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Ehab Abouheif, Daphne J. Fairbairn

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A COMPARATIVE ANALYSIS OF ALLOMETRY FOR SEXUAL SIZE DIMORPHISM: ASSESSING RENSCH'S RULE

EHAB ABOUHEIF* AND DAPHNE J. FAIRBAIRN†

Department of Biology, Concordia University, 1455 de Maisonneuve Blvd., West, Montreal, Quebec H3G 1M8, Canada

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Abstract.—Rensch's rule states that sexual size dimorphism (SSD) increases with body size (hyperallometry) in taxa in which males are the larger sex and decreases with body size (hypoallometry) in those in which females are larger. We use the independent contrasts method to assess the validity and generality of Rensch's rule within 21 independent animal taxa. Allometry is estimated as the slope of the major axis regression of contrasts for log(female size) versus contrasts for log(male size). Allometry consistent with Rensch's rule is significant in 33% of the taxa examined across a diverse range of invertebrate and vertebrate taxa. Significant allometry inconsistent with Rensch's rule occurs in only one taxon. Meta-analysis of these results reveals that Rensch's rule is general and highly significant. Only owls have allometry inconsistent with this trend. Rensch's rule is also shown to be associated with male-biased SSD, which is consistent with the hypothesis that sexual selection acting on male size drives the evolution of this pattern of allometry.

Sexual differences in size and morphology are widespread in the animal kingdom. In most species of animals, females attain larger body sizes than do males (e.g., most spiders, insects, fish, amphibians, reptiles), whereas in most birds and mammals, males are the larger sex (Darwin 1874; Selander 1972; Ghiselin 1974; Ralls 1977; Alexander et al. 1979; Greenwood and Wheeler 1983; Arak 1988; Lewin 1988; Shine 1988; Hedrick and Temeles 1989). Rensch (1960) proposed a general rule relating sexual dimorphism to body size in birds and other animals. He stated, "Thus, the rule is valid that in numerous animal groups the sexual dimorphism increases with body size (B. Rensch, 1950). This rule, however, applies only to subspecies of a species, to related species of a genus, or to related genera of a family. In species of birds in which the male is larger than the female, the relative sexual difference increases with body size. If by way of exception, the females are larger than the males, as among many species of birds of prey, the opposite correlation applies, i.e. the greater sexual difference is found in the smaller species" (p. 159).

Rensch's rule thus predicts that sexual size dimorphism (SSD: size of the larger sex/size of the smaller sex) will be positively correlated with mean body size

* Present address: Department of Ecology and Evolution, State University of New York at Stony Brook, Stony Brook, New York 11794-5245; E-mail: ehab@life.bio.sunysb.edu.

† To whom correspondence should be addressed; E-mail: fairbrn@vax2.concordia.ca.

(hyperallometry) in taxa in which males are the larger sex and negatively correlated with mean body size (hypoallometry) in taxa in which females are the larger sex.

Rensch's rule has been widely accepted, and numerous hypotheses have been proposed to account for the covariation of body size and SSD, particularly in taxa in which males are the larger sex (e.g., Ralls 1977; Leutenegger 1978; Webster 1992; Fairbairn and Preziosi 1994). However, the generality of Rensch's rule has been questioned (Selander 1966; Reiss 1986), and empirical support is equivocal. A review of previous assessments of allometry for SSD indicates support for Rensch's rule in only 19 of 41 taxa (app. A). Moreover, these empirical assessments tend to be flawed by lack of control for phylogenetic autocorrelation and by absent or inappropriate statistical analyses. As an example of the latter, allometry is frequently assessed by regressing SSD or some other index of size dimorphism against the mean size of one or both sexes (e.g., Earhart and Johnson 1970; Wiley 1974; Moors 1980; Gibbons and Lovich 1990). This method is incorrect because the dependent and independent variables both contain mean size and are therefore not mathematically independent (LaBarbera 1989). The null hypothesis for such a relationship is not a slope of 0, and statistical tests of the derived slopes are therefore invalid. Of the 46 independent studies listed in appendix A, 12 use no statistical tests, 25 incorrectly assess allometry for SSD as described earlier, and only three remove the confounding influence of phylogeny using modern comparative methods. Although the allometric trends described by Rensch have been well documented within a few taxa, notably primates, New World blackbirds, and water striders (app. A), the generality of the trends, and hence the validity of Rensch's rule as a true ecological rule, have not been established.

The goal of this study is to determine the validity of Rensch's rule by quantitatively assessing allometry for SSD in 21 taxa within five classes: Mammalia, Aves, Reptilia, Insecta, and Arachnida. We quantify allometric trends using the regression method of Fairbairn and Preziosi (1994) and correct for phylogenetic effects using the method of independent contrasts (Felsenstein 1985; Harvey and Pagel 1991). The generality of allometric trends is then assessed quantitatively using the methods of meta-analysis (Hedges and Olkin 1985; Mullen and Rosenthal 1985; Gurevitch and Hedges 1993).

Although Rensch (1960) proposed a general pattern, several lines of evidence suggest that allometry consistent with Rensch's rule may be more common in taxa in which males are the larger sex. Previous empirical studies of allometry have found the predicted pattern in 66% of taxa with male-biased SSD but in only 48% of taxa with female-biased SSD (app. A). Further, allometry inconsistent with Rensch's rule has been reported in several taxa in which females are the larger sex (Earhart and Johnson 1970; Vollrath and Parker 1992; Head 1995). In addition to these empirical findings, several authors have proposed that allometry consistent with Rensch's rule evolves in response to sexual selection on male size (Clutton-Brock et al. 1977; Maynard Smith 1977; Leutenegger 1978; Webster 1992; Fairbairn and Preziosi 1994). Because such selection can be expected to occur more frequently in association with male-biased size ratios, allometry con-

sistent with Rensch's rule should occur more often in these taxa. To test this hypothesis, we assess allometry independently for taxa with female-biased SSD (females larger than males in >80% of species), male-biased SSD (males larger than females in >80% of species), and mixed SSD (both male- and female-biased SSD in 20%–80% of species). We also estimate the correlation across all 21 taxa between allometry, as indicated by the within-taxon effect sizes from the meta-analysis (Mullen and Rosenthal 1985), and the sexual dimorphism index of Gibbons and Lovich (1990).

