WHEN RENSCH MEETS BERGMANN: DOES SEXUAL SIZE DIMORPHISM CHANGE SYSTEMATICALLY WITH LATITUDE?

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Abstract.—Bergmann's and Rensch's rules describe common large-scale patterns of body size variation, but their underlying causes remain elusive. Bergmann's rule states that organisms are larger at higher latitudes (or in colder climates). Rensch's rule states that male body size varies (or evolutionarily diverges) more than female body size among species, resulting in slopes greater than one when male size is regressed on female size. We use published studies of sex-specific latitudinal body size clines in vertebrates and invertebrates to investigate patterns equivalent to Rensch's rule among populations within species and to evaluate their possible relation to Bergmann's rule. Consistent with previous studies, we found a continuum of Bergmann (larger at higher latitudes: 58 species) and converse Bergmann body size clines (larger at lower latitudes: 40 species). Ignoring latitude, male size was more variable than female size in only 55 of 98 species, suggesting that intraspecific variation in sexual size dimorphism does not generally conform to Rensch's rule. In contrast, in a significant majority of species (66 of 98) male latitudinal body size clines were steeper than those of females. This pattern is consistent with a latitudinal version of Rensch's rule, and suggests that some factor that varies systematically with latitude is responsible for producing Rensch's rule among populations within species. Identifying the underlying mechanisms will require studies quantifying latitudinal variation in sex-specific natural and sexual selection on body size.

Key words.—Bergmann's rule, body size, meta analysis, Rensch's rule, sexual size dimorphism, sexual selection.

Received February 24, 2006.   Accepted July 3, 2006.

Large-scale patterns of body size variation have occupied biologists for over a century, yet the causes of some of these patterns remain elusive. One prominent pattern is Bergmann's rule, which describes the observation that organisms tend to be larger in colder climates and thus at higher latitudes (i.e., Bergmann clines: Bergmann 1847; Ashton 2004; Blanckenhorn and Demont 2004). This pattern initially described geographic variation among endothermic (warm-blooded) species only, but was later applied predominantly to patterns within species (Blackburn et al. 1999). The adaptive explanation originally suggested by Bergmann (1847) was that larger individuals have smaller surface-to-volume ratios, allowing them to conserve heat more efficiently in cold climates. However, evidence for birds and mammals is inconsistent, so the generality of this mechanism across taxa is doubtful (Geist 1987, 1990; Paterson 1990; Blackburn et al. 1999; Ashton et al. 2000; Ashton 2002). Moreover, Bergmann's rule also holds in many ectothermic (cold-blooded) organisms (Ray 1960; Ashton and Feldman 2003; Blanckenhorn and Demont 2004), for which the cause must be different because small ectotherms such as many insects acclimate to ambient temperature almost instantly (Stevenson 1985). A unifying explanation for Bergmann's rule is still lacking, although there is a growing consensus that Bergmann's rule seems to be effected by temperature per se rather than seasonality (Atkinson and Sibly 1997).

Ectotherms also display converse Bergmann clines, in which body size decreases toward the poles (Park 1949; Brennan and Fairbairn 1995; Mousseau 1997; Ashton 2004; Blanckenhorn and Demont 2004). This effect is clearly mediated by season length rather than temperature: shorter growing seasons at higher latitudes progressively limit the time available for foraging, growth, and development and hence the phenotypic body size that can be attained. As this outcome is predicted by optimality theory (Roff 1980; Rowe and Ludwig 1991), converse Bergmann clines are likely adaptive. Blanckenhorn and Demont (2004) recently demonstrated a continuum of Bergmann and converse Bergmann clines in arthropods, suggesting that both patterns are caused by different proximate factors (temperature and season length, respectively) that are not mutually exclusive.

A second prominent body size pattern is Rensch's rule, the observation widespread in the animal kingdom that male body size varies (or evolutionarily diverges) more than female body size among related species, such that male-biased sexual size dimorphism increases and female-biased sexual size dimorphism decreases with body size (Rensch 1950; Abouheif and Fairbairn 1997; Fairbairn 1997). Rensch's rule is manifested statistically in allometric slopes greater than one when male size is regressed on female size (Fairbairn 1997). The reasons for this pattern are unclear, and it is unlikely that any single mechanism is responsible for Rensch's rule across the broad range of taxa in which it is observed (Fairbairn 1997, 2005). However, it has been suggested that Rensch's rule may be driven by sexual selection for large male size in combination with a high genetic correlation in body size between the sexes (Fairbairn and Preziosi 1994; Fairbairn 1997, 2005; Székely et al. 2004). Though originally formulated to explain interspecific variation in sexual size dimorphism, a few studies have addressed
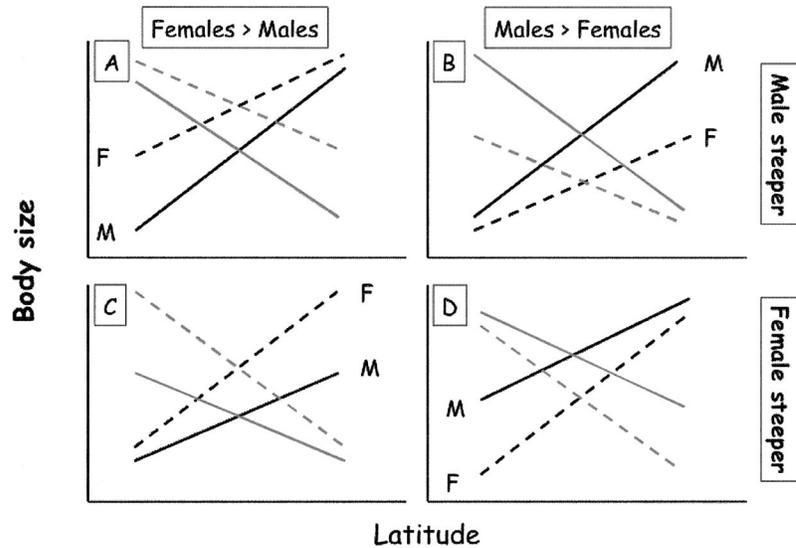
FIG. 1. The possible combinations of sex-specific (males, solid lines; females, broken lines) Bergmann (black and increasing with latitude) or converse Bergmann (gray and decreasing with latitude) body size clines with sexual size dimorphism (A, C, females larger; B, D, males larger); the male cline is steeper in (A, B), and the female cline is steeper in (C, D).

