A Comparative Analysis of the Allometry for Sexual Size Dimorphism: Testing Rensch's Rule

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ABSTRACT

A Comparative Analysis of the Allometry for Sexual Size Dimorphism: Testing Rensch's Rule.

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Rensch's rule states that sexual size dimorphism (SSD) increases with body size (hyperallometry) in taxa where males are the larger sex, and decreases with body size (hypoallometry) where females are larger. Using the recently developed independent contrasts method, I test the validity and generality of Rensch's rule within 21 independent animal taxa, and use these results to compare the parameter estimates and statistical conclusions of independent contrasts and cross-species analyses. Rensch's rule is not universal, but occurs in 33% of the taxa examined across a diverse range of invertebrate and vertebrate taxa. Significant allometry inconsistent with Rensch's rule occurred in only one taxon. Rensch's rule occurs more frequently and consistently in taxa where males are the larger sex, and no consistent patterns of allometry for SSD are observed in female-biased taxa. The association of Rensch's rule with taxa in which male-biased SSD is present is consistent with the hypothesis that sexual selection acting on male size drives the evolution of the allometry for SSD. Cross-species slopes are not good predictors of independent contrasts slopes, and type I errors are more likely to occur in cross-species analyses. For accurate parameter estimation and statistical conclusions, I recommend the independent contrasts method.

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INTRODUCTION.

Sexual differences in size and morphology are widespread in the animal kingdom. In most species of animals, females attain larger body sizes than males (e.g. most spiders, insects, fish, amphibians and 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). In 1960, Rensch proposed a general rule relating sexual dimorphism to body size in birds and other animals. He states: "Thus, the rule is valid that in numerous animal groups the sexual dimorphism increases with body size.... 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." (Rensch 1960:159). In terms of allometry, 'Rensch's rule' predicts that the degree of sexual size dimorphism (SSD: size of the larger sex / size of the smaller sex) will be positively correlated with mean body size (hyperallometry) in taxa where males are the larger sex. Conversely, in taxa where females are the larger sex, SSD is predicted to decrease as mean body size increases (hypoallometry).

'Rensch's rule' has been widely accepted as a general trend across the animal kingdom (e.g. Ralls 1977; Leutenneger 1978; Webster 1992; Fairbairn and Preziosi 1994), and has been observed in many animal taxa (Table 1). However, empirical support for the trend is equivocal. A review of relevant studies indicates support for Rensch's rule in only 19 of 41 taxa (Table 1). The

Table 1. Previous evidence for Rensch's rule.

Taxon	Scientific name	Reference	Larger sex M, F, M&F [1]	Supports Rensch's rule? Yes/No	Sample size	Quality of data[2]
Birds						
Waterfowl	Anseriformes	Sigurjonsdottir (1981)	M	Yes	105	1
Shorebirds	Charadriformes	Payne (1984)	M&F	Yes	24	0
		Jehl and Murray (1986)		No	. .	1
Seabirds	Procelariiformes and Pelecaniformes	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
		Storrer (1966)		Yes	3	0
		Synder and Wiley (1976)		No	35	0
		Newton (1979)		No	...	0
		Andersson and Norberg (1981)		Yes	...	0
		Sigurjonsdottir (1981)		Yes	65	1
		Greenwood and Wheeler (1983)		Yes	...	0

Table 1, continued:

Taxon	Scientific name	Reference	Larger sex M, F, M&F	Supports Rensch's rule? Yes/No	Sample size	Quality of data
Hummingbirds	Trocholiformes	Payne (1984)	M&F	Yes	32	0
Gamebirds	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
Honeyguides	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

Table 1, continued:

Taxon	Scientific name	Reference	Larger sex M, F, M&F	Supports Rensch's rule? Yes/No	Sample size	Quality of data
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
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

Table 1, continued:

Taxon	Scientific name	Reference	Larger sex M, F, M&F	Supports Rensch's rule? Yes/No	Sample size	Quality of data
Pinnepeds	Pinnepedia	Ralls (1977)	M	Yes	...	0
		Alexander et al. (1979)		No	13	1
Ungulates	Perrisodactyla,	Ralls (1977)	M	Yes	...	0
	Artiodactyla	Alexander et al. (1979)		No	17	1
	Bovidae	Jarman (1983)		Yes	65	1
Elephants	Proboscidea	Ralls (1977)	M&F	Yes	...	0
Bats	Chiroptera	Ralls (1977)	F	Yes	...	0
		Myers (1978)		No	...	0
Small mammals		Reiss (1986)	M&F	No	88	3
Squirrels, Marmots & Chipmunks	Sciuridae	Reiss (1986)	M	Yes	10	3
		Levenson (1990)		No	21	1
Gophers	Geomyidae	Reiss (1986)	M	No	3	3

Table 1, continued:

Taxon	Scientific name	Reference	Larger sex M, F, M&F	Supports Rensch's rule? Yes/No	Sample size	Quality of data
Pocket mice & Kangaroo rats	Heteromyidae	Reiss (1986)	M&F	No	5	3
Mice & Hamsters	Cricetidae	Reiss (1986)	M&F	Yes	21	3
Rats, Voles, 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 & Toads	Anura	Crump (1974)	M&F	No	61	1
		Emerson (1994)		No	20	2

Table 1, continued:

Taxon	Scientific name	Reference	Larger sex M, F, M&F	Supports Rensch's rule? Yes/No	Sample size	Quality of data
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						
Waterstriders	Gerridae	Fairbairn (1990)	F	Yes	15	3
		Fairbairn and Presiozi (1994)		Yes	40	3
		Andersen (1994)		Yes	46	3
Tephritid fruit flies	Tephritidae	Sivinski and Dodson (1992)	F	Yes	27	3

Table 1, continued:

Taxon	Scientific name	Reference	Larger sex M, F, M&F	Supports Rensch's rule? Yes/No	Sample size	Quality of data
Stick insects	Phasmatodea	Sivinski (1978)	F	No	152	3
Arachnids						
Spiders	Araneae	Vollrath and Parker (1992)	F	No	802	2
Crustaceans						
Copepods	Copepoda	Bayly (1978)	F	Yes	28	0
		Geddes and Cole (1981)		No	34	1
		Maier (1994)		No	18	1

[1] M = males are generally the larger sex, F = females are generally the larger sex, M&F = there are species that are male-biased in size dimorphism, and species that are female-biased in size dimorphism.

[2] 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 is used; the influence of phylogenetic history is statistically removed. The maximum score is 4.

validity and generality of Rensch's rule has been previously questioned by Selander (1966) and Reiss (1986). Selander (1966:142) stated, " Actually the correlations {between SSD and body size} are weak and the exceptions so numerous as to raise questions concerning the validity of the 'rule'." Reiss (1986) reviewed the evidence for hyperallometry in taxa with male-biased SSD, and found that the data presented in Rensch's original paper are weak and unconvincing as no statistical tests were employed. He concluded that there is statistical evidence for hyperallometry in taxa with male-biased SSD in some taxonomic groups (e.g. primates, small mammals, grouse), but that these conclusions are tentative as the influence of phylogenetic history (which causes the species data points to be non-independent) had not been statistically removed from the data.

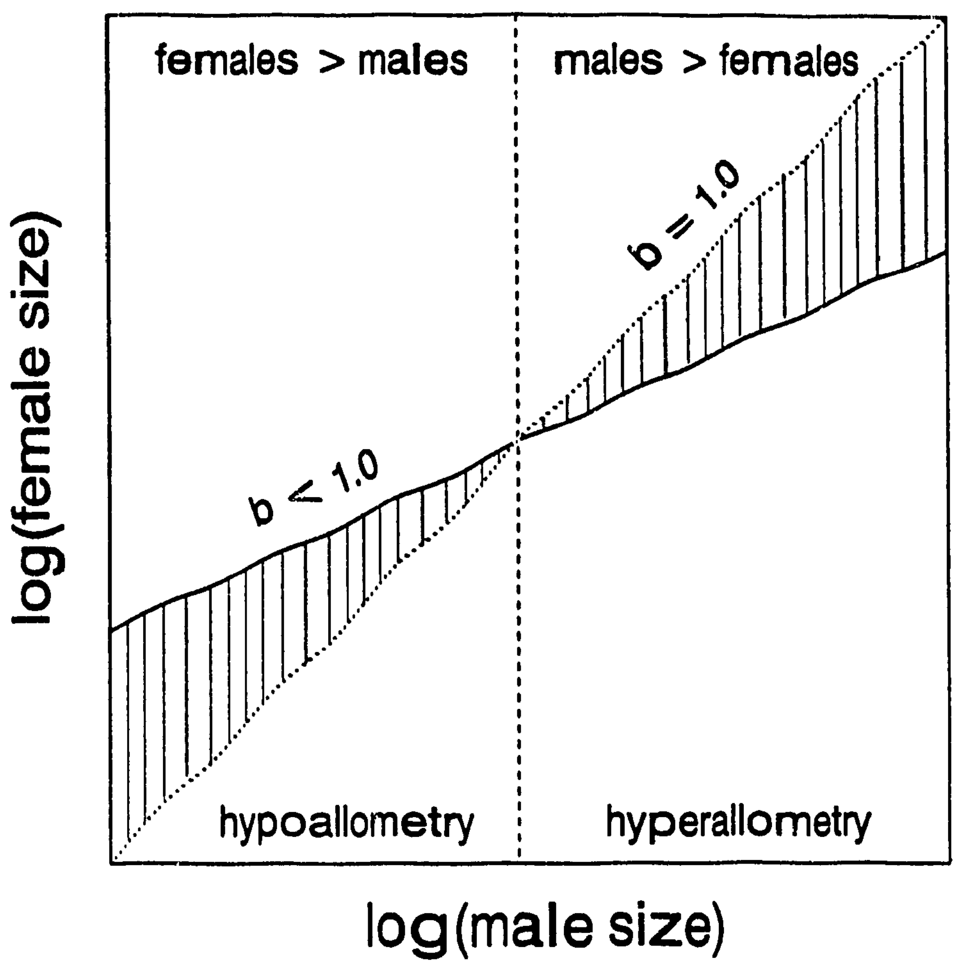
Current evidence for or against Rensch's rule is also flawed by lack of statistical testing or use of inappropriate statistical methodology. Regressing an index of SSD, such as size ratio or the difference between the sexes, against mean size has been widely used in the literature (e.g. Earhart and Johnson 1970; Wiley 1974; Moors 1980; Gibbons and Lovich 1990; Fairbairn and Shine 1993). This method of assessing the allometry for SSD is incorrect because the mean size for males and females appears in both the dependent and independent variables, and therefore the variables are not mathematically independent (LaBarbera 1989). The null hypothesis for such a relationship is not $\beta = 0$, and statistical tests of the derived slopes are therefore invalid. Of the 45 independent studies listed in Table 1, 12 use no statistical tests, and 25 incorrectly assess allometry for SSD as described above. Thus, studies that accurately assess allometry for SSD are relatively rare.

Fairbairn and Preziosi (1994) provide a method of quantitatively assessing Rensch's rule, in which they resolve both hyper- and hypoallometric trends into a single logarithmically scaled plot regressing female size vs. male size (Figure 1). The dotted line indicates a constant size ratio of 1.0, and the solid line illustrates the predicted relationship, according to Rensch's rule, between male and female size. The difference between the two lines (vertical hatching) illustrates the degree of sexual size dimorphism. As given by Rensch's rule, size dimorphism increases with body size where males are the larger sex, and decreases with body size where females are the larger sex. The resolution of both hyper- and hypoallometric trends reveals a slope consistently less than 1.0, indicating that there is greater variance among taxa for males than for females. This means that there is greater evolutionary divergence in male size regardless of which sex is larger. Testing Rensch's rule under this allometric model, I predict a slope of less than one in all taxonomic groups regardless of which sex is larger.

The goal of this study is to determine the validity and generality of Rensch's rule across a diverse range of animal taxa. To this end, I use the method of Fairbairn and Preziosi (1994) to quantify the relationship between size and SSD in 35 taxa across five classes in the animal kingdom: Mammalia, Aves, Reptilia, Insecta, and Arachnida.

Comparative methodology involves making comparisons of two phenotypic traits, or a phenotypic trait with an environmental variable, across a broad range of species or higher taxa. The results of these comparisons can then be used to test hypotheses regarding the generality of evolutionary phenomena (Felsenstein 1985; Harvey and Pagel 1991; Miles and

FIGURE 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(male size)^b. The allometric exponent, b, becomes the slope of the regression of log (female size) on log (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, Δ (male size) > Δ (female size). Regression of log (male size) on log (female size) would yield the same conclusion, but b would be greater than one.


females > males
males > females
b = 1.0
b < 1.0
hypoallometry
hyperallometry
log(female size)
log(male size)

Dunham 1993). The association between variables being considered in any comparative analyses may be confounded by the phylogenetic history of the taxa in question. The main problem arises from the fact that species are part of a hierarchical phylogeny, and closely related species tend to be more similar in morphology, physiology, life history, and behaviour than are distantly related species (Harvey and Pagel 1991). This introduces a correlation between species which share a common ancestor, and thus, these species cannot be considered as biologically and statistically independent points for comparative analyses. To deal with the problem of non-independence of species data points, I employ the recently developed 'independent contrasts' technique which removes the confounding influence of phylogeny (Felsenstein 1985; Harvey and Pagel 1991; Garland et al. 1992; Purvis and Garland 1993). This method is based on extracting difference scores (contrasts) in the value of a trait between sister taxa or nodes, that are free of phylogenetic effects. Contrasts are separately calculated for two or more variables (male and female body size in this study) and are subsequently used in regression and correlational analyses. Very few assessments of allometry for SSD, and thus Rensch's rule, have adequately corrected for phylogenetic effects: of the 45 independent studies reviewed in Table 1, only two removed the confounding influence of phylogeny using modern comparative methods. In the present study, I use both standard cross-species regressions and independent contrasts analyses to examine allometric trends for SSD to determine the generality of Rensch's rule. These data are then used to assess the impact of using the independent contrasts method on my parameter estimates and statistical conclusions.