METHODS

We obtained body size measurements and phylogenies for taxa in which at least 85% of species were reported as sexually dimorphic for body size (apps. B, C). The body size data consist of total body mass (g) for birds and mammals, total body length (mm) for spiders and insects, and snout-to-vent length (mm) for reptiles. All data sets include only sexually mature adults, with a minimum sample size (where reported) of nine for each sex.

To control for the confounding influence of phylogeny, we used Felsenstein's method of independent contrasts (Felsenstein 1985; Garland et al. 1992; Pagel 1992). We considered all unresolved nodes to be soft polytomies and used $n - 1$ contrasts and $c - 1$ degrees of freedom (where n represents the number of species and c , the number of nodes) throughout our analyses, as recommended by Purvis and Garland (1993). When branch length information was unavailable, we used Grafen's (1989) algorithm of assigning arbitrary branch lengths. These methods assume a Brownian motion model of character evolution (Felsenstein 1985). Although violations of this assumption may lead to inflated Type I error rates, computer simulation studies demonstrate that these become bounded at 0.1 for a nominal alpha of 0.05 when branch lengths are empirically verified and transformed (Díaz-Uriarte and Garland 1996). We empirically verified all proposed branch lengths and the adequate standardization of all contrasts by plotting the absolute value of each standardized contrast against its standard deviation (the square root of the sum of its branch lengths) (Garland et al. 1992). When significant linear or nonlinear trends were detected, we successfully removed them by a direct logarithmic transformation of all branch lengths.

Independent contrasts for $\log(\text{female size})$ and $\log(\text{male size})$ were calculated using the Phenotypic Diversity Analysis Program (PDAP version 2.0; Jones et al. 1993). We followed the convention of Garland et al. (1992) in giving a positive sign to the contrasts graphed on the horizontal axis, simultaneously switching the sign of the other contrasts as needed to standardize all graphical representations of independent contrasts.

To estimate the allometric exponent from the independent contrasts, we used Model II major axis regression through the origin (Garland et al. 1992) and regressed the contrasts of $\log(\text{female body size})$ against the contrasts of $\log(\text{male body size})$. As in the basic regression model (fig. 1; Fairbairn and Preziosi 1994), a slope < 1 indicates allometry consistent with Rensch's rule, a slope > 1 indicates

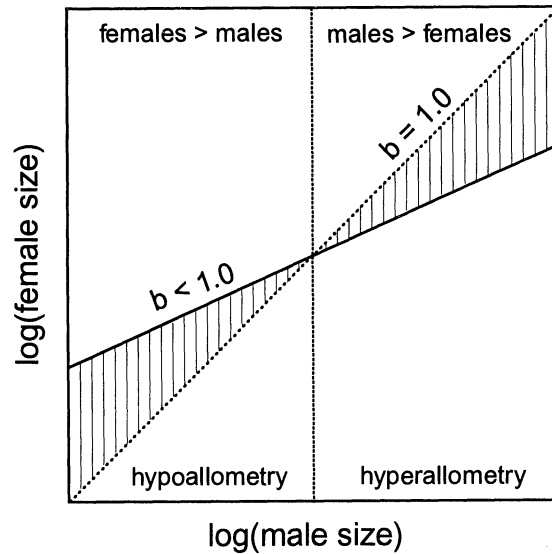


FIG. 1.—Quantitative resolution of Rensch's rule (from Fairbairn and Preziosi 1994). Allometry for SSD is based on the general allometric model, female size = $a(\text{male size})^b$ (Leutenegger 1978; LaBarbera 1989). The allometric exponent, b , becomes the slope of the regression of $\log(\text{female size})$ on $\log(\text{male size})$. The dotted line with a slope of 1.0 defines a size ratio of 1.0. The solid line illustrates $b < 1.0$, and the vertical stripes illustrate the degree of SSD. If females are larger than males and $b < 1.0$, SSD declines as size increases (hypoallometry). If males are larger than females, $b < 1.0$ yields a positive correlation between size and SSD (hyperallometry). Throughout the full range in size of males and females, $\Delta(\text{male size}) > \Delta(\text{female size})$. Regression of $\log(\text{male size})$ on $\log(\text{female size})$ would yield the same conclusion, but b would be > 1 .

allometry inconsistent with Rensch's rule, and a slope of 1 indicates isometry (absence of allometry).

Rensch's rule predicts a greater evolutionary divergence in male size than in female size, regardless of which sex is larger (fig. 1; Fairbairn and Preziosi 1994). Because each independent contrast is an estimate of the standardized evolutionary divergence as one hypothetical ancestor diverged to yield two daughter species (Garland 1992), paired t -tests comparing male and female contrasts can be used to test for differences between the sexes in the minimum amount of evolutionary divergence. Significant t -values indicating that male contrasts exceed female contrasts are consistent with Rensch's rule. Post hoc estimates of the mean power of our paired t -tests (Zar 1984) and regression analyses (power estimated using Monte Carlo simulation) yielded values (\pm SE) of 0.616 ± 0.063 and 0.369 ± 0.083 , respectively (Abouheif 1995). Thus, although the regression analyses are essential for estimating the allometric exponent, the paired t -tests have more power for hypothesis testing. We therefore use both methods to assess allometric trends within taxa (figs. 2–4).