Rensch's rule by examining intraspecific, among-population variation in dimorphism, thereby testing the basic assumption that macroevolutionary patterns should be grounded in equivalent microevolutionary mechanisms. The results suggest, however, that Rensch's rule may (Fairbairn and Preziosi 1994; but see Fairbairn 2005; Young 2005) or may not hold among populations within species (Kraushaar and Blanckenhorn 2002; Gustafsson and Lindenfors 2004), depending on the taxon studied.

Although intraspecific (i.e., among-population) investigations of Rensch's rule are rare, intraspecific studies of Bergmann clines are common and typically investigate male and female body size by sampling several populations along a latitudinal gradient (Ashton 2004; Blanckenhorn and Demont 2004). Here we use published data on sex-specific latitudinal clines from 98 vertebrate and invertebrate species to comprehensively investigate patterns of Rensch's rule within species and their possible relationship with Bergmann clines. A logical null hypothesis is that male and female latitudinal clines have the same slope, regardless of whether the species exhibits Bergmann or converse Bergmann clines or whether males or females are larger. Two alternative hypotheses can be derived that are not mutually exclusive. First, if Rensch's rule is associated with clinal variation in body size, we predict that the slope of the body size on latitude regression should be steeper for males than females, which would result in greater among-population variation in male than female body size (male = steeper hypothesis; Fig. 1A,B). Thus, if males have steeper body size–latitude relationships than females, regardless of which sex is larger or whether the species exhibits Bergmann or converse Bergmann clines, we can conclude that the equivalent of Rensch's rule within species results from sex-specific latitudinal variation in body size. An alternative hypothesis derives from the positive relationship between mean and variance that is common in metric data: often a dataset with a greater mean also displays greater variance, which is one of the prime reasons for statistical

data transformation (Sokal and Rohlf 1995). This predicts that whichever sex is larger should be more variable and hence display a steeper latitudinal slope (larger = steeper hypothesis; Fig. 1B,C). Although log-transformation of data is thought to eliminate such mean-variance correlations in allometric studies and in general, this may not be true in all cases (Gould 1966; Lewontin 1966; Lande 1977; Bryant 1986; LaBarbera 1989; Sokal and Rohlf 1995; Eberhard et al. 1998). Thus, we ask a number of interrelated questions: Is latitude-independent geographic variation in sexual size dimorphism within species consistent with Rensch's rule? Do latitudinal clines differ systematically between the sexes; that is, does sexual size dimorphism increase, decrease, or show no consistent pattern with latitude? Is Rensch's rule within species mediated by consistently steeper latitudinal (Bergmann) clines in males than females?

MATERIALS AND METHODS

From the literature we obtained sex-specific body size data for 98 species (60 vertebrates and 38 invertebrates), displaying both Bergmann and converse Bergmann clines (see Appendix available online only at http://dx.doi.org/10.1554/06-110.1.s1). Studies reporting field (i.e., phenotypic) sizes and those reporting genetic sizes (i.e., when populations were reared under common-garden laboratory conditions) were included. We did not further differentiate these two study types for our purposes here because field estimates are typically qualitatively similar to genetic estimates for the few invertebrates for which both estimates are available (cf. Blanckenhorn and Demont 2004). Most species had at least five populations spanning a range of at least 4° latitude (see online Appendix).