METHODS.

Body Size Data:

I used total body mass (in grams) to estimate overall body size for birds and mammals, total body length (in millimeters) for spiders and insects, and snout to vent length (in millimeters) for reptiles. All body size measurements were obtained from the literature (Table 2). For each species, I recorded the mean body mass (birds and mammals), mean length (spiders and insects), or mean snout to vent length (reptiles) for each sex (Table A1). I considered a species to be dimorphic if the mean male and female sizes for the species were reported as different in the original source. Three principle criteria were used in selecting the data: (1) I used body size measurements only from sexually mature animals; (2) whenever sample sizes were available, I accepted the male and female means for each species only if the sample size for each sex was ≥ 9; and (3) species were selected for analysis only if a hypothesis of their phylogenetic relationships was available.

Statistical Analysis:

Whenever two continuous traits are being compared across a number of extant species for the purpose of analyzing possible evolutionary relationships, it is important to account for the biological and statistical non-independence of species data points. I use Felsenstein's (1985) method of phylogenetically independent contrasts to control for the confounding influence of phylogeny. This method produces a set of independent contrasts among pairs of species and higher nodes of a phylogeny, on the assumption that the difference between a pair of taxa that share an immediate common

Table 2. References from which body size data were extracted (see text).

Taxon	Reference
Birds[1]	Palmer (1962); Ffrench (1973); Cramp and Simmons (1977); Strauch (1977); Thomas (1982); Yanez et al (1982); Pierce (1984); Johnsgard (1973; 1981; 1983a; 1983b; 1986; 1988); Ross (1988); Fry et al. (1988); Lessells and Ovenden (1989); Livezey (1990); Bretagnolle et al. (1990); Clements (1991); Fairbairn and Shine (1993); Dunning (1993).
Mammals	Primates - Gaulin and Sailer (1984); Carnivores - Gittleman (1986); Mustelids - Gittleman (1985), 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).

[1] The principle reference for all bird taxa was Dunning (1993)

ancestor is independent of other difference scores extracted elsewhere in the phylogenetic tree under a brownian motion model of evolutionary change. The method requires complete phylogenetic information for the taxa under study (i.e. a phylogeny and branch length information), and knowledge of the rate and mode of character change (i.e. must assume either a gradualistic or punctuational mode of evolution). For a detailed description of the independent contrasts method see Felsenstein (1985), Garland et al. (1992), and Pagel (1992).

Unfortunately, comparative biologists must often work with only estimates of the true phylogeny linking species in their data set (working phylogenies *sensu* Grafen 1992) with little knowledge of branch length information. These working phylogenies often contain incompletely resolved nodes, which may represent true multi-way speciation events (termed "hard polytomies"), or may simply reflect our ignorance of the true dichotomous branching pattern (termed "soft polytomies") (Purvis and Garland 1993). Recently, several investigators have modified Felsenstein's (1985) independent contrasts approach to account for unresolved phylogenies and missing branch length information (Grafen 1989; Harvey and Pagel 1991; Pagel 1992; Purvis and Garland 1993). Following the guidelines of Purvis and Garland (1993), I considered all unresolved nodes contained within my working phylogenies to be soft polytomies Soft polytomies will cause those species that share a common ancestor within the unresolved nodes to be statistically non-independent. Purvis and Garland (1993) deal with soft polytomies by emphasizing the distinction between statistical estimation and hypothesis testing. They recommend that, in terms of statistical estimation, the full n-1 contrasts (n_c) should always be computed and subsequently analysed by correlation or regression through the origin. With respect to hypothesis testing, since the primary objective of this method is to avoid over-estimating the degrees of freedom (inflation of type I error rates), one should claim only p-1 degrees of freedom, where p = the number of nodes. Alternatively, Grafen (1989) and Pagel (1992) recommend collapsing the information at unresolved nodes into a single linear contrast, thus extracting one piece of information from each node, and claiming only one degree of freedom for hypothesis testing. Computing only a single contrast for each unresolved node may lead to poor estimates of evolutionary correlations and slopes if only a few contrasts are computed for an entire tree (Purvis and Garland 1993). Thus, I have chosen Purvis and Garland's (1993) method because the procedure is simpler, less arbitrary, and may lead to better parameter estimates.

Since the mode of evolutionary change is modelled as a brownian motion process, all contrasts must be adequately standardized so that equal weighting is given to all difference scores in regression analyses (Garland et al. 1992). I verified 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). Any significant linear or non-linear trends in the plot indicate that the contrasts are not adequately standardized. When significant trends were detected, I successfully removed them by logarithmically transforming all branch lengths.

I used a standard log/log analysis to detect the allometry for sexual size dimorphism for both cross-species and independent contrasts approaches: If male and female size are related by the general allometric equation the relationship can be expressed as log (Female size) = log (a) + b (log {Male size}), where b is the allometric slope (Leutenneger 1978; LaBarbara 1989; Fairbairn 1990; Fairbairn and Preziosi 1994). I calculated model II major-axis regressions of log (female size) vs. log (male size) with 95% confidence intervals (Sokal and Rohlf 1995), and tested against the null hypothesis of a slope equal to 1.0 (isometry) (all probability tests were two tailed, alpha = 0.05). To estimate the slope of the line for standardized independent contrasts I used Model II major axis regression through the origin (Garland et. al. 1992). I 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 in order to standardize all graphical representations of independent contrasts.

In both the cross-species and independent contrasts regression analyses, both statistical conclusions (the slope is or is not significantly different from one) are crucial to drawing statistical conclusions regarding the generality of Rensch's rule. To help guard against making type II errors (the probability of failing to reject a false null hypothesis), I estimated the power of the regression analyses to detect a slope significantly different from 1.0 (power = 1-ß, where ß is the probability of making a type II error) by constructing a randomization program. The randomization program first generates a set of normally-distributed, random X values (male body size) with the same mean and standard deviation as the original X values. Then, a set of Y values (female body size) are generated using the model I least squares regression equation. To each Y value, a normally distributed random error term with a mean of zero and a standard deviation equal to the square root of the unexplained mean square ($\sqrt{SS/n-1}$) from the above model I least-squares regression equation is added. The model II major axis slope and 95% confidence intervals are then estimated from the X and Y values. The process is repeated 5000 times, and the frequency with which the confidence intervals exclude 1.0 is equivalent to the power of the regression analyses to detect a slope significantly different from 1.0, given that particular data set.

An alternative statistical method of assessing the allometry for SSD, which is simpler and more powerful, is the paired t-test (performed on independent contrasts). Rensch's rule predicts that there will be a greater evolutionary divergence in male size regardless of which sex is larger (Fairbairn and Preziosi 1994). If each independent contrast extracted from the data is considered as an estimate of the minimum standardized amount of evolutionary divergence as one hypothetical ancestor diverged to yield two daughter species (Garland et al. 1992), then a paired t-test can test for differences between the sexes in the minimum amount of evolutionary divergence. Thus, the paired t-test is another way of testing Rensch's rule in which a greater evolutionary divergence in male size is predicted (i.e. the male contrasts are predicted to be significantly greater than the female contrasts). I calculated paired t-tests as in Sokal and Rohlf (1995), and tested against the null hypothesis of no difference between male and female contrasts. I also calculated the power of the paired t-test as specified in Zar (1984). All probability tests are two-tailed (alpha = 0.05).

I analyzed 35 taxa across five classes (Mammalia, Aves, Reptilia, Insecta, and Arachnida). However, these taxa are hierarchical, and the estimates of allometry for SSD are therefore not all independent of one another. The non-exclusive, hierarchical nature of the 35 analyses was a result of analyzing subtaxa within given taxonomic groups. This was done to confirm previous hypotheses regarding the allometry for SSD, and to control for the fact that an allometric relationship across a taxon may differ from the allometric relationships found independently within the subtaxa of that taxon (Harvey and Pagel 1991). Only 21 of the 35 taxa were considered to be non-hierarchical and independent estimates of the allometry for SSD (Table 3). For the 21 independent analyses, the taxonomic level chosen for analyses (for a given taxonomic group) was the level in which no heterogeneity of slopes was detected among the subtaxa within that taxon. I used species-level comparisons for all 21 independent analyses.

I only analyzed taxa in which at least 85% of species were reported as dimorphic in size, and I placed each taxon in one of three groups; (1) taxa which contain species in which males are larger than females, and species in which females are larger than males (male/female-biased SSD), (2) taxa in which SSD is primarily male-biased, and (3) taxa in which SSD is primarily female-biased (Table 3). I placed a taxon in the male/female-biased group if the frequency of bias in each direction was less than 80% (e.g. 30% female-biased and 70% male-biased). I placed a taxon in the male-biased group if males were the larger sex in more than 80% of the species, and in the female-biased group if females were the larger sex in more than 80% of the species (Table A2).

The published phylogenetic hypotheses used for each taxon are listed

Table 3. Taxa analyzed and associated published phylogenies.

Common name	Scientific name	n	df_c[1] (p-1)	Phylogenetic hypothesis
Male/Female-Biased Taxa[2]				
Mammals				
Carnivores	Carnivora	17	15	Garland et al. (1993)
Birds				
Shorebirds - excluding Sandpipers and Allies	Charadriiformes	65	35	Sibley and Alquist (1990)
Hummingbirds	Trocholiformes	14	12	Johnsgard (1983b)
Seabirds	Procellariiformes, Pelicaniformes	40	29	Brush and Witt (1983); Sibley and Alquist (1990).
Reptiles				
Snakes				
Australian Elapids - Division B	Acanthopiinae Division B	31	29	Wallach (1985); Mengden (1985); Shine (1985); Schwaner et al. (1985).
Australian Elapids - Division C	Acanthopiinae Division C	16	14	Wallach (1985); Mengden (1985); Shine (1985); Schwaner et al. (1985).
Colubrids - Terrestrial, Arboreal Neotropical Oldworld swamp	Colubrinae Lycodontinae Xenodontinae	18	16	Dowling et al. (1983)
Male-Biased Taxa[3]				
Mammals				
Ungulates	Artiodactlya, Persilodactlya	27	25	Garland et al. (1993)

Table 3, continued:

Common name	Scientific name	n	df_c (p-1)	Phylogenetic hypothesis
Mustelids	Mustelidae	26	15	Bryant et al. (1993)
Primates	Primates	37	33	Sillen- Tullberg and Moller (1993)
Birds				
Waterfowl	Anseriformes	28	18	Kessler and Avise (1984); Sibley and Alquist (1990); Quinn et al. (1991).
Gamebirds - Grouse, Quails, Pheasants, Partridges.	Galliformes	27	20	Johnsgard (1973;1983a); Sibley and Alquist (1990); Crowe et al. (1992).
Reptiles				
Snakes				
Vipers, Pitvipers	Viperidae	16	13	Klauber (1972); Ashe and Marx (1988); Knight et al. (1993);
Lizards				
Iguanids (American arboreal)	Iguanidae	90	77	Presch (1969); Ballinger and Tinkle (1972); Lopez et al. (1992); Etheridge and de Queiroz (1988); Losos (1990); Sites et al. (1992).
Female-Biased Taxa[4]				
Birds				
Raptors	Falconiformes	22	11	Sibley and Alquist (1990); Griffiths (1994);

Table 3, continued:

Common name	Scientific name	n	df_c (p-1)	Phylogenetic hypothesis
Owls	Strigiformes	25	15	Sibley and Alquist (1990); Randi et al. (1990).
Shorebirds - Sandpipers and allies	Scolopacidae	35	17	Sibley and Alquist (1990).
Insects				
Waterstriders[5]	Gerridae	46	44	Andersen (1994)
Arachnids				
True spiders[6]	Araneomorphae	44	17	Platnick et al. (1991); Coddington and Levi (1991).
Reptiles				
Snakes				
Colubrids - Watersnakes and Allies	Natracinae	14	12	Dowling et al. (1983); Lawson (1987*).
Australian Elapids - Division A	Acanthopiinae Division A	19	17	Wallach (1985); Mengden (1985); Shine (1985); Schwaner et al. (1985).

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[1]Degrees of Freedom associated with the independent contrasts analysis (the number of nodes -1).

2 Taxa that contain species in which males are larger than females, and species in which females are larger than males (see text)

[3] Taxa in which the males are larger than the females (see text).

4 Taxa in which females are larger than the males (see text).

[5] Both long winged and short winged morphs were included for each species.

[6] True spiders excluding orbweaving spiders (Araneidae)

in Table 3. When branch length information for the working phylogeny of a given taxa was unavailable, I used Grafen's (1989) algorithm of assigning arbitrary branch lengths. Computations for the independent contrasts analysis were done using the Phenotypic Diversity Analysis Program (PDAP version 2.0, copyright 1, September 1993) by J.A. Jones, A.W. Dickerman, and T.H. Garland.

RESULTS.

The paired t-tests had the highest mean power of the three analyses (Table 4). Since power is 1-ß where ß is the probability of committing a type II error (failing to reject a false null hypothesis), the mean probability of making type II errors in the cross-species and independent contrasts regressions is high: mean ß ± SE = 0.831 ± 0.051 , and 0.795 ± 0.052 respectively, for comparisons in which the H_0 was not rejected. Therefore, I used the results of the paired t-test in conjunction with the independent contrasts regressions to test the Fairbairn and Preziosi allometric model. A given taxonomic group was considered to show significant allometry for SSD if the slope of the independent contrasts regression was significantly different from 1.0 (i.e. the 95% confidence intervals exclude 1.0) or if the paired t-test detected significant differences between male and female contrasts.

In the male/female-biased taxa (Figure 2), five of the seven cross-species slopes are less than 1.0, while all of the slopes derived from the independent contrasts analyses are less than 1.0. Overall, three of these taxa showed significant allometry for SSD; hummingbirds, seabirds, and Australian elapids - Division B. All were in the direction predicted by the Fairbairn and Preziosi (1994) allometric model, and are thus consistent with Rensch's rule. It should be noted that the slope of the colubrids (terrestrial, arboreal, neotropical, and swampsnakes) is almost significantly less than one ($p < 0.1$).

