-to-volume ratio of large animals versus small animals leads to the prediction that animals should be larger in colder environments to avoid heat loss (Bergmann 1847). This idea has persisted for more than 150 years, but recent work has found that clines in birds and mammals are not consistent with this hypothesis (Ashton et al. 2000; Ashton 2002). Also, Bergmann clines exist in many ectotherms, including small ectotherms, such as insects, that acclimate to ambient temperature almost instantly (Stevenson 1985; Blanckenhorn et al. 2006), an observation clearly not explainable by surface-to-volume ratios and metabolic heat loss.

Alternatively, latitudinal clines in animals may be produced by other environmental and ecological variables that co-vary with latitude (Blackburn et al. 1999; Ashton et al. 2000). For example, recent studies have found that moisture, or a combination of moisture and temperature, is often a better predictor of variation in body size than is temperature (James 1970; Burnett 1983; Yom-Tov and Nix 1986; Wigginton and Dobson 1999; Yom-Tov and Geffen 2006): dry environments may select for individuals that are larger perhaps to resist dehydration. Other studies have found that seasonality explains clines better than does temperature (Boyce 1978; Lindstedt and Boyce 1985; Murphy 1985; Cushman et al. 1993; Arnett and Gotelli 1999), possibly because of greater starvation resistance of larger individuals (as a result of increased storage reserves) during periods of unfavorable environmental conditions that are often characteristic of seasonal environments. Thus, geographic variation in body size may be generated by multiple sources of selection that could interact (Jones et al. 2005).

Geographic patterns in body size often differ between males and females. Most animals show some degree of sexual size dimorphism, but the direction and magnitude of this dimorphism varies considerably among species and often among populations within species (Teder and Tammaru 2005; Blanckenhorn et al. 2006). Although studies of geographic patterns of body size are common and typically investigate both males and females, they seldom explore how dimorphism varies with latitude. In a meta-analysis of geographic variation in body size of 98 species of animals, Blanckenhorn et al. (2006) found that male body size varies more with latitude than does female body size, following an intraspecific version of Rensch's rule. This suggests that two classic evolutionary rules (Berg-

mann's and Rensch's rules) are related. Although the cause of gender differences in latitudinal clines is not clear, any latitudinal change in an environmental factor that affects one sex more than the other can create gender differences in cline slope and thus create clines in sexual dimorphism (Blanckenhorn et al. 2006).

Here we examine geographic variation in body size and sexual size dimorphism of the seed beetle *Stator limbatus* (Coleoptera: Chrysomelidae: Bruchinae), a generalist seed-feeding beetle that is multivoltine and widely distributed from northern South America to the southwestern United States. Throughout its large geographic range, *S. limbatus* is exposed to considerable variation in climatic conditions ranging from a tropical climate in the southern part of its distribution to a desert climate in the northern part of its distribution. In addition to variation in climate, populations of *S. limbatus* vary in the hosts on which they develop, which vary considerably in the sizes of seeds they produce. Because larvae develop inside of seeds and cannot move among seeds, they are subject to substantial larval competition (Mitchell 1977). Many plant species exhibit latitudinal clines in seed size (Moles and Westoby 2003), which will likely affect the size of insects living within these seeds through variation in the intensity of competition. We thus expect both climatological variables and host seed size to contribute to clinal variation in body size of *S. limbatus*.

In this study we explore geographic variation in adult body size of male and female *S. limbatus* collected from 95 locations along a 38° range in latitude (fig. 1). We ask three related questions concerning the evolution of body size clines. First, is there clinal variation in body size of *S. limbatus*? Second, do males and females exhibit different size versus latitude relationships, creating clinal variation in sexual dimorphism? Finally, are latitudinal gradients in mean temperature associated with clines in body size and dimorphism, or do other ecological/environmental variables better explain this pattern?

Methods

Natural History of Stator limbatus

Stator limbatus (Horn) is distributed from northern South America to the southwestern United States (Johnson and Kingsolver 1976; Johnson et al. 1989; Nilsson and Johnson 1993). It is a generalist seed parasite of legumes in the dry tropical forests of South and Central America and in the deserts of Mexico and the southwestern United States. Although only a few hosts are encountered in most locations, *S. limbatus* has been collected from >70 species of legumes throughout its wide geographic range, most of which are native (~50 spp., primarily mimosoid or cae-