Some taxa may show allometry for SSD that is inconsistent with Rensch's rule (Earhart and Johnson 1970; Vollrath and Parker 1992; Head 1995); thus, any

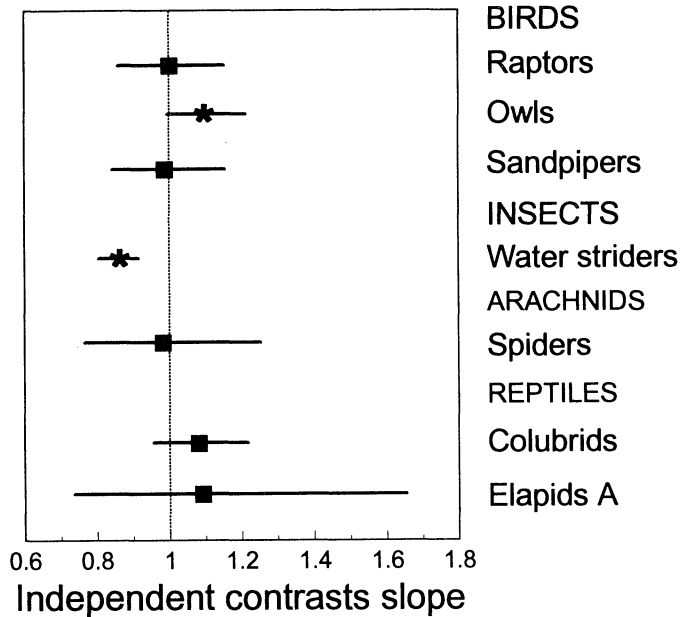


FIG. 2.—Allometric slopes and 95% confidence intervals derived from independent contrasts analyses for taxa with female-biased SSD. The vertical dashed line is the line of isometry (i.e., a slope of 1.0). Slopes represented by asterisks indicate statistically significant allometry as determined by 95% confidence intervals that do not overlap one or significant paired *t*-tests for contrasts (see the text for explanation). *Elapids A* refers to Australian elapids, division A. *Spiders* refers to true spiders excluding orb weavers. *Sandpipers* includes allied taxa (family Scolopacidae). See appendix C for the scientific names of taxa.

statistical evaluation of Rensch's rule should distinguish three possible outcomes: allometry consistent with Rensch's rule, no significant allometry, and allometry inconsistent with Rensch's rule. Our assessments of the statistical significance of allometry within each taxon are therefore based on two-tailed probabilities.

Allometric relationships within any higher taxon may differ from the allometric relationships found independently within the subtaxa of that taxon (Harvey and Pagel 1991). To select the taxonomic level appropriate for assessing allometry, we performed a series of hierarchical analyses (e.g., species within orders, families, subfamilies, etc.). For each taxonomic group, the taxonomic level chosen for analysis was the level at which no heterogeneity of slopes was detected among the subtaxa within that taxon. This method resolved 21 taxa for independent assessments of allometry (app. C).

Because we use the results of our 21 independent analyses to assess general trends rather than to highlight trends within individual taxa, we do not correct the probabilities to an experiment-wide error rate of 0.05 (for discussions of the issue of probability values for multiple comparisons, see Cox 1965; Rice 1989; Saville 1990). The statistical conclusions for the individual taxa should therefore be viewed as generating hypotheses for further tests rather than as definitive

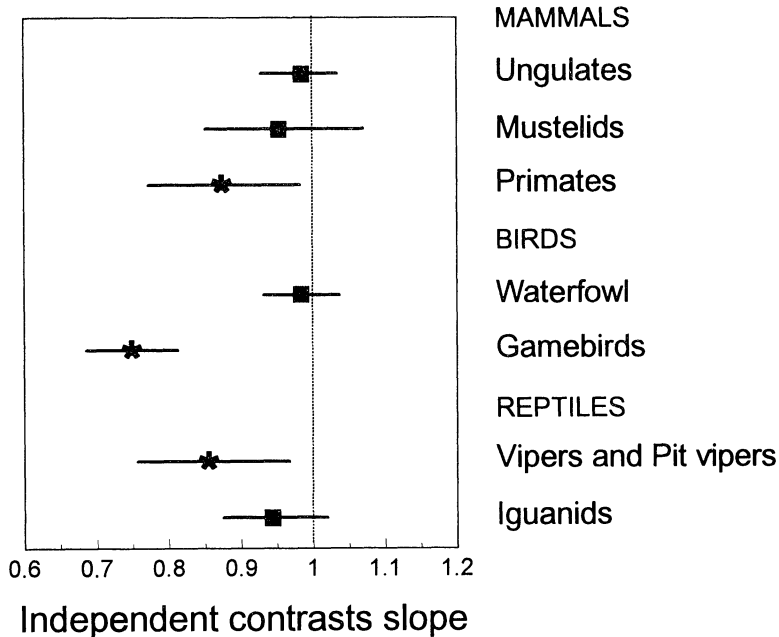


FIG. 3.—Allometric slopes and 95% confidence intervals derived from independent contrasts analyses for taxa with male-biased SSD. The vertical dashed line is the line of isometry (i.e., a slope of 1.0). Slopes represented by asterisks indicate statistically significant allometry as determined by 95% confidence intervals that do not overlap one or significant paired *t*-tests for contrasts (see the text for explanation). See appendix C for the scientific names of taxa.

tests themselves (Saville 1990). To assess the generality and overall statistical significance of allometric trends, we use a meta-analytic approach based on the *t*-values from the 21 independent analyses (Hedges and Olkin 1985; Mullen and Rosenthal 1985).