For each species and each sex, we obtained or calculated from the publication an estimate of the overall mean body size as the mean of population means, a corresponding estimate of the standard deviation (SD) among populations,
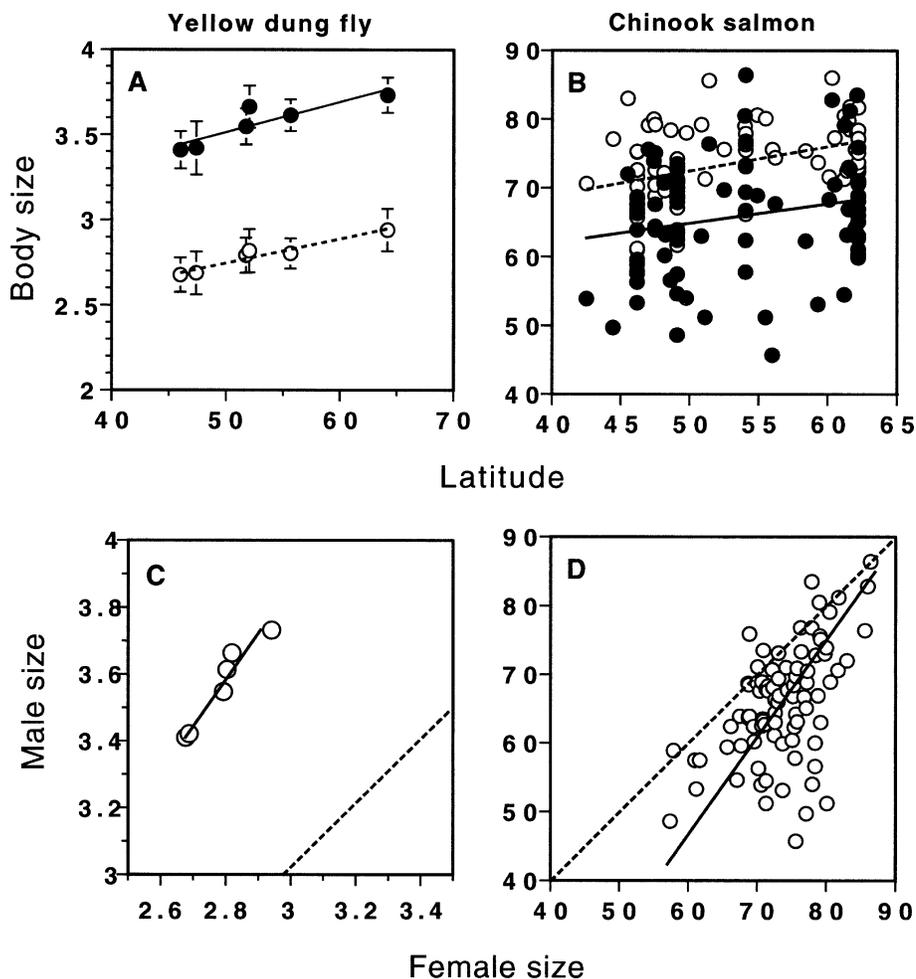
FIG. 2. Exemplary plots of (A, B) sex-specific latitudinal clines (males, filled circles and solid least-squares lines; females, open circles and broken lines), and (C, D) standard allometric plots of male on female body size (main diagonal hatched; solid major axis line, not taking logarithms here for clarity), for six populations of the yellow dung fly (A, C; body size, hind tibia length in mm) and 88 populations of Chinook salmon (B, D; body size, standard length in cm).

and an estimate of the linear regression slope of body size on latitude. Body size indices differed for the various taxa (see online Appendix), but because we only compared the sexes within species, this was of little concern here. If there was a choice, we used the estimate that best represents total body size. We made sure that all body size measures used were linear by computing the cube-root of body mass when body mass was given and otherwise using linear body length measures (LaBarbera 1989).

Because we wanted to relate sexual size dimorphism to the sex-specific slopes of latitudinal body size clines (Fig. 1), we produced an index of dimorphism and an analogous index of the latitudinal slopes for each species. We calculated Lovich and Gibbons's (1992) preferred index of sexual size dimorphism, SSD = (mean size of larger sex/mean size of smaller sex) − 1, arbitrarily set positive when males are larger and negative when females are larger. This index is symmetrical around zero and has the best statistical properties of all indices proposed (Lovich and Gibbons 1992). We analogously calculated a ratio of sex-specific latitudinal slopes. However, the ratio of slopes scales with sexual dimorphism. For ex-

ample, if males are twice as large as females at all latitudes (i.e., dimorphism does not vary with latitude), the slope of the size on latitude regression of males will be two times that of females. We corrected for this scaling effect by dividing the slope ratio by the ratio of mean body sizes (i.e., dimorphism), such that the expected slope ratio is unity if dimorphism does not vary with latitude (the null hypothesis). Hence we computed the corrected slope ratio = [(slope of larger sex/slope of smaller sex)/(size of larger sex/size of smaller sex)] − 1, arbitrarily positive when the male slope is larger and negative when the female slope is larger. Our correction neutralizes the scaling effect in a manner equivalent to log-transforming the original data (which were not available for many species).

We were also interested in whether the data conform to Rensch's rule independent of latitude. The standard analysis tests whether male size is more variable than female size among populations (Fairbairn 1997; cf. Fig. 2C,D). Thus, we calculated the reduced major axis slope of male size on female size. Least squares regression is inappropriate for tests of allometry because it assumes the independent variable
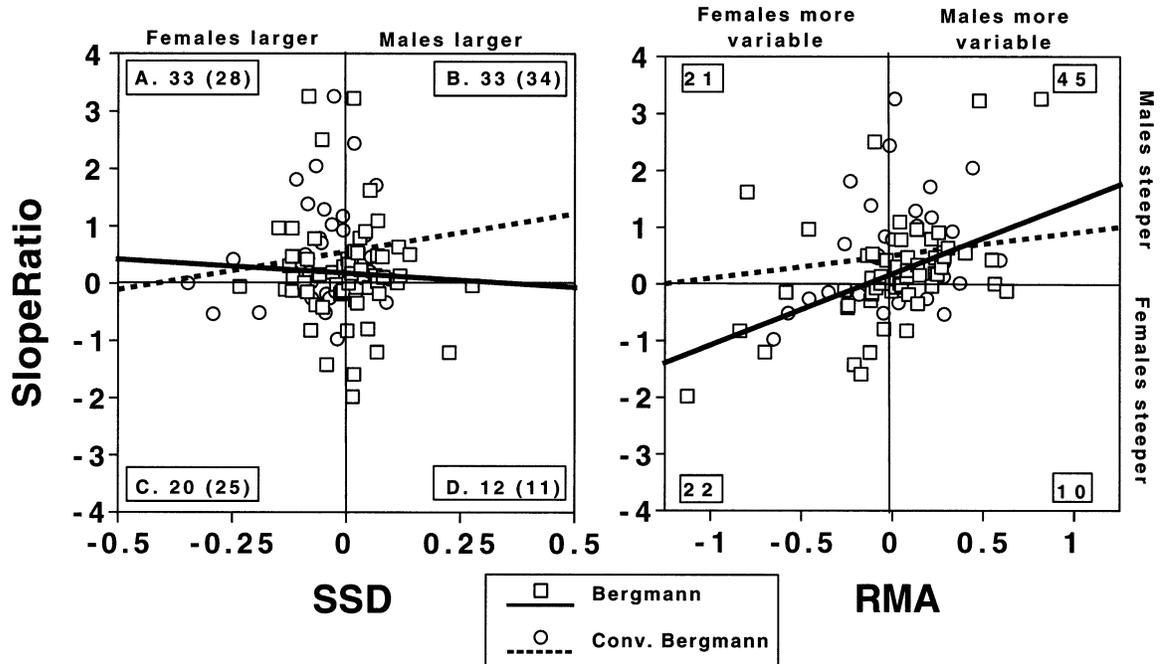
Fig. 3. Ratio of Bergmann (squares and solid least-squares line) or converse Bergmann (circles and broken line) latitudinal slopes (slope ratio) as a function of sexual size dimorphism (SSD; left panel) and the allometric slope of male on female body size across populations (RMA; right panel) for 98 animal species. The numbers denote the number of species falling into each of the four quadrants (the numbers in parentheses referring the uncorrected slope ratio), with letters corresponding to Figure 1 for the left panel.