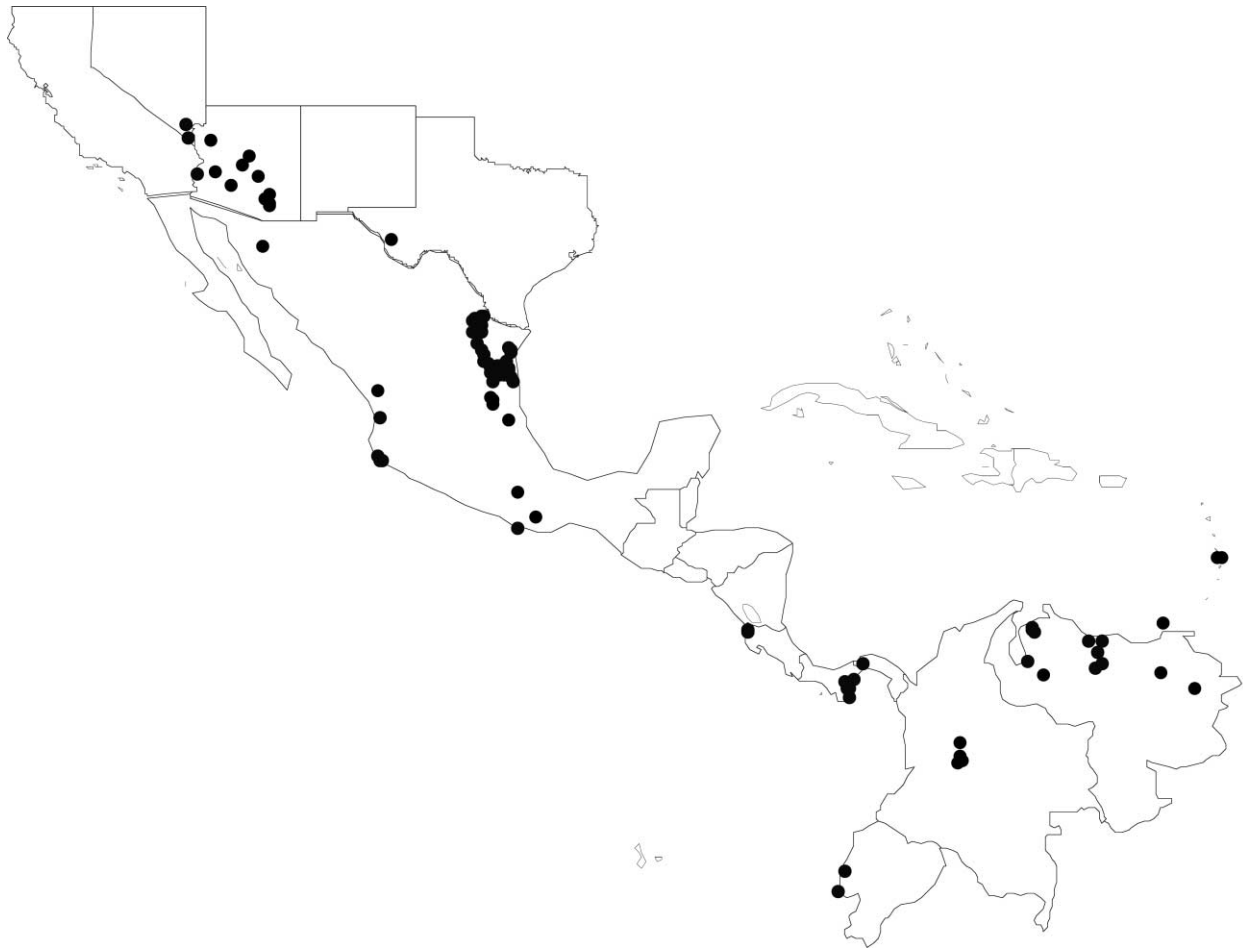


Figure 1: Distribution of sampled populations of *Stator limbatus*. Each dot denotes a collection locality. Some localities are close together and illustrated with a single point.

salpinioid legumes; Morse and Farrell 2005a, 2005b), though many are aliens (>20 spp.).

The life cycle of *S. limbatus* revolves around seeds. Females oviposit directly onto host seeds inside of seed pods that have either dehisced or been damaged by other organisms (e.g., mice, other bruchine beetles such as *Mimosestes* spp., etc.). Eggs hatch and larvae burrow into the seed directly underneath the egg. Larval growth and pupation take place entirely within a single seed. On emergence from the seed, adults mate, and females begin to lay eggs within ~24–48 h.

Collection of Study Populations

Specimens were collected from 1998 to 2004 in 95 locations throughout the entire geographic range of *S. limbatus*

during multiple trips to northern South America, Central America, Mexico, and the southwestern United States. The collection localities are depicted in figure 1 and listed in table A1 in the online edition of the *American Naturalist*. Adults of *S. limbatus* were either collected in the field or reared from field-collected seeds in the laboratory. Because our assessment of latitudinal variation in size of *S. limbatus* is based on measures of field-collected beetles, environmental effects on the phenotype (phenotypic plasticity) cannot be ruled out. However, variation in body size among beetle populations collected from three regions of the geographic range (Colombia vs. Arizona vs. Texas) persist after >10 generations of laboratory rearing (Amarillo-Suárez 2006; Amarillo-Suárez and Fox 2006), indicating that the differences are genetically based. Thus, any detectable cline in body size among the populations

of *S. limbatus* used in this study is likely a result of genetic differentiation among populations. In total, we collected and measured 1,739 individuals (874 females and 865 males) from 95 locations spanning a 38° latitudinal range (Ecuador to Nevada).