RESULTS

As predicted, allometry for SSD is weak and variable in taxa in which females are the larger sex (fig. 2): three slopes are <1 , three are >1 , and the slope for the raptors is essentially equal to 1. The allometry is statistically significant only in the water striders and owls and is consistent with Rensch's rule only in the former. In contrast, all seven taxa with male-biased SSD have slopes <1 (consistent with Rensch's rule), and three are significantly so: primates, game birds, and vipers and pit vipers (fig. 3). Similarly, all seven slopes for taxa with mixed SSD are <1.0 (fig. 4). The slopes for hummingbirds, seabirds, and Australian elapids, division B, are statistically significant, and the slope for the colubrids approaches significance ($P < .1$).

Overall, 17 of the 21 slopes are <1 , and only three are >1 (χ^2 comparison to a 50:50 ratio, $\chi^2 = 9.8$, $P < .005$). Further, seven of the eight significant slopes

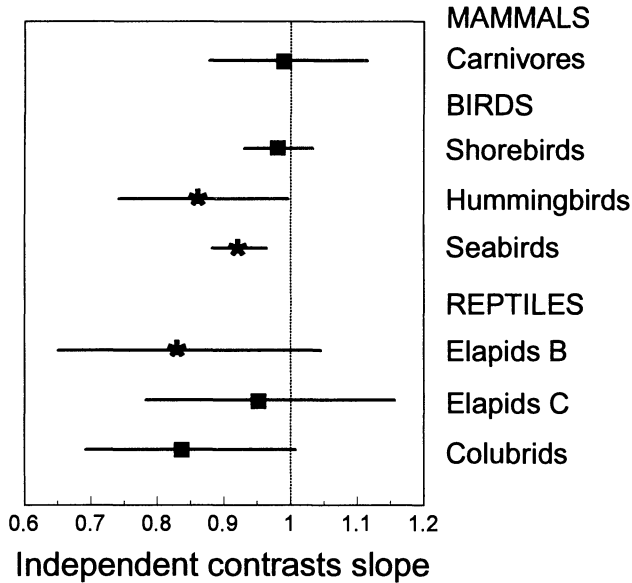


FIG. 4.—Allometric slopes and 95% confidence intervals derived from independent contrasts analyses for taxa with mixed SSD. The vertical dashed line is the line of isometry (i.e., a slope of 1.0). Slopes represented by asterisks indicate statistically significant allometry as determined by 95% confidence intervals that do not overlap one or significant paired *t*-tests for contrasts (see the text for explanation). *Elapids B* and *Elapids C* refer to Australian elapids, divisions B and C. *Shorebirds* excludes the Scolopacidae (sandpipers and allies). See appendix C for the scientific names of taxa.

are < 1 . This preliminary comparison of the 21 independent estimates thus suggests that SSD does show allometry among species and that the allometric trend is generally, but not always, consistent with Rensch's rule.

Meta-analysis confirms the trends suggested by the preliminary survey of regression slopes (table 1). The combined effect sizes are positive in all three groups, which indicates that male contrasts exceed female contrasts on average within each group. This is consistent with Rensch's rule. The diffuse tests for homogeneity of effect sizes indicate no significant heterogeneity among taxa within the male-biased and mixed SSD groups. The combined significance levels test the hypothesis that the combined results of the seven studies within each group could have occurred by chance alone, if the null hypothesis of $d \leq 0$ within taxa (Rensch's rule not followed) were true. These significance levels are extremely low for the male-biased and mixed SSD groups. Thus, the meta-analysis indicates that these two groups show positive, homogeneous effect sizes that are highly statistically significant for each group: Rensch's rule appears to apply within taxa in which more than 20% of species have male-biased size ratios. In contrast, the female-biased group shows a much weaker overall effect size that is not statistically significant. Further, the test for homogeneity of effect sizes reveals significant heterogeneity among the taxa in this group. These results

TABLE 1
RESULTS OF META-ANALYSIS WITHIN GROUPS

	GROUP		
	Female-Biased SSD	Male-Biased SSD	Mixed SSD
Combined effect size (d_+)*	.193	.675	.887
Diffuse test for homogeneity of effect sizes	$\chi^2 = 14.121, df = 6, P = .028$	$\chi^2 = 8.568, df = 6, P = .199$	$\chi^2 = 4.146, df = 6, P = .657$
Combined significance level	$P = .061$	$P = .12 \times 10^{-4}$	$P = .13 \times 10^{-6}$

* Weighted, standardized mean difference between male and female contrasts for log(body size).

confirm our previous conclusion that where females are the larger sex, allometry for SSD is generally weak and inconsistent.

Within the female-biased group, some taxa, most notably the water striders (Gerridae), show allometry consistent with Rensch's rule and thus resemble taxa in the male-biased and mixed SSD groups. This heterogeneity within the female-biased group, and the apparent similarity of the other two groups to each other, suggest that our a priori division of taxa may not capture the true pattern of variation in allometry for SSD. To address this question, we performed a disjoint cluster analysis (Mullen and Rosenthal 1985) on all 21 taxa. With a significance level of .05 as the criterion for separating clusters, owls (Strigiformes) formed a separate cluster, while the remaining 20 taxa formed a single cluster. Diffuse tests of homogeneity confirm this result: for all 21 taxa the test indicates significant heterogeneity of effect sizes ($\chi^2 = 36.622$, $df = 20$, $P = .013$), but this heterogeneity disappears when the owls are removed ($\chi^2 = 20.573$, $df = 19$, $P = .361$). The overall effect size (d_+) for the 20-taxa group is 0.667, and the combined significance level is less than 10^{-9} . These results provide strong evidence for the generality of Rensch's rule. Although the patterns of allometry are weaker and more variable in taxa in which females are the larger sex, only one taxon in this group stands out as statistically distinct from the general trend.