(here female size) is measured without error, which is not the case (Sokal and Rohlf 1995; Abouheif and Fairbairn 1997; Fairbairn 1997). The reduced major axis (RMA) slope can be estimated as the ratio of male to female standard deviations (Sokal and Rohlf 1995). Like the ratio of latitudinal slopes described above (based on population means), the population SD estimates scale with the degree of dimorphism. So we calculated an equivalent RMA = [(SD of larger sex/SD of smaller sex)/(size of larger sex/size of smaller sex)] − 1, arbitrarily set positive when males are more variable and negative when females are more variable. Again, our correction is equivalent to the log-transformation of the original data necessary when investigating allometry (Gould 1966; Fairbairn 1997). Rensch's rule holds when the slope of RMA regression is greater than unity, that is, when RMA (which is scaled for the degree of dimorphism) is greater than zero.

In addition to simple binomial and *t*-tests, we analyzed variation in RMA, SSD, and slope ratio using nested ANCOVAs to test for effects (and hence remove variation) due to cline type (Bergmann vs. converse Bergmann), latitudinal range, population sample size, and phylogenetic effects (i.e., class, order within class, and family within order; e.g., Kappeler 1996; Jannot and Kerans 2003). All three indices met the assumptions of ANCOVA (i.e., the residuals were normally distributed), such that potential problems that can arise when analyzing ratios (e.g., LaBarbera 1989; Ranta et al. 1994) did not occur here due to the good statistical properties of the Lovich and Gibbons (1992) ratios. We did not test for significance of the SSDs, RMAs and latitudinal slopes of the individual species because, on average, we would not expect to reject the null hypothesis of no sex differences overall

unless there are systematic biases in these indices, as small random deviations should cancel out.

RESULTS

To illustrate the typical nature of the original data, Figure 2A,B shows Bergmann clines for males and females of six European yellow dung fly populations (*Scathophaga stercoraria*; Diptera: Scathophagidae; data redrawn from Blanckenhorn and Demont 2004) and 88 North American chinook salmon populations (*Oncorhynchus tshawytscha*; Salmoniformes: Salmonidae; data redrawn from Young 2005). In yellow dung flies, males are larger than females, yielding a positive SSD = 0.276 (Fig. 2A,C; see online Appendix). The species also follows Rensch's rule, with male size being more variable than female size, yielding RMA = 0.340 (Fig. 2C). Whereas for the raw data the male Bergmann cline is steeper than the female cline (uncorrected slope ratio = 0.254; Fig. 2A), the female Bergmann cline is actually slightly steeper when corrected (corrected slope ratio = −0.018) because SSD is greater than the uncorrected ratio of latitudinal slopes. This puts the datapoint of this species in quadrant D of Figure 3 (cf. Fig. 1), such that it confirms neither the male = steeper nor the larger = steeper hypotheses outlined in the introduction. This example also clearly illustrates the importance of removing scaling effects from the analysis, as the sign of the slope ratio changed after correction (which, however, occurred in only a small fraction of species analyzed). In contrast, chinook salmon females are larger on average, yielding a negative SSD = −0.119 (Fig. 2B,D; see online Appendix). In agreement with the larger = steeper hypothesis,

but contradicting the male = steeper hypothesis, the female Bergmann slope is steeper (Fig. 2B), with a corrected slope ratio = -0.125, putting the datapoint of this species in quadrant C of Figure 3 (cf. Fig. 1). Nevertheless, a positive RMA = 0.313 indicates that when the populations are not ordered by latitude, male body size is more variable, following Rensch's rule (Fig. 2D).