Morphological Measurements

We took dorsal photographs of each individual using a Nikon D1 digital camera attached to a Leica dissecting microscope. A micrometer was included in each image for scale. Ten dorsal landmarks on each individual were mapped using ImageJ, version 1.32j, from the National Institutes of Health (<http://rsb.info.nih.gov/ij/>; Abramoff et al. 2004). These landmarks were used to measure three morphological characters: elytron length, elytron width, and pronotum width. Two of these characters, elytron length and pronotum width, are considered to be the best characters for describing body size variation in bruchine seed beetles by Colgoni and Vamosi (2006). Elytron length is the average length of the maximum distance along the midline of the two elytra. Elytron width is the average width of the widest section of the two elytra. Pronotum width is the widest section of the pronotum.

We estimated sexual size dimorphism (SSD) for each population using the Lovich and Gibbons (1992) index, in which $SSD = (\text{size of the larger sex} / \text{size of the smaller sex}) - 1$, made positive when females are the larger sex and negative when males are the larger sex. Using this index, $SSD = 0$ when the sexes are equal in size, and $SSD < 0$ or $SSD > 0$ indicates that males or females are larger, respectively. This index has the best statistical properties of all dimorphism indexes that have been proposed (Lovich and Gibbons 1992; Smith 1999). We used this index for measuring dimorphism instead of examining sex-by-latitude and sex-by-environment interactions in ANOVA because these interactions are biased by scale effects (Dobson and Wigginton 1996; Blanckenhorn et al. 2006).

Environmental Data

Climatic data were obtained from the National Oceanic and Atmospheric Administration's Global Surface Summary of Day database, version 6.0 (<http://www.ncdc.noaa.gov>; National Climatic Data Center, Asheville, NC) for an 11-year period (January 1994–December 2004). To estimate the climatic conditions for each site, we gathered data from the weather station nearest to each population.

Thirteen climatic variables were estimated for each population: average annual mean temperature, average annual minimum temperature, average annual maximum temperature, average annual dew point temperature (an es-

timate of water content of air [absolute humidity]; analyses using relative humidity gave qualitatively similar results—however, we did not use relative humidity because it is a function of dew point temperature and temperature and our model includes both dew point temperature and temperature separately), average annual precipitation, average mean temperature during the season in which beetles were most active, average minimum temperature during the season in which beetles were most active, average maximum temperature during the season in which beetles were most active, average dew point temperature during the season in which beetles were most active, average precipitation during the season in which beetles were most active, average within-year variance in temperature, average within-year variance in dew point temperature, and average within-year variance in precipitation. Annual means were calculated by averaging the daily mean temperatures within each month and then among months within each year. We also calculated means for the period of the season when *S. limbatus* were believed to be most active (estimated as the month before, during, and after the month of collection, a 3-month period). We adjusted mean temperatures for adiabatic heating and cooling ($0.65^\circ\text{C}/100\text{ m}$) because some weather stations had different elevations from those of collection sites (average difference = 118 m). Within-year variances were estimated by taking the average (among years) of the variance among months within years (we did not use the coefficient of variation because it is calculated using the mean in the denominator and is thus not independent of the means included in the analysis; we thus examined means and variances separately). Years that were missing data for any month were not used in estimates. Uninfested seeds (seeds without beetle emergence holes) from each collection locality were weighed on an electronic balance to estimate seed mass.

Statistical Analyses

All data were analyzed with SAS 9.1 (SAS Institute, Cary, NC). Population means rather than individuals were used as data points to avoid the nonindependence of individuals within sites (Gilchrist et al. 2004). We used principal component analysis (PROC PRINCOMP, standardized variables) on the population means to create a single variable for body size from our three morphological measures (population means of the three morphological traits and the three dimorphism indexes are listed in table A1). The first principal component (PC1), which represents body size, was used as the dependent variable in the analysis of clinal patterns. PC1 explained 97% of the variance in elytron length, elytron width, and pronotum width. Principal component analysis was also used to generate a single index of SSD from the three estimates of SSD generated

from our morphological measures. PC1 for sexual dimorphism explained 95% of the variance in our three dimorphism indexes. Both PC1 for body size and PC1 for SSD were normally distributed and thus were not transformed before analysis. Because the other principal components for body size and dimorphism accounted for so little of the remaining variation, we do not consider them further.

Regression analysis was used to examine the influence of the environmental variables on body size. However, because of the large number of separate variables that are correlated with each other, we first used principal component analysis on standardized variables (correlation matrix) to group related variables into three distinct climate indexes: temperature (annual mean temperature, annual minimum temperature, annual maximum temperature, active season mean temperature, active season minimum temperature, and active season maximum temperature; PC1 accounted for 53% of the variation), moisture (mean annual humidity, mean annual precipitation, mean active season humidity, and mean active season precipitation; PC1 accounted for 67% of the variation), and seasonality (within-year variation in temperature, within-year variation in humidity, and within-year variation in precipitation; PC1 accounted for 73% of the variation). Although PC1_{temperature} accounted for only 53% of the variation in temperature among populations, PC2_{temperature} (which accounts for an additional 29%) represents primarily seasonality (positive loadings of annual minimum temperature and active season minimum temperature and negative loadings of annual maximum temperature and active season maximum temperature) and is thus included in our analyses as PC1_{seasonality}. These three variables plus latitude and seed size were examined using linear regression to test whether they correlated with body size. We used this approach to identify a suite of climate variables to be used in a model selection procedure to determine which individual variables explain the variation in body size.