In the male-biased taxa (Figure 3), cross-species slopes are less than 1.0 in five of seven taxa. All of the independent contrasts slopes are less than one, and three are significantly so: primates, gamebirds, and vipers and pit

Table 4. Power analyses of cross-species and independent contrasts regressions, and paired t-test.

Taxon	Power of cross-species regression[1]	Power of independent contrasts regression[2]	Power of paired t-test (on independent contrasts)[3]
Male/Female-Biased Taxa[4]			
Mammals			
Carnivores	0.542	0.028	0.756
Birds			
Shorebirds - excluding Sandpipers and Allies.	0.678	0.010	0.626
Hummingbirds	0.811	0.807	0.108
Seabirds	0.914	0.962	0.710
Reptiles			
Snakes			
Australian Elapids-Division B	0.039	0.371	0.881
Australian Elapids-Division C	0.051	0.020	0.848
Colubrids - Terestrial, Arboreal, Neotropical, and Swampsnakes.	0.915	0.712	0.205
Male-Biased Taxa[5]			
Mammals			
Ungulates	0.085	0.115	0.841
Mustelids	0.321	0.071	0.523
Primates	0.863	0.728	0.717

Table 4, continued:

Taxon	Power of cross-species regression	Power of independent contrasts regression	Power of paired t-test (on independent contrasts)
Birds			
Waterfowl	0.457	0.024	0.063
Gamebirds	1.000	1.000	0.965
Reptiles			
Snakes			
Vipers & Pitvipers	0.794	0.732	0.344
Lizards			
Iguanids	0.060	0.403	0.116
Female-Biased Taxa[6]			
Birds			
Raptors	0.047	0.003	0.909
Owls	0.315	0.473	0.529
Shorebirds - Sandpipers and Allies	0.536	0.004	0.497
Insects			
Waterstriders	0.701	0.998	0.906

Table 4, continued:

Taxon	Power of cross-species regression	Power of independent contrasts regression	Power of paired t-test (on independent contrasts)
Arachnids			
True Spiders - excluding Orbweavers	0.043	0.002	0.764
Reptiles			
Snakes			
Colubrids - Watersnakes and Allies	0.673	0.179	0.812
Australian Elapids-Division A	0.033	0.103	0.824
Mean Power ± SE[7]	0.145 ± 0.050	0.168 ± 0.057	0.581 ± 0.078

---

[1] Power of the cross-species regression to detect a slope significantly different from 1.0.

[2] Power of the independent contrasts analysis to detect a slope significantly different from 1.0.

[3] Power of the paired t-test to detect a significant difference between male and female contrasts.

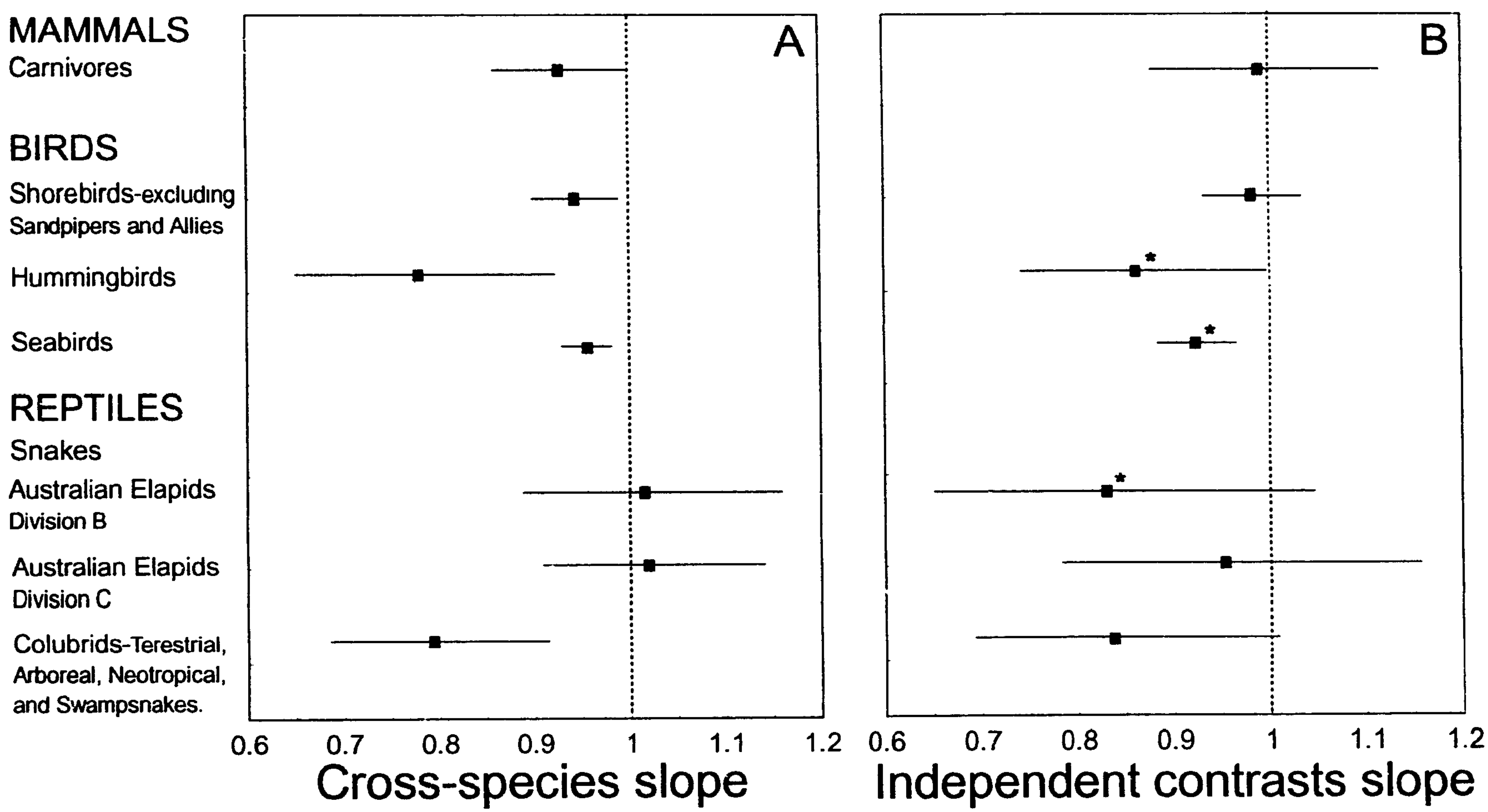
[4] Taxa that contain species that are male-biased in size and species that are female biased in size (see text).

[5] Taxa in which males are larger the sex (see text).

[6] Taxa in which females are larger the sex (see text).

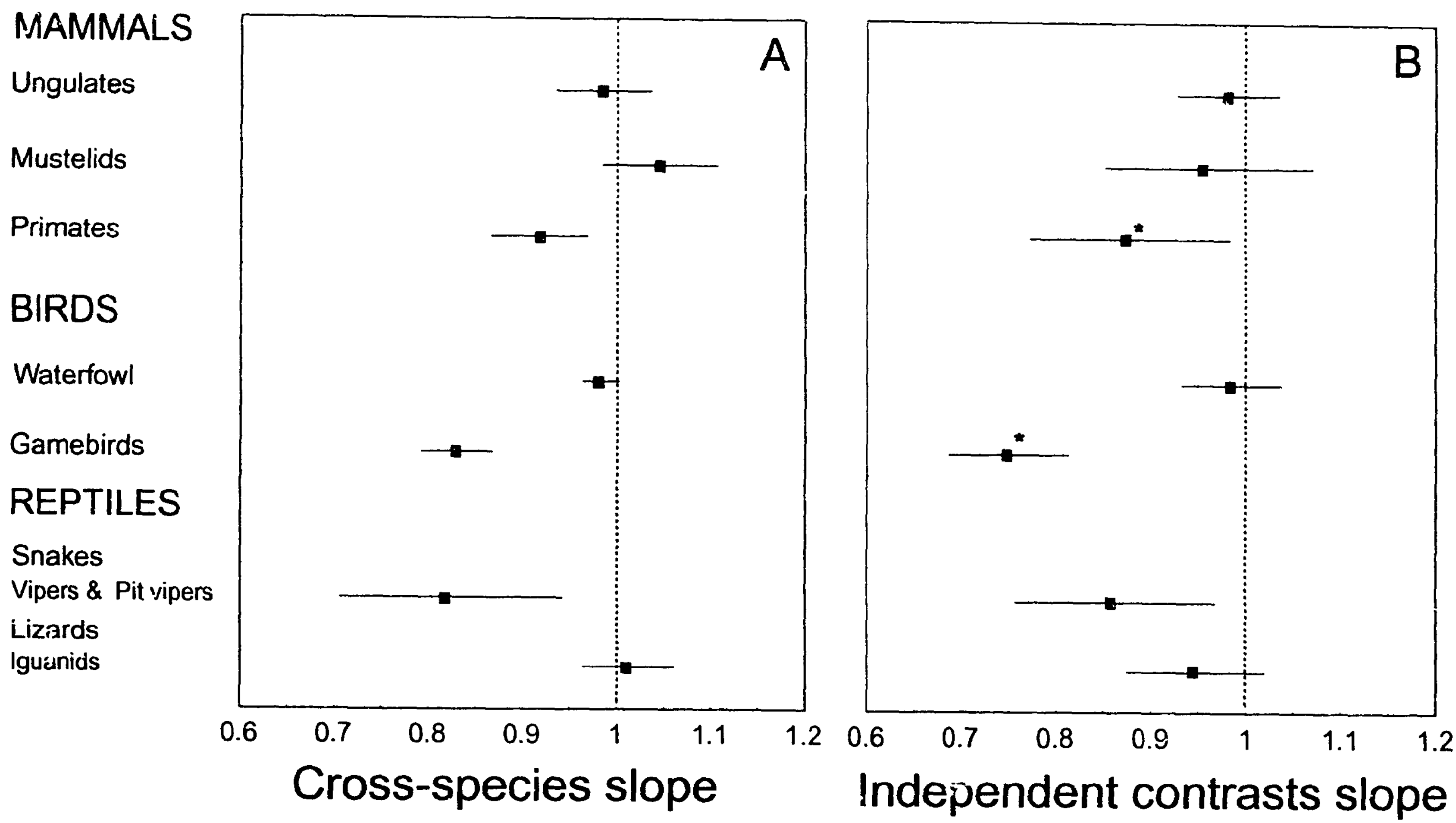
7 Mean power for those taxa in which the 95% confidence intervals of the slope overlap 1 for the cross-species and independent contrasts regressions, and for those taxa in which non-significant results were recorded for the paired t-test, and their standard errors (Figures 2,3,4).

FIGURE 2: Allometric slopes and 95% confidence intervals for male/female-biased taxa derived from cross-species (A) and independent contrasts (B) analyses. The vertical dashed line is the line of isometry (i.e. a slope of 1.0). The solid squares represent the model II-major axis slope, and the horizontal solid lines represent the 95% confidence intervals. The asterisk (*) denotes significant differences between male and female contrasts as determined by the paired t-tests. See Table 3 for scientific names of taxa.



MAMMALS
Carnivores
BIRDS
Shorebirds-excluding Sandpipers and Allies
Hummingbirds
Seabirds
REPTILES
Snakes
Australian Elapids Division B
Australian Elapids Division C
Colubrids-Terestrial, Arboreal, Neotropical, and Swampsnakes.
A
B
0.6
0.7
0.8
0.9
1
1.1
1.2
Cross-species slope
Independent contrasts slope

FIGURE 3: Allometric slopes and 95% confidence intervals for male-biased taxa derived from cross-species (A) and independent contrasts (B) analyses. The vertical dashed line is the line of isometry (i.e. a slope of 1.0). The solid squares represent the model II-major axis slope, and the horizontal solid lines represent the 95% confidence intervals. The asterisk (*) denotes significant differences between male and female contrasts as determined by the paired t-tests. See Table 3 for scientific names of taxa.


MAMMALS
Ungulates
Mustelids
Primates
BIRDS
Waterfowl
Gamebirds
REPTILES
Snakes
Vipers & Pit vipers
Lizards
Iguanids
A
B
0.6
0.7
0.8
0.9
1
1.1
1.2
Cross-species slope
Independent contrasts slope
*

vipers. Again, all significant slopes are consistent with Rensch's rule.

In taxa with female-biased SSD (Figure 4), cross-species regressions revealed slopes less than 1.0 in three taxa, and greater than 1.0 in four. In the independent contrasts regressions, the slopes for four taxa are less than one, while three are greater than one. Significant allometry for SSD occurred only in the waterstriders and owls, and only in the waterstriders was it in the predicted direction.

The overall patterns revealed by the 21 independent estimates of the allometry for SSD are summarized in Figure 5. The slopes are significantly less than 1.0 in 33% of the taxa analyzed (Figure 5A). However, of the taxa with significant allometry for SSD, 88% have slopes significantly less than 1.0. A chi-square test detected significant deviation from a 50:50 ratio between the number of taxa in which the slopes are significantly less than 1.0 and the number of taxa in which the slopes are significantly greater than 1.0 ($x^2 = 4.5$, $p < 0.05$). Thus allometry for SSD is not universal, but when it does occur it is almost always in the direction predicted by Rensch's rule.

The allometry for SSD is found across a diverse range of taxonomic groups (Figure 5B), and occurs regardless of the direction of dimorphism (Figure 5C). However, there appears to be no consistent pattern of allometry in taxa where females are the larger sex (two cases of significant allometry; waterstriders are hypoallometric, while owls are hyperallometric). Allometry consistent with Rensch's rule occurs more frequently and consistently in taxa in which male-biased SSD is present.