To further test our a priori hypothesis of an association between male-biased SSD and Rensch's rule, we calculated the sexual size dimorphism index (SDI) of Gibbons and Lovich (1990) for each of the 21 taxa. The SDI has the advantage over a standard size ratio of being symmetrical near 0 (monomorphism for size), and it is a more appropriate estimate of dimorphism when the direction of dimorphism varies among studies. As predicted, the effect sizes are significantly negatively correlated with SDI (fig. 5; $r = -0.518$, $df = 19$, one-tailed $P = .008$), which remains true even if the owls are removed ($r = -0.455$, $df = 18$, one-tailed $P = .025$). As the size of males relative to females declines (as SDI increases), the probability of observing allometry consistent with Rensch's rule also declines: strong allometry consistent with Rensch's rule (slopes $\ll 1.0$) is associated primarily with male-biased SSD.

DISCUSSION

Allometry consistent with Rensch's rule is clearly a significant component of variation in SSD among species. However, our ability to detect allometry for SSD in any given taxon is limited by a paucity of appropriate data and the low power of the methods necessary for parameter estimation. Major axis regression, necessitated by sampling error in the independent variable (male size), has lower power than ordinary least squares regression (McArdle 1988). Power is also reduced by phylogenetic correction because the number of nodes used to estimate degrees of freedom is always less than the number of species in the phylogeny (app. C). The probability of a Type II error (failing to detect allometry when it in fact exists) is thus high in individual comparisons, particularly if the number of species is low or the phylogeny unresolved. When the power of individual tests is low, assessing general trends or overall significance by simply counting

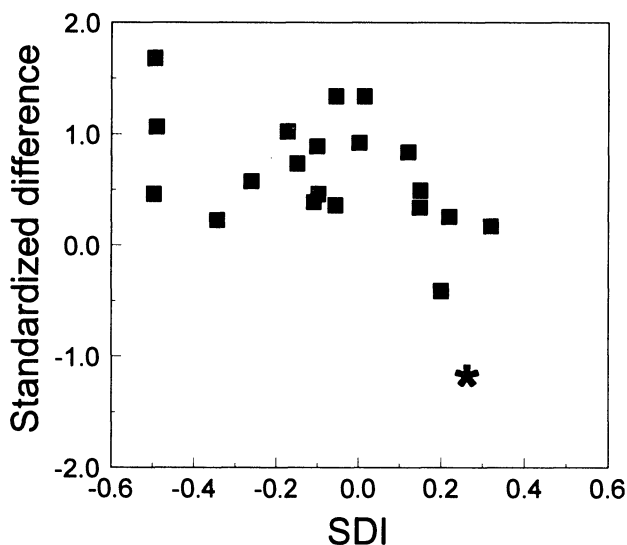


FIG. 5.—The standardized mean difference between male and female contrasts for log (body size) plotted against the sexual dimorphism index (SDI) of Gibbons and Lovich (1990). The SDI is $[(\text{size of the larger sex/size of the smaller sex}) - 1]$, arbitrarily set as negative when males are the larger sex and positive when females are the larger. The mean standardized difference is derived following the meta-analytic techniques of Mullen and Rosenthal (1985), and the contrasts are derived from independent contrasts analyses within taxa (see the text for explanation). The owls (*Strigiformes*) are indicated by the asterisk.

the numbers of statistically significant and statistically nonsignificant comparisons (“vote counting”) compounds the problem of low power, yielding a very high probability of a Type II error (Hedges and Olkin 1985). Meta-analysis provides a method of quantitatively assessing general trends by estimating both a weighted average effect size and an overall probability for the null hypothesis of no effect. A vote-counting approach to our results yielded seven positive results (significant allometry consistent with Rensch’s rule), and our χ^2 comparison of the numbers of slopes >1 and <1 confirmed an overall tendency for the slopes to be <1 . However, the meta-analysis consolidated this information and allowed us to conclude that allometry in the direction predicted by Rensch’s rule is both general and highly statistically significant. Of the 21 taxa examined, only owls are a clear exception to this general trend.

Evolutionary Processes Underlying Rensch’s Rule

The prevalence of allometry consistent with Rensch’s rule suggests a common, causative evolutionary process. Many functional hypotheses have been proposed for specific taxa (reviewed in Reiss 1986; Webster 1992), but the only hypothesis that can be generalized across taxa, regardless of the direction of SSD, attributes allometry to sexual selection on males (Fairbairn and Preziosi 1994). This hypothesis has a long history. Rensch (1960) attributed the allometry to selection on male secondary sexual characteristics, whereas more recent studies emphasize

the role of sexual selection favoring large male size directly (Clutton-Brock et al. 1977; Maynard Smith 1977; Leutenegger 1978; Webster 1992; Fairbairn and Preziosi 1994). According to this hypothesis, sexual selection favoring large males produces an increase in male size and a smaller, correlated increase in female size because of the high genetic correlations between the sexes (Leutenegger 1978; Lande 1980; Fairbairn and Preziosi 1994). In taxa in which males are the larger sex, increases in the size of both sexes are accompanied by increasing SSD because males are the larger sex and increase in size faster than do females. Conversely, in taxa in which females are the larger sex, these responses are accompanied by decreasing SSD. Thus, regardless of which sex is initially larger, sexual selection favoring large males can be expected to push taxa from left to right along the allometric line in figure 1. This hypothesis remains controversial because females are predicted to return to their natural selection optimum at equilibrium (Lande 1980), and female size therefore becomes statistically independent of male size. The model thus predicts allometry only if SSD is not at equilibrium in the constituent species (Clutton-Brock 1985; Webster 1992).