The left panel of Figure 3 shows the distribution of the data for all 98 species into the four quadrants corresponding to the four slope ratio/SSD combinations outlined in Figure 1A–D. Although with great scatter, there is clear evidence of a nonrandom distribution of datapoints: species are over-represented in quadrants A and B, supporting the male = steeper hypothesis (66 vs. 32 species; one-tailed binomial test: $P = 0.0004$; Fig. 3). (Note that this was the case even before slope correction: 62 vs. 36 species, $P = 0.006$.) In contrast, the data do not generally support the larger = steeper hypothesis when comparing quadrants B plus C on the main diagonal with quadrants A plus D (53 vs. 45 species, $P = 0.240$), although this difference had been significant before slope correction (59 vs. 39 species, $P = 0.027$). At the same time, the RMA is positive (i.e., consistent with Rensch's rule) in 55 species and negative in 43 species ($P = 0.133$), indicating little overall support for within-species (among-population) Rensch's rule in our sample of 98 species when latitude is ignored (right panel of Fig. 3). Analyzing the three indices using parametric, one-sample t-tests yielded consistent results. The overall mean slope ratio was 0.312 ± 0.182 (95% CI) and hence significantly male biased ($t_{97} = 3.36$, $P = 0.001$), while the overall mean SSD was only slightly but significantly female biased (-0.025 ± 0.023; $t_{97} = -2.13$, $P = 0.035$), and the overall mean RMA was not significantly different from zero (-0.009 ± 0.076; $t_{97} = -0.23$, $P = 0.818$). Note also that the mean slope ratio was significantly more positive than the mean RMA (paired t-test: $t_{97} = 3.66$, $P < 0.001$).

Using nested ANCOVA, we simultaneously tested for effects of cline type (Bergmann vs. converse Bergmann), latitudinal range, population sample size and phylogenetic effects (i.e., class, order within class, and family within order) on slope ratio, SSD, and RMA. Slope ratio showed no phylogenetic signal whatsoever, with class, order, and family effects all $P > 0.4$, so they were dropped from the final model. The number of populations and the latitudinal range sampled also did not affect the slope ratio (both $F_{1,92} < 1$, $P > 0.4$). However, the slope ratio was overall greater, that is, the male slope relatively steeper, in those 40 species exhibiting converse Bergmann clines (mean $\pm$ 95% CI: 0.532 ± 0.274) than in the 58 species exhibiting Bergmann clines (0.161 ± 0.237; effect of cline type: $F_{1,92} = 4.97$, $P = 0.028$; Fig. 3).

Analogously analyzing SSD revealed some phylogenetic signal at the order ($F_{19,21} = 2.53$, $P = 0.021$) and family levels (marginally nonsignificant: $F_{21,47} = 1.62$, $P = 0.084$), but not the class ($F_{5,19} = 1.16$, $P = 0.365$). The other effects of cline type, number of populations, and the latitudinal range sampled were all nonsignificant in the full model (all $F_{1,47} < 2$, $P > 0.2$).

Likewise, RMA showed no phylogenetic signal, so class, order, and family were dropped from the model. However, all other main effects were significant or nearly so. RMA

tended to be negative, opposite to Rensch's rule, for the 40 species exhibiting converse Bergmann clines but slightly positive for those 58 species that exhibit Bergmann clines: -0.047 ± 0.133 (95% CI) versus 0.017 ± 0.080 (marginal effect of cline type, $F_{1,92} = 3.17$, $P = 0.078$). RMA further correlated positively with slope ratio ($F_{1,92} = 13.83$, $P < 0.001$, partial $r = 0.31$; right panel in Fig. 3) and the number of populations sampled (marginally significant: $F_{1,92} = 3.89$, $P = 0.052$, partial $r = 0.18$), negatively with latitudinal range ($F_{1,92} = 9.82$, $P = 0.002$, partial $r = -0.29$), but not at all with SSD ($F_{1,92} = 0.23$, $P = 0.636$, partial $r = -0.02$).

Lack of phylogenetic effects on slope ratio and RMA justifies our simple analyses performed first (where phylogeny was ignored) and rendered control via phylogenetic methods unnecessary (e.g., Purvis and Rambaut 1995).

DISCUSSION

The few studies to date testing whether intraspecific variation in sexual size dimorphism conforms to Rensch's rule have yielded mixed results (Fairbairn and Preziosi 1994; Kraushaar and Blanckenhorn 2002; Gustafsson and Lindenfors 2004; Fairbairn 2005; Young 2005). In contrast, within-species studies of Bergmann's rule are common and often report patterns of latitudinal variation in both male and female body size. We took advantage of 98 such studies to test whether the equivalent of Rensch's rule holds within species, whether males and females display consistently different latitudinal clines in body size, and whether there is a relationship between sex-specific latitudinal body size variation and Rensch's rule within species. Our dataset displayed the full range of male-biased (45 species) and female-biased (53 species) patterns of dimorphism, with the overall mean close to monomorphism, so it can be considered representative. We found that among-population geographic variation in size dimorphism conforms to Rensch's rule in only about half of all species when latitude is ignored; males have steeper latitudinal body size clines than females in two-thirds of all species; and the magnitude of the allometric slope between male and female size increases significantly with the ratio of male to female latitudinal clines in body size (but not with dimorphism). This latter statistical relationship between dimorphism allometry and sex-specific latitudinal clines in body size provides the first evidence that Rensch's and Bergmann's rule may be related within species.