In addition to the 21 independent estimates of the allometry for SSD, I analyzed 12 species of grouse (Tetraoninae), and 14 mustelid genera

FIGURE 4: Allometric slopes and 95% confidence intervals for female-biased taxa derived from cross-species (A) and independent contrasts analyses (B). The vertical dashed line is the line of isometry (i.e. a slope of 1.0). The solid squares represent the model II-major axis slope, and the horizontal solid lines represent the 95% confidence intervals. The asterisk (*) denotes significant differences between male and female contrasts as determined by a paired t-test. See Table 3 for scientific names of taxa.

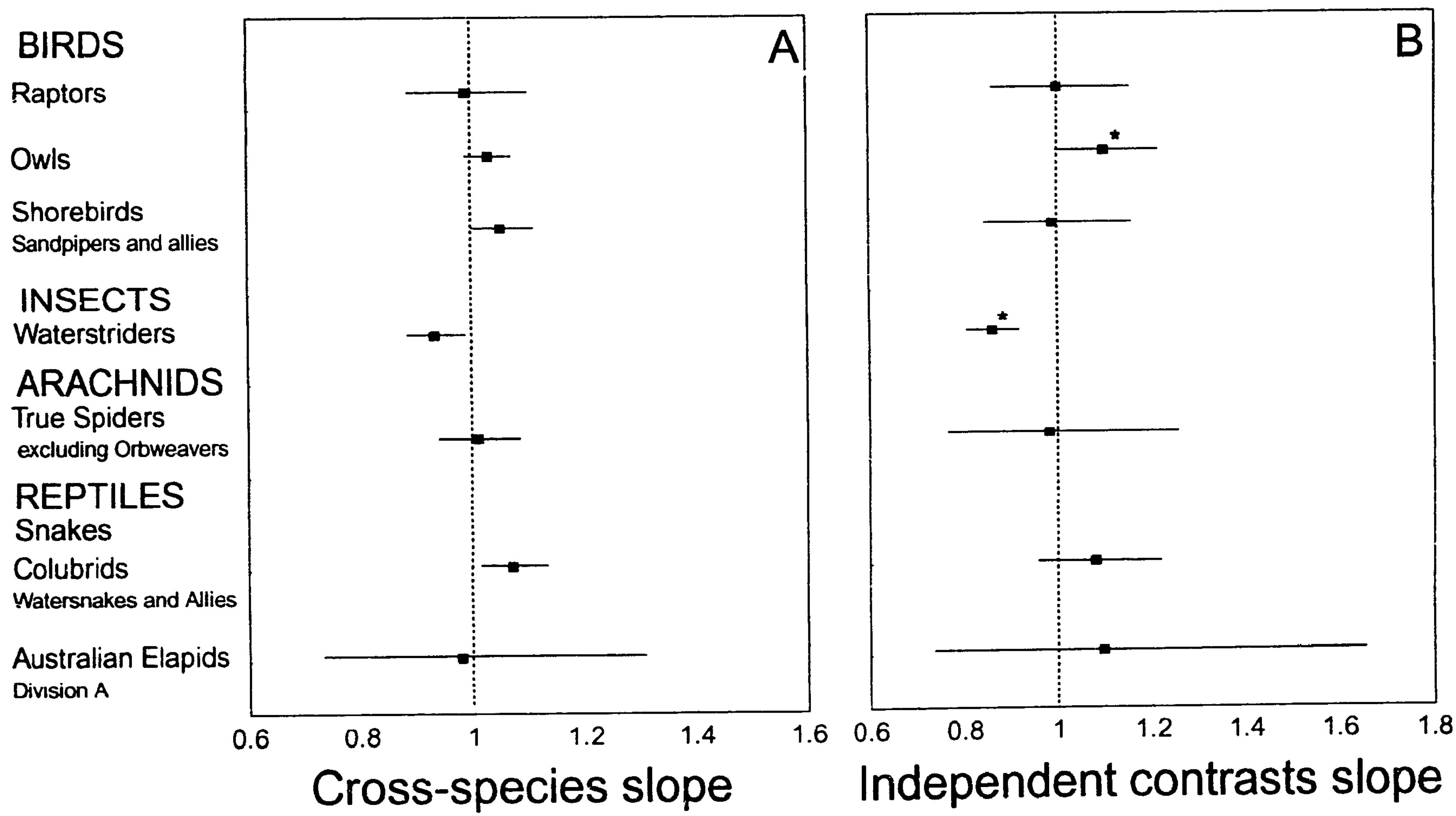
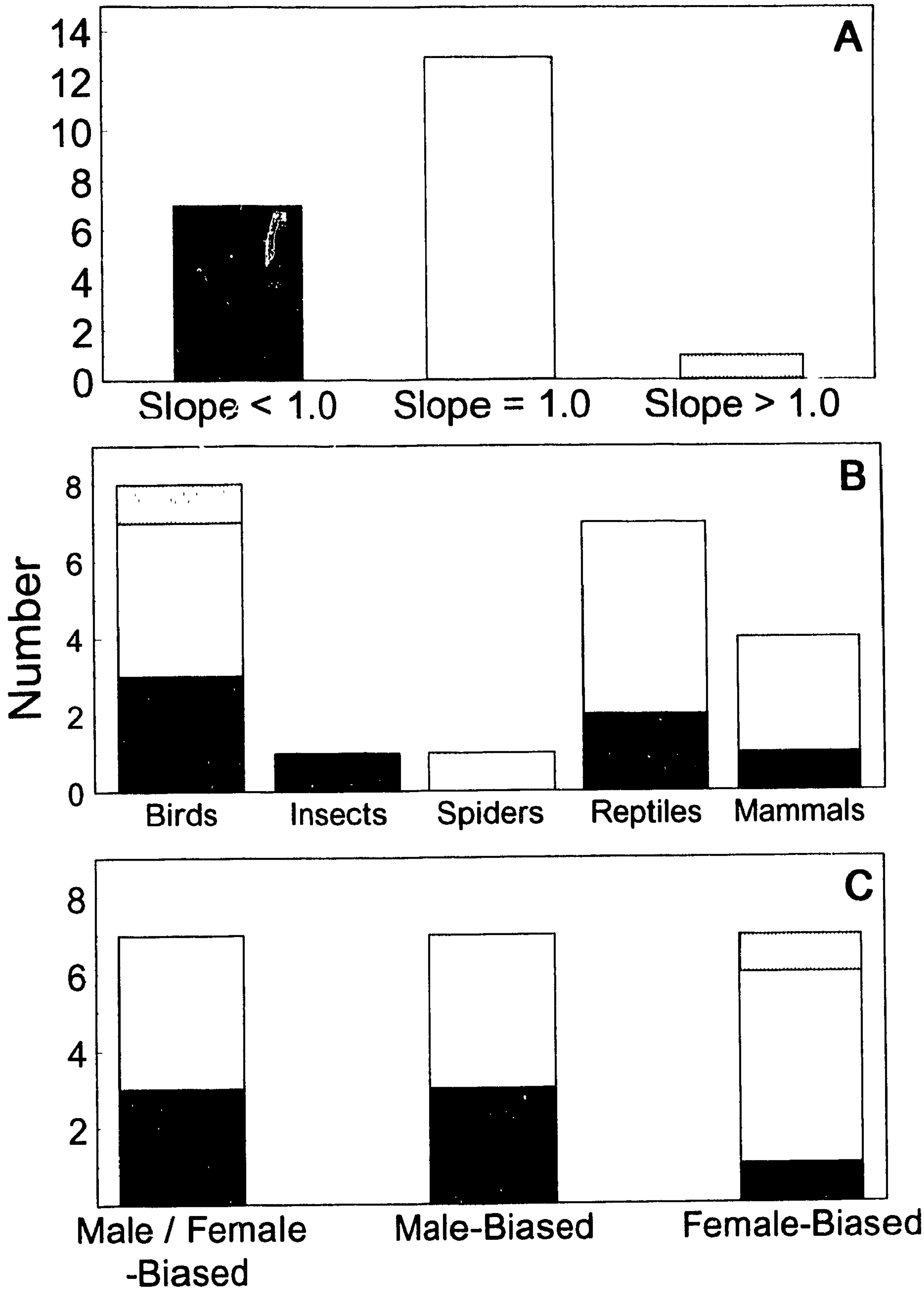

BIRDS
Raptors
Owls
Shorebirds
Sandpipers and allies
INSECTS
Waterstriders
ARACHNIDS
True Spiders
excluding Orbweavers
REPTILES
Snakes
Colubrids
Watersnakes and Allies
Australian Elapids
Division A
A
0.6
0.8
1
1.2
1.4
1.6
Cross-species slope
B
*
*
0.6
0.8
1
1.2
1.4
1.6
1.8
Independent contrasts slope

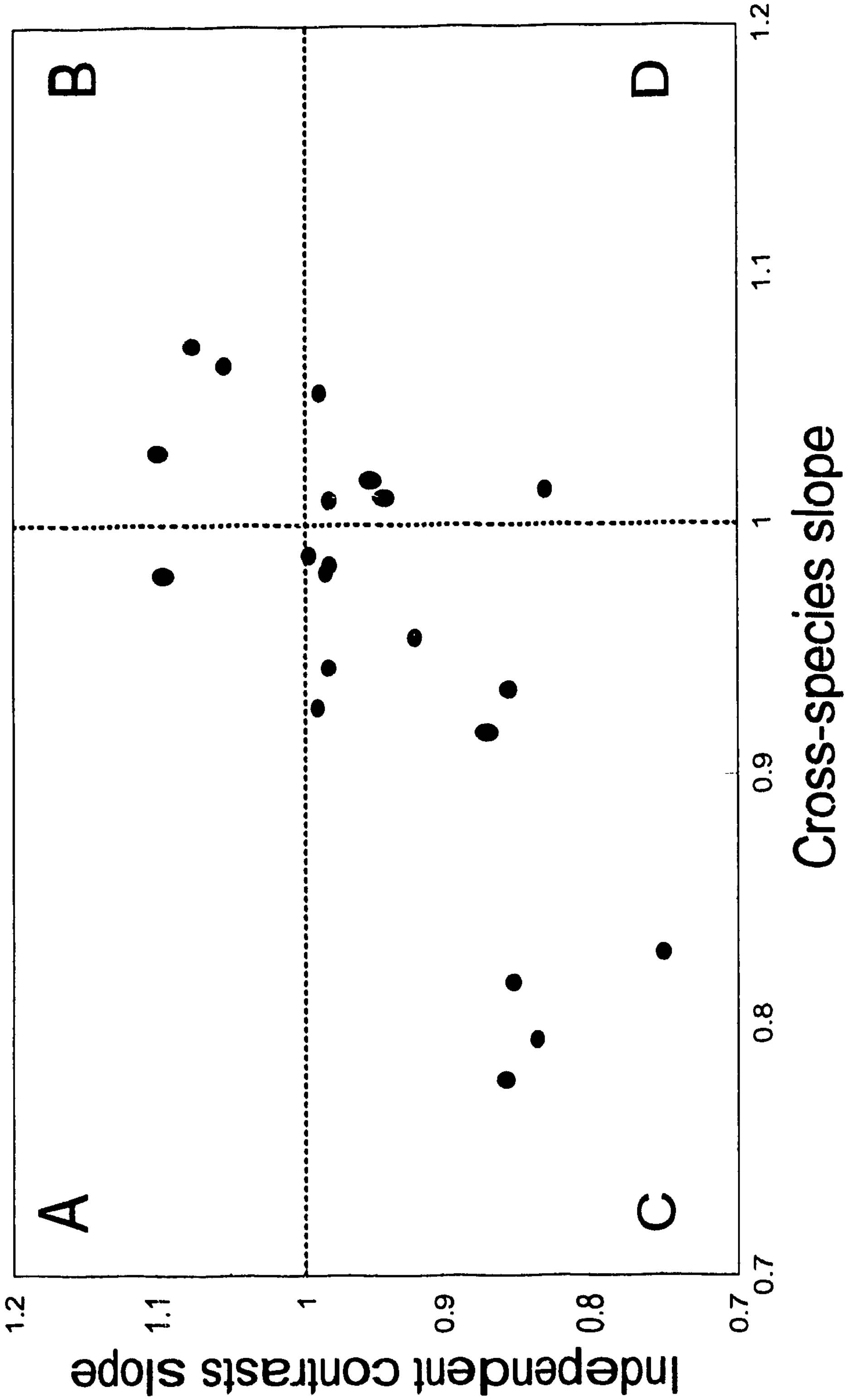
FIGURE 5: The number of independent estimates of the allometry for SSD grouped by direction of slope (A) taxonomic group (B), and direction of dimorphism (C). The solid black portion of the bar indicates slopes that are significantly less than 1, the white portion indicates that slopes are not significantly different from 1, and the vertical stripes indicates that slopes are significantly greater than 1.


A
Slope < 1.0
Slope = 1.0
Slope > 1.0
B
Number
Birds
Insects
Spiders
Reptiles
Mammals
C
Male / Female -Biased
Male-Biased
Female-Biased

(Mustelidae) to confirm previous evidence regarding Rensch's rule in these two taxa (Table 1). Wiley (1974) found significant hyperallometry in the grouse (a subtaxon of the gamebirds). My results show that the slope for the grouse is significantly different from 1.0 for both the cross-species (slope = 0.700, 95% C.I. = 0.649-0.754) and the independent contrasts (slope = 0.675, 95% C.I. = 0.618-0.735) analyses, and the paired t-test indicates significant differences between male and female contrasts ($t = 3.671$, $p < 0.005$). Both the independent contrasts and cross-species regressions, as well as the paired t-test are in the predicted direction, and thus, these analyses support Wiley's (1974) conclusions for the grouse, and my conclusions for the gamebirds as a whole. Ralls and Harvey (1985) found significant hypoallometry in 14 mustelid genera. I also find significant hypoallometry in the cross-genera analyses (slope = 1.064. 95% C.I. = 1.010-1.121), but no significant patterns of allometry for SSD are detected in the independent contrasts regressions of genera (slope = 1.054, 95% C.I. = 0.981-1.132) or paired t-test ($t = 0.746$, $p > 0.05$). These results agree with my species-level analysis of 26 mustelid species. Thus, controlling for the confounding influence of phylogeny removes the apparent allometric trend, and puts my results in conflict with the results obtained by Ralls and Harvey (1985).