Our data cannot be used to test this model directly. However, the association of Rensch's rule with taxa in which more than 20% of species have male-biased SSD, and the overall correlation between the effect size and SDI, support the general hypothesis of a functional relationship between sexual selection favoring large males and allometry consistent with Rensch's rule. Furthermore, the only female-biased taxon that shows significant allometry consistent with Rensch's rule is the water striders, and in this taxon there is strong quantitative evidence that sexual selection favors large males (Fairbairn 1990; Arnqvist 1992; Sih and Krupa 1992; Krupa and Sih 1993; Fairbairn and Preziosi 1994; Rowe et al. 1994). The empirical association between Rensch's rule and sexual selection on male size seen in this and previous studies belies the apparent weakness in the quantitative genetic model (Lande 1980; Clutton-Brock 1985; Webster 1992). Theory and empirical data would be reconciled if SSD were found not to be at equilibrium in these taxa. Alternatively, if SSD is at equilibrium, sexual selection may be necessary but not sufficient for the evolution of allometry consistent with Rensch's rule. Other processes such as correlational selection on female size may also be required (Webster 1992).

Allometry within Taxa: Comparisons with Previous Studies

Because we did not correct our individual comparisons to an experiment-wide Type I error rate of 0.05, the results for each taxon must be considered as generating rather than testing the hypothesis for that specific taxon (Saville 1990). However, a priori hypotheses exist for 14 of the taxa that we examined (app. A), and a comparison of our conclusions with these previous studies is appropriate. Our results confirm previous conclusions of significant allometry consistent with Rensch's rule in seabirds, hummingbirds, gamebirds, and water striders. For a fifth taxon, the waterfowl, our analysis yielded a slope < 1.0 (two-tailed $P < .10$). Sigurjonsdottir (1981) had previously found significant allometry consistent with Rensch's rule in 105 species of waterfowl. The lack of significance of our slope probably reflects the low power of our independent contrasts analysis that, be-

cause of the poorly resolved phylogeny, is based on only 18 df. Our slope would be significant with a one-tailed test, and, given the low power of our analysis, we interpret our results as being consistent with those of Sigurjonsdottir.

For shorebirds, raptors, ungulates, lizards, owls, and primates, our results resolve previous conflicting evidence regarding Rensch's rule (app. A). Allometry is weak and not statistically significant in the first four of these taxa. However, owls and primates show significant hyperallometry, in accord with Earhart and Johnson (1970) for owls and with the majority of previous analyses of primates (app. A).

Patterns of allometry in the remaining three taxa (snakes, mustelids, and spiders) are strongly influenced by phylogeny, and our analyses yield conclusions in conflict with previous studies. Fitch (1981) found no significant allometry for SSD in snakes. By comparison, we find that allometry varies among snake taxa: all four male-biased taxa have slopes <1 , and two are statistically significant. In contrast, both taxa with female-biased SSD have nonsignificant slopes >1 . Our data therefore suggest that allometry consistent with Rensch's rule does occur in some snake taxa and is associated with male-biased SSD.

Mustelids have been used as a prime example of an exception to Rensch's rule (Reiss 1986) because, although males are the larger sex, SSD appears to decrease with body size (Moors 1980; Ralls and Harvey 1985). We performed a phylogenetically controlled analysis of the same 14 genera used by Ralls and Harvey (1985) and detected no significant allometry (slope = 1.054, 95% confidence interval = 0.981–1.132; paired *t*-test, *t* = 0.746, one-tailed *P* > .10). These results agree with our species-level analysis of 26 mustelid species. Thus, controlling for the confounding influence of phylogeny removes the apparent hypoallometric trend in the Mustelidae, and this taxon no longer stands out as an example of allometry inconsistent with Rensch's rule.

The final discrepancy between our results and those of previous authors occurs in the spiders. Vollrath and Parker (1992) and Head (1995) concluded that spiders show allometry inconsistent with Rensch's rule: females are the larger sex, but SSD increases with body size. We find no evidence of such a trend. However, our preliminary analyses revealed strong phylogenetic effects among spider families. Orb-weaving spiders (Araneidae) are outliers with a very strongly female-biased SSD and an allometric slope (uncorrected for phylogeny) >1 . Vollrath and Parker (1992) combined species from 31 families including the orb weavers and did not correct for phylogeny. Head (1995) estimated allometry among families (rather than species), with and without orb weavers. (Note that he used linear rather than logarithmic data, and the slope of his regression therefore cannot be interpreted as an allometric coefficient.) We replicated Head's analyses with our data set and obtained similar results: allometry inconsistent with Rensch's rule (E. Abouheif, unpublished data). However, these results reflect differences among families and the strong influence of the orb weavers: our species-level analysis with orb weavers removed revealed no significant allometry. Preliminary analyses suggest that orb weavers may indeed show allometry inconsistent with Rensch's rule (Head 1995; E. Abouheif, unpublished data), but confirmation of this hypothesis must await a phylogeny resolved to the species level within this family. If confirmed,

hyperallometry within the Araneidae would be consistent with our observed trend in owls and our general conclusion that allometric trends inconsistent with Rensch's rule tend to be associated with female-biased SSD. However, we have no evidence for such a trend at the species level in other spider families, and so, for the present, spiders do not stand out as an exception to Rensch's rule.