To find the most parsimonious model describing variation in PC_{body size}, we used Akaike's Information Criteria (AIC). This model selection criterion chooses a model that is a compromise between the amount of variance explained and the number of parameters included in the model (Burnham and Anderson 2002). The model with the lowest AIC score was chosen as the most parsimonious model. We do not present individual parameter estimates from the multiple regression of the variables in the AIC best-fit model because some variables were highly correlated (multicollinear). Multicollinearity is not problematic for determining which set of variables explains variation in the dependent variable (i.e., selection of the AIC best-fit model) or for assessing the fit of the model to the data, but it does make interpretation of the relationship be-

tween each single independent variable and the dependent variable difficult and often misleading (Graham 2003).

It is possible that the most parsimonious model contains variables that contribute little to the overall variation in body size or sexual dimorphism. To test whether variables were essential to the model, we sequentially removed individual terms to see whether deletion of any one of the variables significantly reduced the fit of the model. The fit of the AIC best-fit model was compared to that of the reduced model (missing one parameter) by using a likelihood ratio test with the number of degrees of freedom equal to the difference in the number of parameters between the two models.

Results

Geographic Variation in Body Size of Stator limbatus

Body size of *Stator limbatus* co-varied significantly with latitude (PC_{body size}: $r^2 = 0.18$, slope $[\beta] = 0.05 \pm 0.01$, $t = 4.45$, $df = 93$, $P < .0001$); beetles were smallest in the tropics and increased in size with increasing latitude (fig. 2), consistent with many other studies supporting Bergmann's rule (Blanckenhorn et al. 2006). Although there is a clear cline in body size, three populations were outliers. These populations were below the equator on the coast of Ecuador and were considerably larger than those from the nearest populations in Colombia (fig. 2). Excluding these populations from the analysis increased the strength of the cline ($r^2 = 0.28$, $\beta = 0.07 \pm 0.01$, $t = 5.91$, $df = 90$, $P < .0001$). After considering the climate indexes, only one of these Ecuador populations (Manabi Province) remained a marginal outlier (fig. 3), suggesting that the climate along the west coast of South America, which is drier and cooler than the rest of the continent because of the Humboldt current, explains the large size of these beetles.

Because latitudinal gradients in temperature are frequently hypothesized to produce latitudinal clines in body size of animals, we expected temperature to be the best explanatory variable of the cline in body size. However, the temperature index was not correlated with body size (fig. 3; PC_{temperature}: $r^2 = 0.0002$, $\beta = 0.01 \pm 0.07$, $t = 0.14$, $df = 93$, $P = .89$). Instead, beetle body size was significantly associated with host plant seed size, moisture, and seasonality (fig. 3); body size increased with increasing seed size ($r^2 = 0.12$, $\beta = 6.23 \pm 1.78$, $t = 3.5$, $df = 91$, $P = .0007$), increasing seasonality (PC_{seasonality}: $r^2 = 0.15$, $\beta = 0.31 \pm 0.08$, $t = 4.04$, $df = 93$, $P < .0001$), and decreasing moisture (PC_{moisture}: $r^2 = 0.08$, $\beta = -0.21 \pm 0.07$, $t = -2.90$, $df = 93$, $P = .005$).

We thus examined models that included latitude, seed size, and the individual variables that compose PC_{moisture} and PC_{seasonality} (nine variables = 512 candidate models).

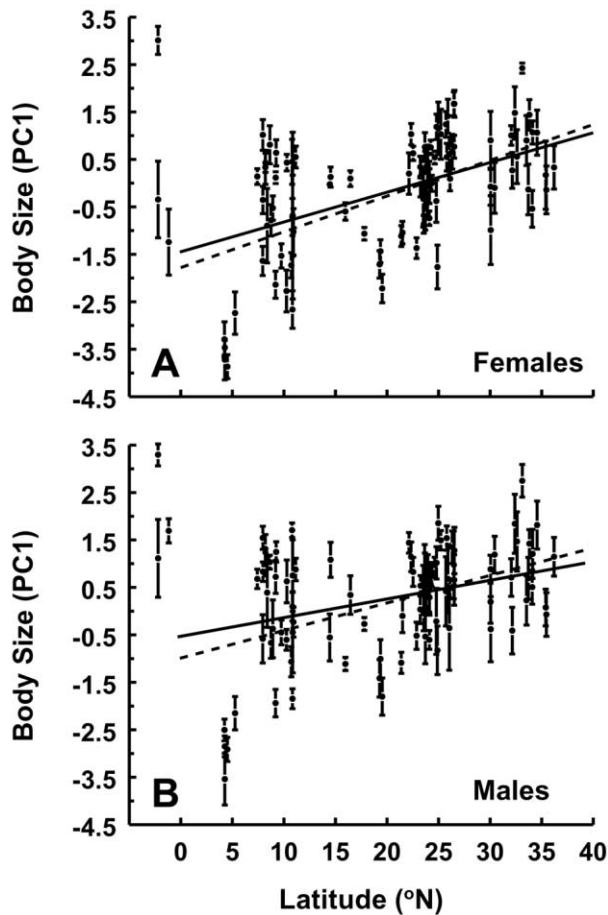


Figure 2: Plot of the first principal component (PC1) for adult body size versus latitude ($^{\circ}\text{N}$) of females (A) and males (B) of *Stator limbatus*. Note that the three populations to the far left of the figure (Ecuador populations) are substantially larger bodied than neighboring populations. The solid line is the regression including all 95 populations. The dashed line is the regression excluding the three Ecuador populations. Latitudes to the left of 0 are south of the equator ($^{\circ}\text{S}$), while latitudes to the right of 0 are north of the equator ($^{\circ}\text{N}$).