To assess the impact of using the independent contrasts method on my parameter estimates and statistical conclusions, I compared the slopes and statistical conclusions of cross-species and independent contrasts analyses. I compared the parameter estimates for the 21 independent analyses by regressing the slopes from the independent contrasts regressions on the slopes from the cross-species regressions (Figure 6). The model II major-axis

FIGURE 6: Scatterplot of the independent contrasts and cross-species slopes, $r = 0.715$, $df = 20$, $p < 0.001$. The dashed lines represents a slope equal to 1.0.



A
B
C
D
Independent contrasts slope
1.2
1.1
1
0.9
0.8
0.7
Cross-species slope
0.7
0.8
0.9
1
1.1
1.2

slope is not significantly different from 1.0 ($Y = -0.12305 + 1.12\{x\}$), 95% C.I. = 0.693-1.86), and a paired t-test indicates no significant differences between the means of the independent contrasts and cross-species slopes ($t = 0.607$, $p > 0.5$). However, only 51 % of the variation in the independent contrasts slopes can be explained by the variation in the cross-species slopes. These results indicate that there are no systematic biases in the parameter estimation of cross-species and independent contrasts slopes, but that the cross-species slopes would not be accurate predictors of independent contrasts slopes. Furthermore, as can be seen from quadrants A and D in Figure 6, there are five taxa in which the cross-species slopes are greater than 1.0, while the independent contrasts slopes are less than 1.0 (quadrant D), and one taxon in which the cross-species slope is less than 1.0 while the independent contrasts slope is greater than 1.0 (quadrant A). This shift in the parameter estimates of the slopes between the cross-species and independent contrasts regressions indicates strong phylogenetic effects on the slopes in 29% (six of 21) of the taxa analysed .

Comparing the statistical conclusions of the independent contrasts and cross-species regressions (excluding the paired t-test) revealed that the statistical conclusions differed in 24% of the taxa (Table 5). In each case, the cross-species regressions show significant allometry for SSD, while the independent contrasts do not. This pattern indicates that either the cross-species analyses are more powerful than the independent contrasts analyses or that type I errors are more likely to occur in the cross-species analyses. However, this is resolved when the more powerful paired t-test is included in the analyses. The difference in statistical conclusions between the two types

Table 5. Statistical conclusions for independent contrasts vs. cross-species analyses.

Analysis	++[1]	--[2]	-+[3]
Independent contrasts vs. cross-species regressions	29%	48%	24%
Independent contrasts regression and paired t-test vs. cross-species regression.	29%	38%	33%

[1] Significant allometry for SSD in the same direction are obtained for both independent contrasts and cross-species analyses.

[2] Independent contrasts and cross-species analyses show no significant patterns of allometry.

3 Cross-species and independent contrasts analyses yield different statistical conclusions for the allometry for SSD.

of analyses increases to 33%. Of the 33% (seven taxa) yielding different statistical conclusions for the two types of analyses, the cross-species analyses showed significant allometry for SSD when the independent contrasts did not in five cases. The paired t-test detected significant allometry when the two types of regression analyses did not in two cases. If differences in power between the two types of analyses is responsible for the difference in statistical conclusions, then the addition of the more powerful paired t-test to the comparisons should decrease the differences in statistical conclusions between the independent contrasts and cross-species analyses. These results indicate that type I errors are more likely in the cross-species analyses. Thus, for accurate statistical conclusions, I recommend using the method of independent contrasts.

DISCUSSION.

Rensch's rule is not universal across the animal kingdom, but occurs in 33% of the taxa examined across a diverse range of invertebrate and vertebrate taxa. The predicted allometry for SSD is most common amongst taxa in which male-biased size dimorphism is present, and no consistent patterns of allometry for SSD are observed in female-biased taxa. These general patterns are fairly consistent with previous evidence which, although often statistically weak, tends to support Rensch's rule in 46% of taxa, and in four of the seven taxonomic classes (Mammalia, Aves, Reptilia, and Insecta) (Table 1). The predicted pattern of allometry appears to be more common among those taxa in which male-biased size dimorphism is present (e.g. gamebirds, blackbirds, kangaroos, primates), but is not restricted to these taxa.

I examined allometry for SSD in 14 taxa that are also listed in Table 1. In five of these taxa (seabirds, hummingbirds, gamebirds, waterstriders, and spiders), my results confirm the conclusions of previous studies. The seabirds, hummingbirds, gamebirds, and waterstriders support Rensch's rule, whereas the spiders do not.

In six of the 14 taxa (owls, shorebirds, raptors, ungulates, primates, and lizards) my results resolve conflicting evidence regarding Rensch's rule. Previous conflicting hypotheses in these six taxa were the result of anecdotal evidence or inadequate statistical analyses (i.e. regressing an index of SSD vs body size, using model I regression, or no phylogenetic controls) to draw conclusions regarding the allometry for SSD. Rigorous quantitative analyses show no significant patterns of allometry for SSD in the shorebirds, raptors, ungulates, and iguanid lizards, and significant hyperallometry in the owls and primates (the primates support Rensch's rule, whereas the owls do not) . These results agree with Jehl and Murray (1986) for the shorebirds; Selander (1966; 1972), Synder and Wiley (1976), and Newton (1979) for the raptors; Alexander et al. (1979) for the ungulates; Fitch (1976) for the iguanid lizards; Earhart and Johnson (1970) for the owls; and Clutton-Brock et al. (1977), Ralls (1977), Leutenegger (1978; 1982), Leutenegger and Cheverud (1982), and Gaulin and Sailer 1984) for the primates.

In an extensive review of patterns of SSD in reptiles, Fitch (1981) found no significant patterns of allometry for SSD across eight different size classes of snake species, and five different size classes of lizard species. My results indicate that Rensch's rule is found in two of six snake taxa, indicating that allometry for SSD occurs in some snake taxa but not others. My finding of no significant allometry for 90 species of iguanid lizards is consistent with Fitch's (1981) results, as well as Stamps (1983) analysis of allometry for SSD across 30 territorial lizard species.

Only in two taxa, mustelids and waterfowl, do my results disagree with the conclusions of previous studies. Ralls and Harvey (1985) found significant hypoallometry for SSD (i.e. a decrease in SSD as body size increases) across 14 mustelid genera, a taxon in which males are the larger sex. Since then, this group has been used as a prime example of an exception to Rensch's rule (Reiss 1986). However, after controlling for the non-independence of generic-data points, I detected no significant allometry for SSD. This discrepancy indicates that in this case, using generic-level comparisons as a method of removing phylogenetic effects is inadequate. In 1980, Moors also found significant hypoallometry for SSD, but across 15 mustelid species. However, he used no phylogenetic corrections, and regressed an index of SSD against body size to assess allometry for SSD. It is important to note that my results show that the slope is greater than 1.0 in the cross-species regression, but less than 1.0 in the independent contrasts regression. This shift indicates that there are major phylogenetic effects in this taxon, and that the direction of the slope resulting from independent contrasts regression is now consistent with Rensch's rule rather than an exception to the rule. My quantitative analyses show no significant patterns of allometry for SSD in this taxon.

Sigurjonsdottir (1981) found significant hyperallometry in 105 species of waterfowl, while my results show no significant allometric patterns. This discrepancy could have arisen because Sigurjonsdottir (1981) used wing length as an estimate of overall body size, and did not remove phylogenetic effects. However, this discrepancy may also be due to the low power in the independent contrasts analyses (paired t-test and regression) resulting from the reduced number of degrees of freedom associated with the poorly resolved phylogeny used in this taxon. My results are in partial agreement with Sigurjonsdottir (1981) and Rensch's rule in that the slope is less than 1.0, but not significantly so ($p < 0.1$). Thus, conclusions regarding Rensch's rule remain uncertain, and must await better phylogenetic resolution for a more powerful test of the patterns of allometry for SSD in this taxon.

Computer simulation studies show the independent comparisons method to almost always yield acceptable levels of type I error, and good estimates of evolutionary correlations or slopes (Martins and Garland 1991; Grafen 1992; Purvis et al. 1994). Conversely, a simple correlation or regression of trait values across the tips of a phylogeny (cross-species correlation or regression) almost always yields inflated type I error rates, and poor estimates of evolutionary correlations or slopes (Martins and Garland 1991; Grafen 1992; Purvis et al. 1994). It is important to note that violations of the assumptions of Felsenstein's methods, such as inaccurate phylogenetic hypotheses, branch length information, or model of character change, adversely affect the method's performance. However, even under these conditions the independent contrasts technique still performs as well as, if not better than, the cross-species regressions (Martins and Garland 1991; Purvis et al. 1994). The empirical observations in this study lend credence to these simulation results. I found no systematic biases in the parameter estimation of independent contrasts and cross-species slopes. However, I did find that cross-species slopes are not good predictors of independent contrasts slopes, and that in some cases, there are strong phylogenetic influences on the cross-species slopes. Differences in statistical conclusions between independent contrasts and cross-species analyses indicate type I errors are more likely in cross-species analyses. Thus, for accurate parameter estimation and statistical conclusions, I recommend the use of the independent contrasts method.

Many functional hypotheses have been proposed to explain Rensch's rule for taxa in which males are the larger sex, and are reviewed in Reiss (1986) and Webster (1992). Several investigators have proposed that hyperallometry in taxa where males are larger than females is caused by sexual selection favouring large male size (Maynard Smith 1977; Clutton-Brock et al. 1977; Leutenneger 1978; Webster 1992). Fairbairn and Preziosi (1994) extend the sexual selection hypothesis and provide quantitative evidence to show that the greater evolutionary divergence in male size predicted by the Rensch's rule may have evolved in response to sexual selection favouring large males, even in taxa where females are the larger sex. According to the Fairbairn and Preziosi (1994) sexual selection hypothesis, sexual selection favoring large males produces an increase in male size, as well as a smaller, correlated increase in female size, because of the high genetic correlations between the sexes (Lande 1980). These responses to sexual selection favouring large males produce correlated increases in the average size of both sexes, as well as changes in SSD. In female-biased taxa, sexual selection favouring large males would cause increases in the size of both sexes, accompanied by decreasing SSD (i.e. the initially smaller sex {males} increase in size more rapidly than the larger sex), and in male-biased taxa, increases in the size of both sexes will be accompanied by increasing SSD. Thus regardless of which sex is initially larger, sexual selection favouring large males can be expected to push taxa from left to right along the allometric line in Figure 1. The association of Rensch's rule with taxa in which male-biased SSD is present is consistent with the Fairbairn and Preziosi (1994) sexual selection hypothesis, in that both male-biased SSD and allometry are likely to reflect sexual selection acting on males. Furthermore, the only female-biased taxon to support Rensch's rule is the waterstriders, and in this taxon there is strong quantitative evidence to show 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).

In addition to assessing the generality of Rensch's rule, the patterns of allometry for SSD found in my study may inform hypotheses concerning the functional significance of SSD. For example, numerous functional hypotheses have been proposed for the evolution of female-biased SSD in the raptors (reviewed in Anderson and Norberg (1981)). Greenwood and Wheeler (1983) proposed that the key factor which has resulted in the evolution of female-biased SSD in this group is a constraint on female flight performance prior to egg laying. One major prediction of this model is that smaller species should be more sexually dimorphic than larger ones. My results clearly do not support this major prediction, and thus falsify the hypothesis.

In conclusion, I have found that allometry for SSD is not universal, but where found, tends to be in accord with Rensch's rule. Quantitative estimates of the allometric slopes based on modern phylogenetic comparative methods are clearly desirable in estimating allometric trends, and are likely to produce more accurate statistical conclusions than traditional cross-species analyses. My results support the hypothesis that allometry for SSD consistent with Rensch's rule occurs in association with sexual selection acting on male size, and I make this prediction for future studies (Fairbairn and Preziosi 1994). Other patterns of allometry for SSD are rare (found in only one taxon), and await functional explanations.

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APPENDIX

Table A1. Mean male and female body sizes (total weight in grams, total body length and snout to vent length in millimeters). Sources for body size data are listed in Table 2.