As the taxonomically most exhaustive test to date, our results provide convincing evidence that intraspecific, among-population variation in sexual size dimorphism does not generally conform to Rensch's rule. This finding is consistent with the results of four previous studies of intraspecific variation in dimorphism: Fairbairn and Preziosi (1994; but see Fairbairn 2005) and Young (2005) found support for Rensch's rule, whereas Kraushaar and Blanckenhorn (2002) and Gustafsson and Lindenfors (2004) did not. This is contrary to the patterns among closely related species, where a great majority of largely vertebrate taxa display body size variation consistent with Rensch's rule (Abouheif and Fairbairn 1997; Fairbairn 1997). One possible explanation for this discrepancy across taxonomic scales is that establishment of consistent genetic differences in dimorphism among pop-

ulations, presumably due to sex-specific selection (Fairbairn and Preziosi 1994; Blanckenhorn 2000), is likely hampered by factors such as phenotypic plasticity (Fairbairn 2005), gene flow between populations (Kraushaar and Blanckenhorn 2002), temporal variability in selection on male or female size (e.g., Holtby and Healey 1990), or nonequilibrium dimorphism arising from the generally very high genetic correlation between male and female size (Lande 1980). Macroevolutionary patterns of sexual size dimorphism across species are less affected by these factors and should therefore better reflect evolutionary divergence in dimorphism over longer time scales (Fairbairn 1997, 2005). Nevertheless, identifying the putative microevolutionary mechanisms causing Rensch's rule among species requires studying variation in dimorphism among populations in detail in a greater number of species, as any general explanation should apply across taxonomic levels (Fairbairn 1997). Systematic differences among populations in sexual selection currently appear to be the most likely mechanism (Fairbairn and Preziosi 1994; Kraushaar and Blanckenhorn 2002; Fairbairn 2005; Tamate and Maekawa 2006). For example, if directional sexual selection on male body size is stronger than fecundity selection on female body size (with viability selection assumed to be equal), and if this difference varies systematically and consistently among populations depending on environmental factors, male size will increase faster than female size over evolutionary time (Fairbairn and Preziosi 1994; Kraushaar and Blanckenhorn 2002).

Male latitudinal clines were steeper than those of females in a significant majority of species (66 of 98; Fig. 3A,B), confirming the male = steeper hypothesis connecting Bergmann's and Rensch's rules (Fig. 1A,B), regardless of whether the species displays male- or female-biased size dimorphism. This supports the existence of a geographic version of Rensch's rule. Of course, this leaves approximately one-third of the species showing the opposite trend, underscoring the fact that several factors (discussed above and below) must be involved in generating these patterns. As previously shown for arthropods (Blanckenhorn and Demont 2004), we found a continuum of Bergmann (58 species) and converse Bergmann clines (40 species) in this taxonomically more diverse dataset (see also Ashton 2004). Interestingly, regardless of which sex is larger, the latitudinal decrease in male size (relative to female size), and hence change in sexual size dimorphism, in species with converse Bergmann clines was generally more pronounced than the corresponding relative male size increase with latitude in species with Bergmann clines (Fig. 1), implying that dimorphism changes faster with latitude in the former group. This relationship between cline type and magnitude of divergence in male and female size requires further study. We suspect the difference is mediated by sex-specific selection on body size due to season length limitations (producing converse Bergmann clines) being generally stronger than corresponding selection due to temperature (producing Bergmann clines: Roff 1980; Mousseau 1997; Blanckenhorn and Demont 2004). Identifying the mechanisms producing steeper male clines will require more studies quantifying latitudinal variation in sex-specific natural and sexual selection on body size. While the underlying mechanisms are often unclear, any latitudinal change in en-

vironmental factors (e.g., season length, food availability, or winter temperatures) that affects one sex more than the other can generate variation in male and female body size clines and thus in size dimorphism (e.g., Dobson and Wigginton 1996; Tamate and Maekawa 2006). In the house finch, for example, sexual selection favors large males but small females, whereas winter viability selection favors large females but small males, generating consistent spatial variation in sexual size dimorphism (Badyaev and Martin 2000; Badyaev et al. 2000; for a similar example in house sparrows, see Fleischer and Johnston 1984).

We found no general support for the larger = steeper hypothesis after correcting the latitudinal slope ratio for a scaling dependence on dimorphism: the larger sex had the steeper cline in about half the species, that is, as often as expected by chance. However, before correction there was weak support for this hypothesis. Thus, the scaling of the latitudinal body size slope with dimorphism documents an association of mean and variance, because body size of the larger sex has to change faster with latitude if dimorphism is to remain constant (see Materials and Methods). However, our analysis suggests that after correction (equivalent to a log-transformation) there are no further such statistical artifacts. Nevertheless, artifacts due to scaling or association of mean and variance can be a problem in studies of sexual size dimorphism and in general (Lewontin 1966; Lande 1977; Bryant 1986; LaBarbera 1989; cf. Teder and Tammaru 2005).

The mean RMA (cf. Fig. 2C,D) slope linking male to female body size was slightly less than one, (i.e., our RMA index corrected for dimorphism < 0) for those species exhibiting converse Bergmann clines, contrary to Rensch's rule, but it was one or slightly greater than one for species exhibiting Bergmann clines. Considered along with the fact that the mean ratio of male to female latitudinal slopes at the same time was greater than one (i.e., our slope ratio index > 0), this result again underscores the differences between the putative mechanisms mediating these two types of clines (season length vs. temperature) as discussed above (Blanckenhorn and Demont 2004). This result also underscores the important distinction between male on female body size slopes and the ratio of male-to-female latitudinal slopes. The former slope quantifies the relationship between male and female size across populations ignoring latitude (Figs. 2C,D). Thus, statistically, if male and female size are correlated across populations and male size is more variable than female size, the RMA slope will be greater than one (and our RMA index > 0), and the species conforms to Rensch's rule. In contrast, the ratio of male-to-female latitudinal slopes is explicitly spatial because population mean male and female body sizes are plotted against and hence ordered by latitude (Figs. 2A,B). A ratio of male-to-female latitudinal slopes greater than one indicates that the male latitudinal slope is steeper than that of the female, the effect now being generated by the latitudinal order of the populations. We therefore conclude that, while species do not generally conform to the intraspecific equivalent of Rensch's rule when populations are unordered, latitudinal variation in SSD among populations is consistent with Rensch's rule. That is, there is a statistical relationship between Rensch's rule and (converse) Bergmann latitudinal clines. This may also be an interesting

issue to explore among species. However, we cannot yet conclude this relationship is causal, because the mechanisms responsible for Rensch's rule and Bergmann clines (but not converse Bergmann clines) remain largely unclear (Roff 1980; Fairbairn 1997; Mousseau 1997; Blanckenhorn and Demont 2004).