The AIC best-fit model (model $r^2 = 0.43$, $F = 13.1$, $df = 5, 87$, $P < .0001$) included five variables: host plant seed size, annual mean humidity, within-year variation in temperature, within-year variation in humidity, and within-year variation in precipitation. Removal of any one of these five individual variables significantly reduced the fit of the model ($\chi^2 > 6.5$, $df = 1$, $P < .02$ for all variables). Furthermore, addition of all six temperature variables either simultaneously ($\chi^2 = 4.8$, $df = 6$, $P = .57$) or individually ($\chi^2 < 1.2$, $df = 1$, $P > .27$ for all variables) did not significantly improve the fit of the model to the data. Also, although we must be cautious when interpreting significance of specific variables due to multicollinearity (Graham 2003), in no case were the temperature variables

significant in the expanded six-variable ($P > .31$ for each) or 11-variable model ($P > .36$ for each).

Geographic Variation in Sexual Size Dimorphism of *S. limbatus*

Overall, males of *S. limbatus* were considerably larger than females (sex effect in ANOVA: $F = 7.74$, $df = 1, 187$, $P = .006$), consistent with previous studies of *S. limbatus* (Savalli and Fox 1998; Stillwell and Fox 2005). However, sexual size dimorphism varied substantially with latitude ($PC_{\text{dimorphism}}$: $r^2 = 0.15$, $\beta = 0.07 \pm 0.02$, $t = 4.00$, $df = 93$, $P = .0001$); beetles were most dimorphic in the tropics and decreased in dimorphism with increasing latitude (fig. 4). The cline in sexual dimorphism appears to be due to a gender effect on the slope of the latitudinal cline; the cline in female size ($r^2 = 0.22$, $\beta = 0.06 \pm 0.01$) was steeper than the cline in male size ($r^2 = 0.1$, $\beta = 0.04 \pm 0.01$; fig. 2A, 2B).

Temperature and seed size were not correlated with sexual size dimorphism ($PC_{\text{temperature}}$: $r^2 = 0.001$, $\beta = -0.03 \pm 0.10$, $t = -0.30$, $df = 93$, $P = .76$; seed size: $r^2 = 0.007$, $\beta = 2.11 \pm 2.63$, $t = 0.80$, $df = 91$, $P = .43$). However, beetles were most dimorphic in populations where moisture was highest (PC_{moisture} : $r^2 = 0.06$, $\beta = -0.25 \pm 0.10$, $t = -2.45$, $df = 93$, $P = .02$) and where seasonality was lowest ($PC_{\text{seasonality}}$: $r^2 = 0.09$, $\beta = 0.34 \pm 0.11$, $t = 3.07$, $df = 93$, $P = .003$). We thus examined models that included latitude and the individual variables that compose PC_{moisture} and $PC_{\text{seasonality}}$ (eight variables = 256 candidate models). Only one environmental variable (mean humidity during the active season) was present in the AIC best-fit model (model $r^2 = 0.20$, $F = 11.8$, $df = 2, 92$, $P < .0001$). However, the latitudinal cline in dimorphism persists even after removing the humidity effect (the AIC best-fit model includes both latitude and mean humidity of the active season—removal of either variable significantly reduced the fit of the model; $\chi^2 > 6.6$, $df = 1$, $P < .02$ for both variables). This indicates that unmeasured ecological and/or environmental variables must contribute to producing this cline in sexual dimorphism. When we separately examined the environmental variables that affected the clines in female and male size, we found that the AIC best-fit model was the same for both sexes and consisted of the same five variables we found for the overall cline in size.

Discussion

In this study we found that *Stator limbatus* adults were smallest in the tropics and increased in size with increasing latitude; that is, their body size follows Bergmann's rule. This variation in body size is at least partly genetic; in