CONCLUSIONS

Our analysis of allometry for SSD in 21 independent taxa provides quantitative support for Rensch's rule, particularly for taxa in which males are the larger sex or in which sexual selection favors large males. The low power of assessments of allometry within individual taxa makes such analyses poor tests of the general hypothesis. However, quantitative comparisons of the results for our 21 taxa (the χ^2 comparison of slopes and meta-analysis) reveal a highly significant, general trend consistent with Rensch's rule. Exceptions to the rule seem to be confined to taxa in which females are the larger sex. We have documented one such exception, the owls, and suggest that future analyses may reveal similar exceptions in the orb-weaving spiders and several snake lineages. Comparisons of selective regimes in these taxa with those in taxa showing the more typical allometric trend should prove instructive as tests of functional hypotheses for the evolution of allometry consistent with Rensch's rule.

Offering a final caveat, we caution that both SSD and allometry for SSD tend to show strong phylogenetic effects. The controversies over allometric trends in the spiders, snakes, and mustelids illustrate that perceived trends can be strongly dependent on the taxonomic level of the analysis (i.e., family, genus, or species). We restrict our analyses to the species level and combine higher taxa only if the allometric slopes are homogeneous. Even so, correcting for phylogenetic effects using independent contrasts had a noticeable impact on both our estimates of the allometric slopes and our statistical conclusions, particularly for these controversial groups. Because of the strong influence of phylogeny on patterns of allometry, we restrict our conclusions and predictions to allometry among species, and we recommend that future assessments of allometric trends be based on independent contrasts to control for phylogenetic effects.

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APPENDIX A

TABLE A1

PREVIOUS EVIDENCE FOR RENSCH'S RULE

TAXON		REFERENCE	LARGER SEX*	SUPPORTS RENSCH'S RULE?	SAMPLE SIZE	QUALITY OF DATA†
Common Name	Scientific Name					
Birds:						
Waterfowl	Anseriformes	Sigurjonsdottir 1981	M	Yes	105	1
Shorebirds	Charadriiformes	Payne 1984	M&F	Yes	24	0
		Jehl and Murray 1986	...	No	...	1
Seabirds	Procelariiformes and Pelicaniformes	Fairbairn and Shine 1993	M&F	Yes	98	2
Owls	Strigiformes	Earhart and Johnson 1970	F	No	32	1
		Greenwood and Wheeler 1983	...	Yes	...	0
Raptors	Falconiformes	Selander 1966	F	No	12	0
		Storror 1966	...	Yes	3	0
		Snyder and Wiley 1976	...	No	35	0
		Newton 1979	...	No	...	0
		Andersson and Norberg 1981	...	Yes	...	0
		Sigurjonsdottir 1981	...	Yes	6	...
		Greenwood and Wheeler 1983	...	Yes	...	0
Hummingbirds	Trochiliformes	Payne 1984	M&F	Yes	32	0
Game birds	Galliformes	Sigurjonsdottir 1981	M	Yes	89	1
Grouse	Tetraonidae	Payne 1984	M	Yes	15	0
		Wiley 1974	...	Yes	30	1
Blackbirds	Icteridae	Webster 1992	M	Yes	35	3
Parrots	Psittacidae	Payne 1984	M&F	No	...	0
Bustards	Otididae	Payne 1984	M	Yes	17	0
Honey guides	Indicatoridae	Payne 1984	M	No	6	0
Cotingas	Cotingidae	Payne 1984	M&F	Yes	40	0
Manakins	Pipridae	Payne 1984	M&F	Yes	30	0
Birds of paradise	Paradisaeidae	Payne 1984	M	Yes	44	0
Bowerbirds	Ptilonorhynchidae	Payne 1984	M	No	15	0
Euplectine finches	Ploceidae	Payne 1984	M	Yes	18	0

TABLE A1 (continued)

TAXON		REFERENCE	LARGER SEX*	SUPPORTS RENSCH'S RULE?	SAMPLE SIZE	QUALITY OF DATA†
Common Name	Scientific Name					
Mammals:						
Primates	Primates	Clutton-Brock et al. 1977	M	Yes	42	2
		Ralls 1977	...	Yes	...	0
		Leutenegger 1978	...	Yes	53	3
		Alexander et al. 1979	...	No	22	1
		Leutenegger 1982	...	Yes	53	3
		Leutenegger and Cheverud 1982	...	Yes	70	3
		Gaulin and Sailer 1984	...	Yes	60	1
		Ford 1994	...	No	51	1
Kangaroos and wallabies	Macropodidae	Jarman 1983	M	Yes	21	1
Pinnipeds	Pinnipedia	Ralls 1977	M	Yes	...	0
		Alexander et al. 1979	...	No	13	1
Ungulates	Perrisodactyla, Artiodactyla	Ralls 1977	M	Yes	...	0
		Alexander et al. 1979	...	No	17	1
Elephants	Bovidae	Jarman 1983	...	Yes	65	1
Bats	Proboscidea	Ralls 1977	M&F	Yes	...	0
	Chiroptera	Ralls 1977	F	Yes	...	0
		Myers 1978	...	No	...	0
		Reiss 1986	M&F	No	88	3
Small mammals						
Squirrels, marmots, and chipmunks	Sciuridae	Reiss 1986	M	Yes	10	3
		Levenson 1990	...	No	21	1
		Reiss 1986	M	No	3	3
Gophers	Geomysidae					
Pocket mice and kangaroo rats	Heteromyidae	Reiss 1986	M&F	No	5	3
Mice and hamsters	Cricetidae	Reiss 1986	M&F	Yes	21	3
Rats, voles, and lemmings	Muridae	Reiss 1986	M&F	Yes	19	3
Shrews	Soricidae	Reiss 1986	M&F	No	7	3
Rabbits	Leporidae	Reiss 1986	F	No	3	3
Mustelids	Mustelidae	Moors 1980	M	No	15	1
		Ralls and Harvey 1985		No	14	3