The male on female body size RMA slope was positively correlated with the ratio of male-to-female latitudinal slopes (Fig. 3) but not with size dimorphism. The first result confirms our conclusion above, based on the overall positive value of the mean ratio of male-to-female latitudinal slopes, that some systematic latitudinal variable explains a significant proportion of the intraspecific allometry between male and female body size. However, other yet undiscovered processes operating independently of latitude must also be important. The second result indicates that there is no general relationship within species between the ratio of male-to-female variance in body size (i.e., RMA) and the corresponding ratio in body size means (i.e., SSD) after correction of scaling effects. This differs from the positive relationship observed among species and often attributed to variation in sexual selection on males (Fairbairn 1997). The RMA slope, but not the ratio of male-to-female latitudinal slopes or sexual size dimorphism, also correlated positively with the number of populations and negatively with the latitudinal range sampled (see online Appendix). The former may occur because more populations generate more variance and possibly also more differential variance in the larger versus the smaller sex. We cannot make much sense of the latter finding. However, it must be noted that because all these are partial correlations from one ANCOVA, the same argument cannot account for all these effects. It is likely that the two latter correlations merely reflect greater sampling error in studies with small sample size or latitudinal range.

Finally, phylogenetic effects did not explain a significant amount of variation in the relationship between male and female body size or the ratio of male-to-female latitudinal slopes in our dataset. In contrast, sexual size dimorphism did show some phylogenetic signal at the order and (marginally) the family level in our nested ANCOVAs. This result was not unexpected, as it is well known that dimorphism tends to be male biased in mammals and birds and female biased in most ectotherms (reviewed by Abouheif and Fairbairn 1997; Fairbairn 1997).

In summary, in our analysis of 98 species we found no general support for the traditional, nonspatial intraspecific version of Rensch's rule: male body size was more variable than female body size in only about half of all species. Instead we found evidence for a latitudinal version of Rensch's rule within species: male body size varied more with latitude than female body size, as males showed steeper body size–latitude relationships than females in about two-thirds of all species. We did not find support for the alternative hypothesis that the larger sex tends to have the stronger body size–latitude association. We conclude that latitudinal variation among populations is an important correlate or mediator of the intraspecific equivalent of Rensch's rule and that future studies should evaluate whether and how the type of latitudinal body size trend (Bergmann's rule or its converse) relates to sexual size differences and their putative selective causes (Roff

1980; Fairbairn 1997; Blanckenhorn 2000; Ashton 2004; Blanckenhorn and Demont 2004).

LITERATURE CITED

Abouheif, E., and D. J. Fairbairn. 1997. A comparative analysis of allometry for sexual size dimorphism: assessing Rensch's rule. Am. Nat. 149:540–562.

Ashton, K. G. 2002. Patterns of within-species body size variation of birds: strong evidence for Bergmann's rule. Global Ecol. Biogeogr. 11:505–523.

———. 2004. Are there general intraspecific patterns of body size variation in relation to latitude (and temperature) for tetrapod vertebrates? Integr. Comp. Biol. 44:401–412.

Ashton, K. G., and C. R. Feldman. 2003. Bergmann's rule in non-avian reptiles: turtles follow it, lizards and snakes reverse it. Evolution 57:1151–1163.

Ashton, K. G., M. C. Tracy, and A. de Queiroz. 2000. Is Bergmann's rule valid for mammals? Am. Nat. 156:390–415.

Atkinson, D., and R. M. Sibly. 1997. Why are organisms usually bigger in colder environments? Making sense of a life history puzzle. Trends Ecol. Evol. 12:235–239.

Badyaev, A. V., and T. E. Martin. 2000. Sexual dimorphism in relation to current selection in the house finch. Evolution 54: 987–997.

Badyaev, A. V., G. E. Hill, A. M. Stoehr, P. M. Nolan, and K. J. McGraw. 2000. The evolution of sexual size dimorphism in the house finch. II. Population divergence in relation to local selection. Evolution 54:2134–2144.

Bergmann, C. 1847. Über die Verhältnisse der Wärmeökonomie der Thiere zu ihrer Grösse. Göttinger Stud. 1:595–708.

Blackburn, T. M., K. J. Gaston, and N. Loder. 1999. Geographic gradients in body size: a clarification of Bergmann's rule. Divers. Distrib. 5:165–174.

Blanckenhorn, W. U. 2000. The evolution of body size: What keeps organisms small? Q. Rev. Biol. 75:385–407.

Blanckenhorn, W. U., and M. Demont. 2004. Bergmann and converse Bergmann latitudinal clines in arthropods: Two ends of a continuum? Integr. Comp. Biol. 44:413–424.

Brennan, J. M., and D. J. Fairbairn. 1995. Clinal variation in morphology among eastern populations of the waterstrider, *Aquarius remigis* Say (Hemiptera, Gerridae). Biol. J. Linn. Soc. 54: 151–171.