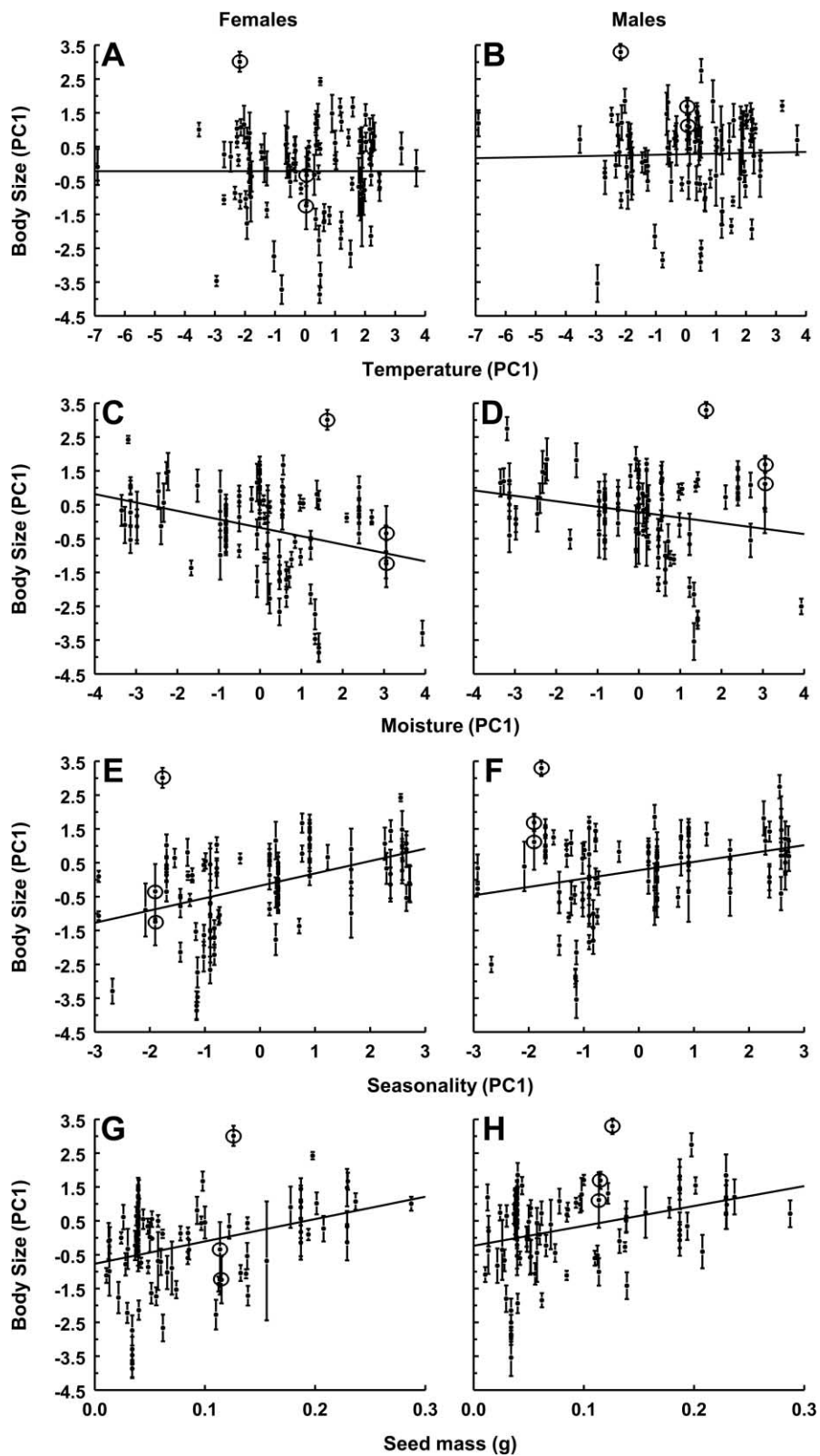


Figure 3: Plot of the first principal component (PC1) for adult body size of *Stator limbatus* versus PC1 for temperature (A, B), PC1 for moisture (C, D), PC1 for seasonality (E, F), and seed mass (G, H). Circles denote the three Ecuador populations.