Taxon	n (males)	Male size (grams)	n (females)	Female size (grams)
Mammalia				
Primates				
Tarsidae				
Tarsius bancanus	...	1200.0	...	1100.0
Callithricidae				
Saguinus geoffroyi	...	500.0	...	500.0
Cebidae				
Cebus capucinus	...	3800.0	...	2700.0
Alouatta seniculus	...	8100.0	...	6400.0
Aotus trivirgatus	...	920.0	...	1000.0
Callicebus moloch	...	680.0	...	680.0
Callicebus torquatus	...	680.0	...	680.0
Ateles belzebuth	...	6000.0	...	6000.0
Ateles geoffroyi	...	7400.0	...	7600.0
Saimiri oerstedii	...	890.0	...	740.0
Saimiri sciureus	...	1040.0	...	670.0
Cercopithecus aethiops	...	4500.0	...	3600.0
Cercopithecus cephus	...	4100.0	...	2900.0
Cercopithecus mitis	...	4500.0	...	4500.0
Cercopithecus neglectus	...	7000.0	...	4000.0
Cercopithecus nictitans	...	6600.0	...	4200.0
Miopithecus talapoin	...	1400.0	...	1100.0
Cercocebus galeritus	...	10200.0	...	5500.0
Cercocebus albigena	...	9000.0	...	6400.0
Macaca fascicularis	...	5900.0	...	4100.0

Table A1, continued:

Taxon	n (males)	Male size (grams)	n (females)	Female size (grams)
Macaca fuscata	...	11000.0	...	9200.0
Macaca nemestrina	...	10000.0	...	7000.0
Macaca sinica	...	5700.0	...	3600.0
Papio hamadryas	...	18300.0	...	9400.0
Theropithecus gelada	...	20500.0	...	13600.0
Colobus guereza	...	10700.0	...	9000.0
Colobus satanas	...	10000.0	...	9000.0
Presbytis entellus	...	15200.0	...	10400.0
Presbytis melalophos	...	6200.0	...	6000.0
Presbytis obscurus	...	6300.0	...	6000.0
Nasalis larvatus	...	20400.0	...	9980.0
Hylobatidae				
Hylobates agilis	...	5820.0	...	5500.0
Hylobates hoolock	...	6900.0	...	6100.0
Hylobates lar	...	5700.0	...	5300.0
Pongidae				
Pongo pygmaeus	...	69000.0	...	37000.0
Pan troglodytes	...	49000.0	...	41000.0
Gorilla gorilla	...	160000.0	...	93000.0
Perissodactyla				
Rhinocerotidae	...		...	
Ceratotherium simum	...	2200000.0	...	1600000.0
Equidae				
Equus caballus	...	350000.0	...	320000.0
Equus burchelli	...	248900.0	...	219500.0
Artiodactyla				
Camelidae				
Lama guanicoe	...	100000.0	...	82500.0

Table A1, continued:

Taxon	n (males)	Male size (grams)	n (females)	Female size (grams)
Camelus dromedarius	...	545000.0	...	545000.0
Giraffidae				
Giraffa Camelopardus	...	1175000.0	...	912500.0
Bovidae				
Syncerus caffer	...	623300.0	...	420000.0
Bison bison	...	836500.0	...	472500.0
Taurotragus oryx	...	545700.0	...	366000.0
Gazella granti	...	70000.0	...	47500.0
Gazella thomsoni	...	20430.0	...	16210.0
Antilope cervicapra	...	41750.0	...	32250.0
Madoqua kirki	...	5000.0	...	5000.0
Oreamnos americanus	...	114000.0	...	96750.0
Ovis canadensis	...	83000.0	...	48000.0
Hippotragus equinus	...	257500.0	...	239000.0
Aepyceros melampus	...	56900.0	...	42080.0
Connochaetes taurinus	...	220000.0	...	178000.0
Damaliscus lunatus	...	142500.0	...	129250.0
Alcelaphus buselaphus	...	146000.0	...	122500.0
Antilocapridae				
Antilocapra americana	...	55000.0	...	45000.0
Cervidae				
Cervus canadensis	...	400000.0	...	250000.0
Dama dama	...	67000.0	...	44000.0
Alces alces	...	450000.0	...	318000.0
Rangifer tarandus	...	156300.0	...	93700.0
Odocoileus virginianus	...	77000.0	...	48500.0
Odocoileus hemionus	...	87500.0	...	56000.0
Carnivora				
Ursidae				

Table A1, continued:

Taxon	n (males)	Male size (grams)	n (females)	Female size (grams)
Ursus maritimus	...	490000.0	...	225000.0
Ursus arctos	...	298500.0	...	298500.0
Ursus americanus	...	124000.0	...	97000.0
Procyonidae				
Nasua narica	...	5000.0	...	5000.0
Procyon lotor	...	6100.0	...	6700.0
Mustelidae				
Mephitis mephitis	...	2800.0	...	2000.0
Meles meles	...	12300.0	...	10900.0
Martes americana	...	970.0	...	770.0
Martes pennanti	...	5250.0	...	2250.0
Martes martes	...	1200.0	...	1200.0
Martes zibellina	...	1330.0	...	1030.0
Gulo gulo	...	12850.0	...	10350.0
Vormela peregusna	...	670.0	...	530.0
Ictonyx striatus	...	910.0	...	630.0
Mustela vison	...	1210.0	...	610.0
Mustela erminea	...	1280.0	...	620.0
Mustela nivalis	...	100.0	...	60.0
Mustela nixosa	...	50.0	...	50.0
Mustela altaica	...	250.0	...	130.0
Mustela sibirica	...	740.0	...	400.0
Mustela lutreola	...	740.0	...	440.0
Mustela putorius	...	1260.0	...	800.0
Poecilogale albinucha	...	350.0	...	250.0
Mellivora capensis	...	8570.0	...	7590.0
Taxidea taxus	...	4000.0	...	4100.0
Spilogale interupta	...	670.0	...	430.0
Lutra lutra	...	10700.0	...	7100.0
Lutra canadensis	...	8600.0	...	7800.0

Table A1, continued:

Taxon	n (males)	Male size (grams)	n (females)	Female size (grams)
Lutra maculicollis	...	4580.0	...	3500.0
Aonyx capensis	...	20000.0	...	18000.0
Enhydra lutris		32200.0	...	24400.0
Canidae				
Canis lupus	...	35100.0	...	31100.0
Canis latrans	...	11500.0	...	9700.0
Lycaon pictus	...	21800.0	...	22200.0
Urocyon cinereoargenteus	...	4100.0	...	3300.0
Hyanidae				
Hyaena hyaena	...	27000.0	...	26600.0
Crocuta crocuta	...	48700.0	...	55300.0
Felidae				
Acinonyx jubatus	...	57600.0	...	60000.0
Panthera pardus	...	65500.0	...	39300.0
Panthera tigris	...	191000.0	...	131000.0
Panthera leo	...	176100.0	...	135500.0
Aves				
Dinornithiformes				
Apterigidae				
Apteryx australis	15	2120.0	31	2540.0
Apteryx owenii	61	1135.0	41	1351.0
Tinamiformes				
Tinamidae				
Crypturellus boucardi	22	418.0	18	468.0
Galliformes				
Cracidae				

Table A1, continued:

Taxon	n (males)	Male size (grams)	n (females)	Female size (grams)
Ortalis vetula	106	584.0	102	542.0
Phasianidae				
Alectoris chukar	22	619.0	24	537.0
Francolinus pondicerianus	114	274.0	91	228.0
Francolinus francolinus asiae	19	482.0	18	424.0
Francolinus clappertoni	12	604.0	10	463.0
Francolinus adspersus	12	465.0	24	394.0
Francolinus leucoscepus	173	753.0	223	545.0
Francolinus swainsonnii	90	706.0	100	505.0
Coturnix coturnix	144	90.0	[illegible]	103.0
Coturnix delguorgeui	11	72.4	[illegible]	78.5
Dendragapus canadensis	62	492.0	34	456.0
Dendragapus obscurus	359	1188.0	410	891.0
Lagopus lagopus	498	601.0	326	516.0
Lagopus mutus	38	437.0	28	401.0
Lagopus leucurus	25	359.0	30	351.0
Tetrao tetrix	26	1255.0	35	910.0
Tetrao urogallus	75	4100.0	10	1800.0
Bonasa bonasia	32	435.0	24	422.0
Bonasa umbellus	180	621.0	214	532.0
Centrocerus urophasianus	465	3190.0	221	1745.0
Tympanuchus phasianellus	236	953.0	247	817.0
Tympanuchus cupido	22	999.0	16	772.0
Meleagris gallopavo	54	7400.0	55	4222.0
Callipepla squamata	143	191.0	132	177.0
Callipepla californica	418	176.0	272	170.0
Callipepla gambelii	145	170.0	103	162.0
Cyrtonyx montezumae	45	195.0	22	176.0

Table A1, continued:

Taxon	n (males)	Male size (grams)	n (females)	Female size (grams)
Anseriformes				
Anatidae				
Dendrocygna autumnalis	44	813.0	45	849.0
Oxyura jamaicensis	12	590.0	17	499.0
Cygnus olor	59	11800.0	35	9670.0
Cygnus atratus	270	6200.0	243	5100.0
Cygnus buccinator	27	11400.0	47	10300.0
Cygnus columbianus	76	7100.0	86	6200.0
Cygnus columbianus bewickii	96	6400.0	95	5700.0
Branta canadensis canadensis	232	3814.0	159	3314.0
Branta canadensis intertior	128	4181.0	121	3514.0
Branta canadensis moffitti	99	4741.0	104	4044.0
Branta canadensis parvipes	113	2679.0	129	2542.0
Branta canadensis occidentalis	175	3690.0	134	3043.0
Branta canadensis hutchinsii	31	2043.0	37	1861.0
Branta canadensis minima	52	1480.0	58	1264.0
Branta leucopsis	366	1788.0	253	1586.0
Branta bernicla	430	1370.0	361	1230.0
Aix sponsa	248	681.0	163	635.0
Anas americana	65	792.0	68	719.0
Anas strepera	16	990.0	14	849.0
Anas crecca	194	364.0	81	318.0
Anas platyrhnchos wyvilliana	28	644.0	19	585.0
Anas fulvigula	30	1030.0	11	968.0
Anas acuta	232	1035.0	60	986.0
Anas discors	105	409.0	101	363.0
Anas cyanoptera	26	408.0	19	363.0
Anas clypeata	90	636.0	71	590.0
Melanitta perspicillata	12	1000.0	10	900.0
Mellanitta fusca deglandi	13	1500.0	19	1200.0

Table A1, continued:

Taxon	n (males)	Male size (grams)	n (females)	Female size (grams)
Piciformes				
Megalaimidae				
Lybius leucocephalus	12	63.8	11	61.8
Ramphastidae				
Aulacorhynchus prasinus	15	160.0	16	149.0
Picidae				
Melanerpes formicivorus	47	82.9	39	78.1
Melanerpes rubricapillus	19	55.9	12	49.0
Melanerpes uropygialis	20	69.7	24	60.0
Melanerpes carolinus	22	67.2	9	56.2
Melanerpes aurifrons	29	85.4	14	76.4
Picoides villosus	27	70.0	11	62.5
Picoides albolarvatus	18	63.0	17	59.2
Colaptes auratus auratus	94	135.0	65	129.0
Coraciiformes				
Bucerotidae				
Tockus erythrorhynchus	75	150.0	75	128.0
Tockus leucomelas	75	211.0	75	168.0
Trogoniformes				
Trogonidae				
Trogon collaris	29	63.4	18	65.4
Alcedinidae				
Ceyx argentatus	12	16.5	14	19.3
Ceryle rudis	189	82.4	96	86.4
Cucliformes				
Cuculidae				
Chrysococcyx cupreus	20	38.3	12	36.7

Table A1, continued:

Taxon	n (males)	Male size (grams)	n (females)	Female size (grams)
Chrysococcyx caprius	24	29.0	14	35.0
Crotophagidae				
Crotophaga major	16	157.0	9	140.0
Crotophaga ani	10	119.0	12	91.0
Crotophaga sulcirostris	16	87.3	19	77.1
Psittaciformes				
Psittacidae				
Brotogeris jugularis	14	61.0	9	65.5
Cacatuidae				
Cacatua sanguinea	22	562.0	17	488.0
Apodiformes				
Apodidae				
Cypseloides rutilus	24	20.6	19	19.6
Trochiliformes				
Trochilidae				
Colubri thalassinus	39	5.5	36	5.1
Orthorynchus cristatus	18	2.8	11	2.4
Cynanthus leucotis	158	3.6	51	3.2
Amazilia tzacoti	12	5.4	10	4.7
Lampornis clemenciae	190	8.4	62	6.8
Heliodaxa fulgens	119	7.7	24	6.4
Archilochus anna	81	4.3	40	4.1
Archilochus costae	33	3.1	27	3.2
Archilochus colubris	419	3.3	202	3.0
Archilochus alexandri	34	3.1	24	3.4
Archilochus calliope	46	2.5	26	2.8
Selaphorus rufus	22	3.2	20	3.4

Table A1, continued:

Taxon	n (males)	Male size (grams)	n (females)	Female size (grams)
Selaphorus sasin	57	3.3	44	3.5
Selaphorus platycerus	35	3.2	25	3.6
Phaethornis koepckeae	16	5.4	10	4.7
Strgiformes				
Strigidae				
Otus flammeolus	56	53.9	9	57.2
Otus kennicottii kennicottii	14	152.0	11	186.0
Otus kennicottii cineraceus	35	111.0	18	123.0
Otus kennicottii quercinus	26	134.0	10	152.0
Otus asio navius	31	167.0	66	194.0
Bubo virginianus virginianus	22	1318.0	29	1768.0
Bubo virginianus occidentalis	18	1154.0	18	1555.0
Bubo virginianus pallescens	18	914.0	12	1142.0
Bubo bubo	14	2380.0	12	2992.0
Nycetea scandiaca	23	1806.0	21	2279.0
Strix occidentalis	10	582.0	10	637.0
Strix varia	20	632.0	24	801.0
Strix uralensis macroura	40	706.0	57	863.0
Strix nebulosa	17	789.0	21	1159.0
Glaucidium perlatum	12	69.0	13	91.0
Glaucidium gnoma	42	61.9	10	73.0
Glaucidium brasilianum	29	61.4	16	75.1
Athene noctua	9	162.0	12	166.0
Athene cunicularia	15	151.0	31	159.0
Aegolius funereus	74	101.0	96	167.0
Aegolius acadicus	27	74.9	18	90.8
Asio otus	38	245.0	28	279.0
Asio flammeus	20	315.0	27	378.0
Tytonidae				

Table A1, continued:

Taxon	n (males)	Male size (grams)	n (females)	Female size (grams)
Tyto alba pratincola	33	479.0	41	568.0
Tyto alba guttata	12	292.0	11	296.0
Caprimulgiformes				
Caprimulgidae				
Caprimulgus volciferus	32	55.3	39	50.6
Caprimulgus ruwenzorii	10	46.4	9	51.6
Columbiformes				
Columbidae				
Columba livia	41	369.0	37	340.0
Columba leucocephala	17	263.0	22	231.0
Columba fasciata fasciata	5888	353.0	5291	332.0
Columba fasciata monilis	1880	398.0	942	386.0
Columba iriditorques	15	130.0	18	122.0
Columba mayeri	33	315.0	29	291 0
Streptopelia decaocto	87	152.0	80	146.0
Zenaida macroura	140	123.0	95	115.0
Columbina talpacoti	38	48.1	36	44.8
Gruiformes				
Rallidae				
Galinula chloropus	103	340.0	110	265.0
Fulica americana	27	724.0	20	560.0
Grus canadensis canadensis	33	3350.0	31	2982.0
Grus canadensis tabida	61	5797.0	28	5345.0
Grus rubicunda	321	6383.0	217	5663.0
Pteroclidiformes				
Pteroclididae				