Bryant, E. H. 1986. On use of logarithms to accommodate scale. Syst. Zool. 35:551–559.

Dobson, F. S., and J. D. Wigginton. 1996. Environmental influences on the sexual dimorphism in body size of western bobcats. Oecologia 108:610–616.

Eberhard, W. G., B. A. Huber, R. L. Rodriguez, R. D. Briceno, I. Salas, and V. Rodriquez. 1998. One size fits all? Relationships between the size and degree of variation in genitalia and other body parts in 20 species of insects and spiders. Evolution 52: 415–431.

Fairbairn, D. J. 1997. Allometry for sexual size dimorphism: pattern and process in the coevolution of body size in males and females. Annu. Rev. Ecol. Syst. 28:659–687.

———. 2005. Allometry for sexual size dimorphism: testing two hypotheses for Rensch's rule in the water strider *Aquarius remigis*. Am. Nat. 166:S69–S84.

Fairbairn, D. J., and R. F. Preziosi. 1994. Sexual selection and the evolution of allometry for sexual size dimorphism. Am. Nat. 144:101–118.

Fleischer, R. C., and R. F. Johnston. 1984. The relationships between winter climate and selection on body size of house sparrows. Can. J. Zool. 62:405–410.

Geist, V. 1987. Bergmann's rule is invalid. Can. J. Zool. 65:1035–1038.

———. 1990. Bergmann's rule is invalid: a reply to J. D. Paterson. Can. J. Zool. 68:1613–1615.

Gould, S. J. 1966. Allometry and size in ontogeny and phylogeny. Biol. Rev. 41:587–640.

Gustafsson, A., and P. Lindenfors. 2004. Human size evolution: no evolutionary allometric relationship between male and female stature. J. Hum. Evol. 47:253–266.

Holtby, B., and M. Healey. 1990. Sex-specific life history tactics and risk-taking in coho salmon. Ecology 71:678–690.

Jannot, J. E., and B. L. Kerans. 2003. Body size, sexual size dimorphism, and Rensch's rule in adult hydropsychid caddisflies (Trichoptera: Hydropsychidae). Can. J. Zool. 81:1956–1964.

Kappeler, P. M. 1996. Intrasexual selection and phylogenetic constraints in the evolution of sexual canine dimorphism in strepsirhine primates. J. Evol. Biol. 9:43–65.

Kraushaar, U., and W. U. Blanckenhorn. 2002. Population variation in sexual selection and its effect on body size allometry in two species of flies with contrasting sexual size dimorphism. Evolution 56:307–321.

LaBarbera, M. 1989. Analyzing body size as a factor in ecology and evolution. Annu. Rev. Ecol. Syst. 20:97–117.

Lande, R. 1977. On comparing coefficients of variation. Syst. Zool. 26:214–217.

———. 1980. Sexual dimorphism, sexual selection and adaptation in polygenic characters. Evolution 56:307–321.

Lewontin, R. 1966. On measurement of relative variability. Syst. Zool. 15:141–142.

Lovich, J. E., and J. W. Gibbons. 1992. A review of techniques for quantifying sexual size dimorphism. Growth Dev. Aging 56:269–281.

Mousseau, T. A. 1997. Ectotherms follow the converse Bergmann's rule. Evolution 51:630–632.

Park, O. 1949. Application of the converse Bergmann principle to the carabid beetle, *Dicaelus purpuratus*. Physiol. Zool. 22:359–372.

Paterson, J. D. 1990. Bergmann's rule is invalid: a reply to V. Geist. Can. J. Zool. 68:1610–1612.

Purvis, A., and A. Rambaut. 1995. Comparative-analysis by independent contrasts (CAIC): an Apple-Macintosh application for analyzing comparative data. Comput. Appl. Biosci. 11:247–251.

Ranta, E., A. Laurila, and J. Elmberg. 1994. Reinventing the wheel: analysis of sexual dimorphism in body size. Oikos 70:313–321.

Ray, C. 1960. The application of Bergmann's and Allen's rules to the poikilotherms. J. Morphol. 106:85–108.

Rensch, B. 1950. Die Abhängigkeit der relativen Sexualdifferenz von der Körpergrösse. Bonn. Zool. Beitr. 1:58–69.

Roff, D. A. 1980. Optimizing development time in a seasonal environment: the 'ups and downs' of clinal variation. Oecologia 45:202–208.

Rowe, L., and D. Ludwig. 1991. Size and timing of metamorphosis in complex life cycles: time constraints and variation. Ecology 72:413–427.

Sokal, R. R., and F. J. Rohlf. 1995. Biometry. 3rd ed. Freeman, New York.

Stevenson, R. D. 1985. Body size and limits to daily range of body temperature in terrestrial ectotherms. Am. Nat. 125:102–117.

Székely, T., R. P. Freckleton, and J. D. Reynolds. 2004. Sexual selection explains Rensch's rule of size dimorphism in shorebirds. Proc. Natl. Acad. Sci. USA 101:12224–12227.

Tamate, T., and K. Maekawa. 2006. Latitudinal variation in sexual size dimorphism of sea-run Masu salmon, *Oncorhynchus masou*. Evolution 60:196–201.

Teder, T., and T. Tammaru. 2005. Sexual size dimorphism within species increases with body size in insects. Oikos 108:321–334.

Young, K. A. 2005. Life history variation and allometry for sexual size dimorphism in Pacific salmon and trout. Proc. R. Soc. Lond. B 272:167–172.

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