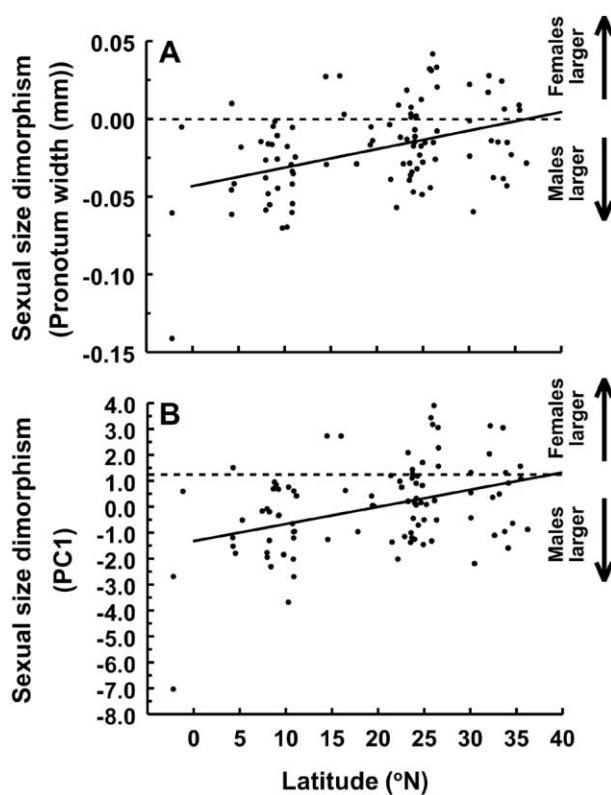


Figure 4: Geographic variation in sexual size dimorphism of pronotum width (A) and the first principal component (PC1; B) for the three dimorphism indexes for adults of 95 populations of *Stator limbatus*. PC1 was used for all analyses; pronotum width is plotted to illustrate the pattern. Sexual size dimorphism was calculated for each population using the Lovich and Gibbons (1992) index, in which size dimorphism = (mean size of the larger sex/mean size of the smaller sex) – 1, made positive when females are the larger sex and negative when males are the larger sex. The dashed lines indicate the point where populations are monomorphic (no dimorphism). Note that populations become less dimorphic with increasing latitude (the regression line approaches the dashed line). Latitudes to the left of 0 are south of the equator (°S), while latitudes to the right of 0 are north of the equator (°N).

laboratory common garden experiments, *S. limbatus* from populations collected at lower latitudes (Colombia) are genetically smaller than beetles from populations collected at higher latitudes (Arizona and Texas; Amarillo-Suárez 2006; Amarillo-Suárez and Fox 2006). In contrast to the most widely accepted hypothesis, the cline in body size we observed is not concordant with a latitudinal gradient in mean temperature. This is not surprising considering that mean annual temperature differs <math><15^{\circ}\text{C}</math> between the dry tropical forests of South and Central America and the deserts of Mexico and the southwestern United States (though variance in temperature varies substantially along the cline). Instead, we found that the cline in body size is better explained by host plant seed size, moisture (hu-

midity), and seasonality (variance in humidity, precipitation, and temperature). Because our study is correlational, we cannot distinguish between cause and effect. However, our results do suggest that these variables, and not average temperature, are the best candidate environmental factors to explain latitudinal clines in seed beetle body size. We also found that sexual size dimorphism varied with latitude; dimorphism was most pronounced in the tropics and decreased with increasing latitude.

Geographic Variation in Moisture

Moisture (rainfall and humidity) often varies as consistently with latitude as does temperature; tropical regions are characterized by high rainfall and humidity, both of which decrease with increasing latitude. Recent studies have shown that moisture can be more highly correlated with intraspecific variation in body size of animals than can temperature (Burnett 1983; Yom-Tov and Nix 1986; Yom-Tov and Geffen 2006), suggesting that moisture is a more important mediator of selection on body size than is temperature.

Large size reduces the surface-to-volume ratio and increases absolute water content (Chown and Gaston 1999). Any gradient in moisture will thus likely generate variation in selection on body size via variation in desiccation resistance (Schoener and Janzen 1968; Le Lagadec et al. 1998). In *Drosophila*, both body size and desiccation resistance increase with increasing latitude (Hoffmann and Harshman 1999; Gilchrist et al. 2001) and co-vary among natural populations (Van Herrewege and David 1997). Selection for increased desiccation resistance also results in a correlated increase in body size (Telonis-Scott et al. 2006), and large body size evolves rapidly in response to low versus high relative humidity (Kennington et al. 2003). These results suggest that gradients in moisture can generate latitudinal clines in insects.

Body sizes of *S. limbatus* were smallest in the wetter tropical regions of its geographic range (northern South America and Central America) and increased in size with decreasing moisture availability. Larval growth and pupation take place entirely within a single seed, where beetles are largely protected from the external environment by an impermeable seed coat. However, adults live outside of seeds exposed to ambient humidity. Consequently, resistance to dehydration in adult *S. limbatus* is likely essential for survival and reproduction in arid habitats, imposing selection on adult body size and potentially generating the observed latitudinal cline. Interestingly, populations of *S. limbatus* from Arizona (the northern end of the distribution) do not require water as adults to reproduce, even in low-humidity conditions. In contrast, populations from Colombia (the southern end of the dis-

tribution) cannot reproduce without access to water and high ambient humidity (Amarillo-Suárez 2006). We suggest that populations from Arizona are able to tolerate drier conditions as adults because they are larger, whereas populations from Colombia are small enough to rapidly desiccate in drier conditions and thus need access to water.

Geographic Variation in Seasonality

Seasonality increases with latitude and could generate the clines in selection that create clines in animal size and life-history traits (Boyce 1978; Murphy 1985; Wigginton and Dobson 1999; Ashton 2001). In seasonal environments, organisms must tolerate periods of stressful conditions. Insects typically tolerate these stressful conditions in a dormant state (diapause). During prolonged intervals of diapause, selection on body size is likely to be significant (Matsuo 2006). For example, there may be selection for large-bodied individuals that are able to resist starvation during periods of food shortage or to resist desiccation during prolonged dry periods. The strength of selection is also likely to increase with the duration of unfavorable periods, which varies geographically.