Amphibians	Amphibia	Shine 1979	F	No	569	0
Frogs and toads	Anura	Crump 1974	M&F	No	61	1
		Emerson 1994	...	No	20	2
Reptiles:						
Turtles	Chelonia	Berry and Shine 1980	M&F	Yes	8	1
		Gibbons and Lovich 1990	...	No	63	1
Lizards	Lacertilia	Schoener 1970	M&F	Yes	54	1
		Fitch 1976	...	No	54	1
		Fitch 1981	...	No	5	1
		Stamps 1983	...	No	30	1
Snakes	Serpentes	Fitch 1981	M&F	No	8	1
Insects:						
Water striders	Gerridae	Fairbairn 1990	F	Yes	15	3
		Fairbairn and Prestozi 1994	...	Yes	40	3
		Andersen 1994	...	Yes	46	3
Tephritid fruit flies	Tephritidae	Sivinski and Dodson 1992	F	Yes	27	3
Stick insects	Phasmatodea	Sivinski 1978	F	No	152	3
Arachnids:						
Spiders	Araneae	Vollrath and Parker 1992	F	No	802	2
		Head 1995	F	No	19	3
Crustaceans:						
Copepods	Copepoda	Bayly 1978	F	Yes	28	0
		Geddes and Cole 1981	...	No	34	1
		Mater 1994	...	No	18	1

* Symbols are as follows: *M*, males are the larger sex; *F*, females are the larger sex; *M&F*, males are larger in some species, and females are larger in others.

† Scores are calculated as follows: 0, no statistical tests used; 1, statistical tests used. A point is also added for each of the following: a standard log/log plot is used where log (size of one sex) is regressed on log (size of the other sex); Model II major axis or reduced major axis regression is used; the influence of phylogenetic history is statistically removed. The maximum score is 4.

APPENDIX B

TABLE B1

REFERENCES FROM WHICH BODY SIZE DATA WERE EXTRACTED

Taxon	Reference
Birds*	Palmer 1962; Ffrench 1973; Johnsgard 1973, 1981, 1983 <i>a</i> , 1983 <i>b</i> , 1986, 1988; Cramp and Simmons 1977; Strauch 1977; Thomas 1982; Yanez et al. 1982; Pierce 1984; Fry et al. 1988; Ross 1988; Lessells and Ovenden 1989; Bretagnolle et al. 1990; Livezey 1990; Clements 1991; Dunning 1993; Fairbairn and Shine 1993
Mammals	Primates: Gaulin and Sailer 1984; carnivores: Gittleman 1986; mustelids: Gittleman 1986; Van Valkenburgh 1990; ungulates: Sachs 1967; Demment 1982; Scott 1983, 1987; Owen-Smith 1988; Janis 1990
Reptiles	Lizards: Fitch 1981; snakes: Shine 1994
Insects	Andersen 1994
Arachnids	Spiders: Locket and Milledge 1951; Kaston and Kaston 1953; Yaginuma 1960; Mascord 1970; Locket et al. 1974

* The principal reference for the birds was Dunning (1993).

APPENDIX C

TABLE C1

TAXA ANALYZED AND ASSOCIATED PUBLISHED PHYLOGENIES

Common Name	Scientific Name	<i>n</i>	<i>df_c</i> *	Source for Phylogenetic Hypothesis
Mammals:				
Carnivores	Carnivora	17	15	Garland et al. 1993
Mustelids	Mustelidae	26	15	Bryant et al. 1993
Primates	Primates	37	33	Sillen-Tullberg and Møller 1993
Ungulates	Artiodactyla and Perissodactyla	27	25	Garland et al. 1993
Birds:				
Game birds	Galliformes	27	20	Johnsgard 1973, 1983 <i>a</i> ; Sibley and Alquist 1990; Crowe et al. 1992
Hummingbirds	Trochiliformes	14	12	Johnsgard 1983 <i>b</i>
Owls	Strigiformes	25	15	Sibley and Alquist 1990
Raptors	Falconiformes	22	11	Sibley and Alquist 1990
Seabirds	Procellariiformes and Pelicaniformes	40	29	Brush and Witt 1983; Sibley and Alquist 1990
Shorebirds	Charadriiformes†	65	35	Sibley and Alquist 1990
	Scolopacidae	35	17	Sibley and Alquist 1990
Waterfowl	Anseriformes	28	18	Kessler and Avise 1984; Sibley and Alquist 1990; Quinn et al. 1991
Reptiles:				
Australian elapid snakes	Acanthopiinae			Mengden 1985; Schwaner et al. 1985; Shine 1985; Wallach 1985
	Division A	19	17	
	Division B	31	29	
	Division C	16	14	
Colubrid snakes	Colubrinae, Lyco-dontinae, and Xenodontinae	18	16	Dowling et al. 1983
	Natracinae	14	12	Dowling et al. 1983; Lawson 1987
Iguanid lizards	Iguanidae	90	77	Presch 1969; Ballinger and Tinkle 1972; Ethridge and de Queiroz 1988; Losos 1990; Lopez et al. 1992; Sites et al. 1992
Vipers, pit vipers	Viperidae	16	13	Klauber 1972; Ashe and Marx 1988; Knight et al. 1993
Arachnids	Araneomorphae‡	44	17	Coddington and Levi 1991; Platnick et al. 1991
Insects	Gerridae	46	44	Andersen 1994

* Degrees of freedom associated with the independent contrasts analysis (number of nodes - 1).

† Excluding sandpipers and allies (Scolopacidae).

‡ True spiders excluding orb weavers (Araneidae).

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