Body sizes of *S. limbatus* generally increased with increasing seasonality of the environment (within-year variation in temperature, humidity, and precipitation). This cline is likely caused by seasonality in host availability, which is driven by seasonality in climate. Bruchine seed beetles undergo reproductive diapause as adults during much of the dry season and the beginning of the rainy season when host seeds are absent or scarce (Biemont and Bonet 1981; Monge et al. 1989; Lenga et al. 1991; Monge and Huignard 1991; Zannou et al. 2003; Amevoin et al. 2005). Although variation in reproductive diapause has not been studied in *S. limbatus*, populations of *Acanthoscelides obtectus* exhibit reproductive diapause in central Mexico during the season when host seeds are absent, but they do not show reproductive diapause in Colombia, where the host plant is available to them throughout much of the year (Biemont and Bonet 1981). Availability of *S. limbatus* hosts is limited to the short wet season at the northern end of the range of *S. limbatus* but is spread out through the year in the tropics, generating geographic variation in the need to undergo diapause and likely geographic variation in selection on traits affecting survival through diapause (such as size).

Geographic Variation in Host Seed Size

Ecological factors, such as predation and competition, may be as important as climate in producing geographic variation in body size (Ashton et al. 2000). For insects that develop inside discrete hosts, such as parasitoids and seed-

feeding beetles, host size constrains growth, imposing substantial selection on body size and life-history traits (Hardy et al. 1992; Mackauer and Chau 2001). Host size can influence the evolution of body size by constraining the resources needed for the growth of a single individual (i.e., an individual cannot grow to be large on very small seeds) or through variation in the intensity of larval competition. *Stator limbatus* are typically found developing at >1 larvae/seed, though larval competition has less effect on offspring in larger seeds (Fox et al. 1996). Consequently, clines in seed size can generate clines in traits of their herbivores. For example, seed size of hosts of the camellia weevil *Curulio camelliae* varies geographically (Toju and Sota 2006). Our reanalysis of the data in table 1 of Toju and Sota (2006) found that both beetle body size (simple linear regression: $r^2 = 0.32$, $P = .03$) and seed size ($r^2 = 0.8$, $P < .0001$) declined substantially with latitude, with seed size explaining 45% of the variance in body size ($r^2 = 0.45$, $P = .006$). In bruchine seed beetles, species that use small seeds are generally smaller bodied than species that use large seeds (Dickason 1960; Center and Johnson 1974; Toquenaga and Fuji 1990; Amarillo-Suárez and Fox 2006), indicating that seed size is likely an important selective agent for adult body size. The hosts of *S. limbatus* vary substantially in seed size, increasing in size from lower latitudes to higher latitudes, and *S. limbatus* were largest on the largest-seeded hosts. This variation in body size is at least partly genetic; in laboratory common garden experiments, *S. limbatus* from populations collected from small-seeded hosts are genetically smaller than beetles from populations collected from larger hosts (Amarillo-Suárez 2006; Amarillo-Suárez and Fox 2006).

Geographic Variation in Sexual Size Dimorphism

In *S. limbatus*, body size of both males and females increased with latitude, but female size exhibited a steeper latitudinal cline than did male size (beetles were most dimorphic at lower latitudes and least dimorphic at higher latitudes), contrary to the general pattern found among animals (Blanckenhorn et al. 2006) and opposite Rensch's rule. A cline in sexual size dimorphism could be generated by systematic variation among populations in sexual selection on males (Fairbairn 2005; Blanckenhorn et al. 2006), possibly as a result of variance in the sex ratio (Garel et al. 2006). For example, sex ratios (proportion males) increase with latitude in some animals (Ketterson and Nolan 1976; Tamate and Maekawa 2006). The genetic sex ratio does not change among populations of *S. limbatus* (G. E. Morse, unpublished data), but we do not have data on operational sex ratios. Alternatively, variation in climate, or other ecological and environmental variables that vary with latitude, may have different fitness consequences

for male versus female body size. The only environmental variable associated with the latitudinal cline in sexual dimorphism of *S. limbatus* was humidity in the season when beetles are most likely to be active; dimorphism was greatest in environments where humidity was highest. Interestingly, sexual size dimorphism of the sugar glider *Petaurus breviceps* and the frog *Limnodynastes peronii* are greatest where precipitation is highest (Quin et al. 1996; Schäuble 2004), suggesting that body size effects on resistance to desiccation differ between males and females. However, for *S. limbatus*, the relationship between latitude and dimorphism persisted after correcting for the humidity effect, indicating that some unmeasured factors probably differentially affect selection on males and females and thus contribute to producing the observed cline. A better understanding of the mechanisms that generate latitudinal clines in dimorphism will require detailed studies of sexual differences in natural and sexual selection on body size.

Conclusions

Both body size and sexual size dimorphism co-vary with latitude in the seed-feeding beetle *S. limbatus*. However, the observed cline in body size is not concordant with a latitudinal gradient in mean temperature. Instead, our results suggest that clinal variation in three factors likely explains this cline in size: host plant seed size, moisture (humidity), and seasonality (within-year variation in humidity, precipitation, and temperature). Researchers should consider environmental variables other than mean temperature when exploring the sources of selection generating latitudinal clines in body sizes of animals. We also found that female size exhibited a steeper latitudinal cline than did male size (sexual size dimorphism was most pronounced in the tropics and decreased with increasing latitude). Future studies should thus focus on gender differences in clinal variation in natural selection to gain a more complete understanding of the mechanisms that generate these patterns.

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