Table A1, continued:

Taxon	n (males)	Male size (grams)	n (females)	Female size (grams)
Pterocles orientalis	9	428.0	11	383.0
Pterocles bicinctus	9	234.0	19	239.0
Charadriiformes				
Jacanidae				
Jacana spinosa	20	78.9	16	112.0
Jacana jacana	16	108.0	15	143.0
Rostratulidae				
Rostratula benghalensis	25	117.6	9	130.0
Scolopacidae				
Scolopax rusticola	250	306.0	234	313.0
Scolopax minor	390	176.0	313	219.0
Gallinago hardwickii	249	151.1	250	161.8
Gallinago media	143	157.0	67	184.0
Gallinago gallinago	15	128.0	14	116.0
Gallinago gallinago raddei	20	97.0	16	113.0
Limosa limosa	11	252.0	11	330.0
Limosa lapponica	69	309.0	20	376.0
Limosa fedoa	10	320 0	9	421.0
Numenius phaeopus	29	355.0	36	404.0
Numenius tahitiensis	10	378.0	10	489.0
Numenius arquata	124	742.0	97	869.0
Numenius americanus	12	531.0	24	642.0
Tringa totanus	100	123.3	100	134.9
Tringa stagnatilis	30	77.0	31	78.0
Tringa nebularia	26	172.0	25	175.0
Tringa glareola	16	62.0	11	73.0
Tringa cinerea	17	69.4	16	74.8
Tringa incana	13	101.0	16	116.0
Arenaria melanocephala	12	114.0	9	124.0

Table A1, continued:

Taxon	n (males)	Male size (grams)	n (females)	Female size (grams)
Limnodromus griseus griseus	12	110.0	30	116.0
Limnodromus scolopaceus	28	100.0	11	109.0
Calidris tenuostris	10	156.0	15	174.0
Calidris canutus	13	126.0	9	148.0
Calidris ruficollis	62	32.0	29	36.0
Calidris bairdi	46	38.6	16	43.5
Calidris melanotos	74	97.8	38	65.0
Calidris acuminata	10	70.3	10	63.5
Calidris maritima	72	76.8	92	86.2
Calidris ptilocnemis	91	76.3	51	83.0
Calidris alpina sakhalina	267	55.4	177	59.7
Calidris alpina schintzii	92	44.2	92	49.6
Micropalama himantopus	24	53.8	15	60.9
Phalaropus lobatus	43	32.7	14	34.9
Phalaropus fulicaria	132	50.2	78	61.1
Haematopus moquini	55	665.0	54	722.0
Haematopus unicolor	69	678.0	75	724.0
Recurvirostridae				
Himantopus leucocephalus	15	193.0	14	192.0
Charadriidae				
Charadrius semipalmatus	26	47.4	24	46.1
Charadrius dubius	232	38.3	229	39.2
Charadrius wilsonia	18	53.8	21	56.2
Charadrius ruficapillus	108	35.0	32	36.0
Anarhynchus frontalis	32	60.7	53	58.0
Vanellus vanellus	32	211.0	40	226.0
Laridae				
Larus canus	96	432.0	72	375.0
Larus delwarensis	48	566.0	51	471.0
Larus californicus californicus	64	657.0	84	556.0

Table A1, continued:

Taxon	n (males)	Male size (grams)	n (females)	Female size (grams)
Larus californicus albertaensis	32	841.0	19	710.0
Larus marinus	116	1829.0	93	1488.0
Larus hyperboreus	39	1576.0	26	1249.0
Larus argentatus	220	1226.0	139	1044.0
Larus cachinnans michabellis	80	1275.0	80	1033.0
Larus fuscus graellsii	22	880.0	31	755.0
Larus fuscus fuscus	52	768.0	64	662.0
Sterna superciliaris	11	47.0	18	46.0
Stercoraridae				
Catharacta skua	219	413.0	189	478.0
Stercorarius pomarinus	73	648.0	52	740.0
Stercorarius parasiticus	20	421.0	11	508.0
Stercorarius longicaudus	26	280.0	18	313.0
Rynchopidae				
Rynchops niger	56	349.0	73	254.0
Alcidae				
Uria aalage	121	1006.0	117	979.0
Falconiformes				
Falconidae				
Polyborus plancus	14	834.0	10	953.0
Milvago chimango	10	288.5	19	299.6
Falco naumanni	34	141.0	25	164.0
Falco tinnunculus	40	186.0	57	217.0
Falco araea	14	72.4	32	87.9
Falco cenchroides	179	168.0	133	186.0
Falco sparverius	69	111.0	111	120.0
Falco columbarius	145	163.0	189	218.0
Falco mexicanus	15	554.0	31	863.0
Falco peregrinus	12	611.0	19	952.0

Table A1, continued:

Taxon	n (males)	Male size (grams)	n (females)	Female size (grams)
Accipitridae				
Circus aeruginosus	19	492.0	25	763.0
Circus cyaneus	186	358.0	174	513.0
Accipiter gentilis	77	912.0	103	1137.0
Accipiter nisus	70	150.0	246	325.0
Accipiter striatus	435	103.0	487	174.0
Accipiter striatus venator	13	94.9	11	171.0
Accipiter cooperii	51	349.0	57	529.0
Buteo lineatus	10	475.0	14	643.0
Buteo platypterus	14	420.0	13	490.0
Buteo jamaicensis	108	1028.0	100	1224.0
Buteo buteo	214	781.0	261	969.0
Buteo lagopus	152	847.0	119	1065.0
Pelecaniformes				
Pelicanidae				
Pelicanus occidentalis	56	3702.0	47	3174.0
Sulidae				
Morus bassanus	27	2932.0	27	3067.0
Sula nebouxii	23	1283.0	28	1801.0
Sula dactylatra personata	26	1880.0	27	2095.0
Sula leucogaster	64	1093.0	69	1382.0
Phalacrocoracidae				
Phalacrocorax auritus	33	1808.0	32	1540.0
Phalacrocorax carbo	36	2283.0	17	1936.0
Fregatidae				
Fregata minor	316	927.0	312	1183.0

Table A1, continued:

Taxon	n (males)	Male size (grams)	n (females)	Female size (grams)
Fregata ariel	29	754.0	45	858.0
Ciconiiformes				
Ardeidae				
Ardea cinerea	17	1505.0	13	1361.0
Ardea herodias	17	2576.0	15	2204.0
Casmerodius albus	12	935.0	9	812.0
Phoenicopteridae				
Phoenicopterus ruber roseus	13	3540.0	12	2530.0
Threskiornithidae				
Eudocimus albus	12	1036.0	16	764.0
Plegadis chihi	32	697.0	35	546.0
Threskiornis aethiopicus	40	1618.0	54	1378.0
Ciconiidae				
Ciconia ciconia	41	3571.0	27	3325.0
Sphenisciformes				
Spheniscidae				
Pygoscelis papua	32	6400.0	32	5500.0
Pygoscelis adelial	15	5000.0	10	4700.0
Spheniscus demersus	127	3310.0	127	2960.0
Procellaritormes				
Procellaridae				
Pterodermu macroptera gouldii	56	560.0	28	505.0
Puffinus tenuirostris	12	560.0	13	528.0
Diomedia immutablis	233	3230.0	134	2853.0
Diomedia melanophris	132	3922.0	94	3206.0
Diomedia hrysostoma	133	3751.0	95	3264.0

Table A1, continued:

Taxon	n (males)	Male size (millimeters)	n (females)	Female size (millimeters)
Reptilia				
Squamata				
Colubridae				
Boaedon lineatus	...	424.0	...	525.0
Coluber constrictor	...	699.0	...	772.0
Coluber viridiflavus	...	1209.0	...	930.0
Diadophis punctatus	...	222.0	...	241.0
Elaphe obsoleta	...	1203.0	...	1095.0
Heterodon nasicus	...	450.0	...	513.0
Heterodon platyrhinos	...	619.0	...	662.0
Nerodia erythrogaster	...	686.0	...	787.0
Nerodia fasciata	...	535.0	...	638.0
Nerodia rhombifera	...	734.0	...	914.0
Nerodia sipedon	...	542.0	...	719.0
Nerodia taxispilota	...	652.0	...	826.0
Nerodia valida	...	453.0	...	547.0
Opheodrys aestivus	...	372.0	...	433.0
Pituophis melanoleucas	...	960.0	...	937.0
Ptyas korros	...	1021.0	...	940.0
Ptyas mucosus	...	1300.0	...	1220.0
Regina grahami	...	478.0	...	571.0
Regina septemvittata	...	408.0	...	465.0
Seminatrix pygaea	...	303.0	...	330.0
Storeria dekayi	...	202.0	...	239.0
Storeria occipitomaculata	...	167.0	...	186.0
Thamnophis elegans	...	404.0	...	475.0
Thamnophis sauritus	...	410.0	...	483.0

Table A1, continued:

Taxon	n (males)	Male size (millimeters)	n (females)	Female size (millimeters)
Thamnophis sirtalis	...	483.0	...	570.0
Xenochrophis piscator	...	424.0	...	571.0
Xenochrophis vittata	...	327.0	...	405.0
Elapidae				
Acanthophis antarcticus	...	439.0	...	580.0
Austrelaps superbus	...	765.0	...	679.0
Cacophis harriettae	...	286.0	...	357.0
Cacophis krefftii	...	235.0	...	264.0
Cacophis squamulosus	...	391.0	...	507.0
Demansia atra	...	785.0	...	730.0
Demansia olivacea	...	459.0	...	429.0
Demansia psammophis	...	570.0	...	525.0
Demansia torquata	...	539.0	...	510.0
Denisonia devisi	...	327.0	...	341.0
Denisonia maculata	...	283.0	...	335.0
Drysdalia coronata	...	318.0	...	321.0
Drysdalia coronoides	..	289.0	...	304.0
Drysdalia mastersi	...	221.0	...	227.0
Drysdalia rhodogaster	...	304.0	...	309.0
Elapognathus minor	...	288.0	...	337.0
Furina barnardi	...	288.0	...	440.0
Furina diadema	...	243.0	...	271.0
Furina ornata	...	291.0	...	365.0
Furina tristis	...	609.0	...	584.0
Hemiaspis damelli	...	402.0	...	432.0
Hemiaspis signata	...	409.0	...	376.0
Hoplocephalus bitorquatus	...	460.0	...	524.0
Hoplocephalus bungariodes	...	545.0	...	572.0
Hoplocephalus stephensi	...	637.0	...	694.0
Notechis scutatus	...	900.0	...	850.0

Table A1, continued:

Taxon	n (males)	Male size (millimeters)	n (females)	Female size (millimeters)
Xenochrophis piscator	...	424.0	...	571.0
Xenochrophis vittata	...	327.0	...	405.0
Pseudechis australis	...	1258.0	...	1028.0
Pseudechis butleri	...	1036.0	...	925.0
Pseudechis colletti	...	1317.0	...	1242.0
Pseudechis guttatus	...	1031.0	...	1019.0
Pseudechis porphyriacus	...	1060.0	...	930.0
Pseudonaja affinis	...	1085.0	...	1088.0
Pseudonaja guttata	...	679.0	...	707.0
Pseudonaja inframacula	...	929.0	...	826.0
Pseudonaja ingrami	...	1203.0	...	1226.0
Pseudonaja modesta	...	343.0	...	399.0
Pseudonaja nuchalis	...	938.0	...	863.0
Pseudonaja textilis	...	1088.0	...	978.0
Rhinoplocephalus bicolor	...	346.0	...	328.0
Rhinoplocephalus nigrescens	...	445.0	...	375.0
Rhinoplocephalus pallidiceps	...	377.0	...	427.0
Simoselaps approximans	...	278.0	...	278.0
Simoselaps australis	...	227.0	...	275.0
Simoselaps bertholdi	...	183.0	...	208.0
Simoselaps bimaculatus	...	293.0	...	336.0
Simoselaps calonotus	...	205.0	...	224.0
Simoselaps fasciolatus	...	258.0	...	294.0
Simoselaps incinctus	...	248.0	...	265.0
Simoselaps littoralis	...	162.0	...	240.0
Simoselaps roperi	...	255.0	...	282.0
Simoselaps semifaciatus	...	242.0	...	271.0
Simoselaps warro	...	290.0	...	335.0
Suta boschmai	...	371.0	...	411.0
Suta dwyeri	...	311.0	...	286.0

Table A1, continued:

Taxon	n (males)	Male size (millimeters)	n (females)	Female size (millimeters)
Suta fasciata	...	384.0	...	387.0
Suta flagellum	...	?72.0	...	272.0
Suta gouldii	...	343.0	...	303.0
Suta monachus	...	298.0	...	286.0
Suta nigriceps	...	354.0	...	320.0
Suta nigrostriatus	...	385.0	...	362.0
Suta punctata	...	364.0	...	342.0
Suta spectabilis	...	299.0	...	267.0
Suta suta	...	444.0	...	391.0
Tropidechis carinatus	...	676.0	...	672.0
Vermicella annulata	...	395.0	...	544.0
Viperidae				
Vipera bersus	...	463.0	...	498.0
Vipera xanthina	...	937.0	...	897.0
Bitis arietans	...	866.0	...	807.0
Echis colorata	...	642.0	...	627.0
Crotalus ruber	...	1285.0	...	1075.0
Crotalus lucasensis	...	1055.0	...	919.0
Crotalus atrox	...	963.0	...	873.0
Crotalus scutulatus	...	857.0	...	754.0
Crotalus tigris	...	767.0	...	632.0
Crotalus viridis	...	726.0	...	626.0
Crotalu: mitchelli	...	925.0	...	792.0
Crotalus cerastes	...	537.0	...	555.0
Crotalus enya	...	796.0	...	736.0
Crotalus durissus	...	754.0	...	731.0
Crotalus molossus	...	1062.0	...	922.0
Crotalus horridus	...	1073.0	...	1010.0
Iguanidae				
Anolis occultus	...	39.0	...	39.2

Table A1, continued:

Taxon	n (males)	Male size (millimeters)	n (females)	Female size (millimeters)
Anolis cuvieri	22	41.7	13	38.4
Anolis evermanni	...	70.7	...	52.4
Anolis gundlachi	...	64.8	...	45.2
Anolis poncensis	...	45.6	...	39.6
Anolis krugi	...	49.7	...	39.3
Anolis puchellus	108	46.1	24	37.0
Anolis cristalellus	327	63.6	204	44.6
Anolis sagrei	192	54.5	62	39.7
Anolis valenciennì	...	79.4	...	68.5
Anolis garmani	...	110.0	...	82.5
Anolis lineatopus	...	60.0	...	42.0
Anolis grahami	...	65.5	...	44.0
Anolis opalinus	...	49.5	...	40.5
Chamaeleolis chamaeleonides	12	161.7	33	160.5
Crotaphytus collaris	24	100.9	56	93.6
Gambelia wizlizenii	36	102.0	25	117.5
Enyaloides laticeps	14	115.0	17	114.5
Phyrnosoma platyrhinos	24	71.5	32	76.0
Phyrnosoma solare	19	90.4	22	98.0
Phyrnosoma cornutum	15	79.6	17	74.4
Phyrnosoma douglassi	11	60.9	23	66.9
Callisauras draconoides	43	78.9	46	70.2
Callisauras draconoides rhodesticus	13	68.8	24	61.6
Holbrookia maculata	31	48.9	70	52.6
Uma inornata	191	102.0	213	81.0
Uma notata	270	96.0	214	76.0
Uma scoparia	248	97.0	236	83.0
Uta palmeri	34	67.0	51	60.7
Uta nolascensis	21	50.1	15	46.6
Uta antigua	33	50.8	27	46.6

Table A1, continued:

Taxon	n (males)	Male size (millimeters)	n (females)	Female size (millimeters)
Uta stansburiana	447	50.0	402	48.0
Uta squamata	25	50.6	27	47.1
Urosaurus ornata	178	49.6	129	48.3
Sceloporus megalepidurus	10	45.2	11	44.9
Sceloporus grammicus	23	51.2	32	49.3
Sceloporus pyrocephalus	9	62.9	12	53.5
Sceloporus nelsoni	26	60.1	21	52.1
Sceloporus scalaris	45	45.3	203	51.3
Sceloporus siniferus	32	60.8	52.3	35.0
Sceloporus utiformis	9	64.4	10	59.7
Sceloporus chrysostictus	81	54.0	82	51.3
Sceloporus variabilis	97	65.8	157	53.1
Sceloporus teapensis	24	58.9	26	52.0
Sceloporus cozumelae	57	50.7	33	45.5
Sceloporus merriami	60	52.3	51	49.8
Sceloporus jarrovi	35	78.8	33	71.9
Sceloporus poinsetti	18	116.4	21	97.0
Sceloporus mucronatus	21	93.3	17	88.5
Sceloporus torquatus	13	103.5	9	102.7
Sceloporus bulleri	10	107.0	10	97.7
Sceloporus insignis	10	89.5	10	82.6
Sceloporus virgatus	11	52.0	11	58.8
Sceloporus woodi		47.6	...	50.5
Sceloporus occidentalis	23	66.1	13	70.4
Sceloporus undulatus	59	56.1	35	62.1
Sceloporus graciosus	106	57.4	121	59.9
Sceloporus orcutti	17	102.0	77	92.0
Sceloporus clarki	29	102.1	21	94.9
Sceloporus magister	42	115.5	33	96.6
Sceloporus spinosus	17	88.3	18	87.2

Table A1, continued:

Taxon	n (males)	Male size (millimeters)	n (females)	Female size (millimeters)
Sceloporus olivaceus	34	82.9	107	93.0
Sceloporus malachitis	146	79.1	208	75.5
Leiocephalus asticus	15	69.2	10	58.7
Leiocephalus exotheatus	19	59.8	16	49.9
Leiocephalus gigas	23	100.7	30	72.1
Leiocephalus paraphrus	9	83.9	17	63.7
Leiocephalus raviceps	23	66.5	11	54.5
Leiocephalus sierrae	33	73.2	30	62.8
Leiocephalus stictigaster	26	66.1	27	54.9
Leiocephalus cubensis	37	88.4	28	68.0
Tropidurus pacificus	17	87.5	32	75.7
Tropidurus albemarlensis	67	82.0	118	65.0
Tropidurus occipitallis	...	64.4	...	52.2
Tropidurus habellii	23	107.1	27	84.6
Tropidurus peruvianis	...	98.3	...	84.6
Tropidurus delanonis	41	119.0	43	90.0
Plica umbra ochrocollaris	16	78.5	12	80.6
Basilicus basilicus	...	218.0	...	170.0
Basilicus vittatus	29	140.9	17	120.5
Polychrus marmoratus	9	385.0	13	478.0
Sauromalus obesus	25	175.0	28	161.0
Dipsosaurus dorsalis	377	127.0	200	120.0
Ctenosaura similis	610	345.0	283	276.0
Cyclura carinata	47	276.3	45	225.4
Cyclura cornuta	...	534.5	...	468.0
Cyclura cychlura	...	303.0	...	283.0
Cyclura pinguis	...	534.5	...	468.0
Iguana iguana	174	361.0	169	327.0
Amblyrhynchus cristatus	...	341.0	...	290.0

Table A1, continued:

Taxon	n (males)	Male size (millimeters)	n (females)	Female size (millimeters)
Insecta				
Hemiptera				
Gerridae				
Aquarius najas	...	12.9	...	16.5
Aquarius cinereus (SW)	...	9.6	...	12.7
Aquarius chilensis (LW)	...	11.0	...	13.5
Aquarius remigis (SW)	...	14.5	...	15.2
Aquarius remigis (LW)	...	14.6	...	15.8
Aquarius antigone	...	12.0	...	13.9
Aquarius paludum (SW)	...	12.6	...	15.2
Aquarius paludum (LW)	...	13.7	...	15.4
Aquarius conformis	...	15.2	...	16.5
Aquarius elongatus	...	23.8	...	24.4
Gerris lateralis (SW)	...	9.1	...	10.2
Gerris lateralis (LW)	...	9.9	...	11.2
Gerris brachynotus	...	7.0	...	8.5
Gerris gracilicornis	...	11.5	...	13.3
Gerris insularis	...	10.6	...	12.7
Gerris incognitus (SW)	...	8.5	...	9.5
Gerris incognitus (LW)	...	9.2	...	9.7
Gerris sphagnetorum	...	8.5	...	8.8
Gerris nepalensis (SW)	...	7.2	...	8.8
Gerris nepalensis (LW)	...	8.2	...	9.7
Gerris thoracicus	...	10.3	...	11.4
Gerris costae	...	12.0	...	13.5
Gerris marginatus	...	9.4	...	10.4
Gerris comatus (SW)	...	9.3	...	10.5
Gerris comatus (LW)	...	9.7	...	10.6
Gerris latiabdominis (SW)	...	7.9	...	9.1

Table A1, continued:

Taxon	n (males)	Male size (millimeters)	n (females)	Female size (millimeters)
Gerris latiabdominis (LW)	...	9.4	...	10.9
Gerris lacustris (SW)	...	8.3	...	9.1
Gerris lacustris (LW)	.	8.8	...	9.7
Gerris gibbifer	...	10.8	...	11.8
Gerris odontogaster (SW)	...	7.9	...	8.7
Gerris odontogaster (LW)	...	7.8	...	8.4
Gerris buenoi (SW)	...	7.4	...	8.2
Gerris buenoi (LW)	...	7.5	...	8.1
Gerris argentatus (SW)	...	6.1	...	7.3
Gerris argentatus (LW)	...	6.5	...	7.4
Gerris swakopensis (SW)	...	6.2	...	7.1
Gerris swakopensis (LW)	...	8.0	...	9.0
Limnoporus canaliculatus (SW)	...	8.4	...	10.2
Limnoporus canaliculatus (LW)	...	8.1	...	10.3
Limnoporus esakii	...	8.0	...	10.0
Limnoporus rufoscutellatus	...	14.2	...	15.5
Limnoporus genitalis	...	12.6	...	13.8
Limnoporus dissortis	...	13.3	...	14.1
Limnoporus notabilis	...	17.4	...	18.1
Gigantometra gigas (LW)	...	33.2	...	33.3
Arachnida				
Araneae				
Hypochilidae				
Hypochilus thorelli	...	11.0	...	14.0
Flistatidae				
Flistata hibernalis	...	9.5	...	16.0
Scytodidae				
Scytodes thoracica	...	4.0	...	4.8

Table A1, continued:

Taxon	n (males)	Male size (millimeters)	n (females)	Female size (millimeters)
Loxoscelidae				
Loxosceles unicolor	...	6.0	...	8.8
Diguetidae				
Digueta canities	...	5.9	...	8.8
Plectreuridae				
Plectreurys tristis	...	12.5	...	12.5
Pholcidae				
Pholcus phalangiodes	...	6.0	...	7.5
Dysderidae				
Dysdera crocata	...	10.5	...	13.0
Dysdera erythina	...	8.0	...	10.0
Segestriidae				
Segestria senoculata	...	8.5	...	8.5
Segestria bavarica	...	11.0	...	11.0
Segestria florentina	...	17.5	...	17.5
Tetragnathidae				
Tetragnatha laboriosa	...	5.0	...	6.0
Tetragnatha versicolor	...	5.0	...	6.5
Tetragnatha straminea	...	6.5	...	8.0
Tetragnatha elongata	...	7.5	...	9.0
Tetragnatha extensa	...	7.5	...	9.5
Tetragnatha pincola	...	5.0	...	8.0
Tetragnatha montana	...	7.3	...	8.3
Tetragnatha obtusa	...	4.5	...	6.0
Tetragnatha nigrita	...	6.5	...	8.3
Tetragnatha praedonia	...	11.0	...	14.0
Tetragnatha japonica	...	9.5	...	11.0
Tetragnatha lauta	...	5.0	...	5.0
Tetragnatha yesoensis	...	6.5	...	8.5
Tetragnatha squamata	...	5.0	...	7.0

Table A1, continued:

Taxon	n (males)	Male size (millimeters)	n (females)	Female size (millimeters)
Tetragnatha shikokiana	...	8.0	...	8.0
Oecobiidae				
Oecobius parietalis	...	2.0	...	2.5
Mimetidae				
Mimetus puritanus	...	4.3	...	5.3
Mimetus epeiroides	...	3.4	...	4.6
Mimetus maculosus	...	5.2	...	8.1
Mimetus audax	...	5.0	...	6.0
Dictynidae				
Dictyna sublata	...	2.3	...	3.0
Dictyna volucripes	...	3.1	...	3.8
Dictyna foliacea	...	1.9	...	2.4
Dictyna annulipes	...	3.1	...	3.7
Dictyna arundinacea	...	2.5	...	2.5
Dictyna pusilla	...	2.0	...	2.1
Dictyna major	...	2.8	...	3.3
Dictyna uncinata	...	2.3	...	2.6
Dictyna latens	...	2.1	...	3.0
Dictyna puella	...	2.4	...	2.8
Dictyna flavescens	...	2.3	...	2.5
Dictyna viridissima	...	3.5	...	4.0
Araneidae				
Araneus pentagrammicus	...	6.0	...	10.0
Araneus semilunarus	...	5.0	...	7.0
Araneus triguttatus	...	4.0	...	4.5
Araneus ejusmodi	...	5.0	...	6.5
Araneus displicatus	...	5.0	...	6.5
Araneus nordmanni	...	7.0	...	12.0
Araneus solitanius	...	11.5	...	17.5
Araneus miniatus	...	2.5	...	3.8

Table A1, continued:

Taxon	n (males)	Male size (millimeters)	n (females)	Female size (millimeters)
Araneus trifolium	. . .	5.0	. . .	13.5
Araneus marmoreus	. . .	5.5	. . .	8.5
Araneus cornutus	. . .	8.5	. . .	11.5
Araneus ventricosus	. . .	20.0	. . .	30.0
Araneus quadratus	. . .	10.0	. . .	16.5
Araneus diaidematus	. . .	9.0	. . .	12.0
Araneus mongolicus	. . .	14.0	. . .	20.0
Araneus ishsawai	. . .	8.0	. . .	19.0
Araneus opimus	. . .	8.0	. . .	13.0
Araneus patagiatus	. . .	6.5	. . .	10.0
Araneus aia	. . .	7.5	. . .	10.0

Table A2. The mean size (total body mass in grams, total body length and snout to vent length in millimeters), size dimorphism index[1], and percentage of male-biased and female-biased species in each taxon.

Taxon	% Species male-biased	% Species female-biased	Mean size	SDI[1]
Male/Female-Biased Taxa[2]				
Mammals				
Carnivores	71	18	78600.0 g	-0.497
Birds				
Shorebirds - excluding Sandpipers and Allies	57	43	505.1 g	-0.098
Hummingbirds	57	43	410.8 g	-0.055
Seabirds	68	32	3379.6 g	-0.173
Reptiles				
Snakes				
Australian Elapids - Division B	42	55	408.0 mm	0.014
Australian Elapids - Division C	75	25	969.0 mm	-0.056
Colubrids - Terestrial, Arboreal, Neotropical, and Swampsnakes	44	56	750.0 mm	0.002

Table A2, continued:

Taxon	% Species male-biased	% Species female-biased	Mean size	SDI
Male-Biased Taxa[3]				
Mammals				
Ungulates	93	0	29300.0 g	-0.344
Mustelids	88	4	4600.0 g	-0.261
Primates	81	5	11600.0 g	-0.491
Birds				
Waterfowl	96	4	2656.6 g	-0.150
Gamebirds	92	8	847.2 g	-0.495
Reptiles				
Snakes				
Vipers and Pitvipers	87.5	12.5	81.8 mm	-0.101
Lizards				
Iguanids	82	18	100.5 mm	-0.109
Female-Biased Taxa[4]				
Birds				
Raptors	0	100	481.9 g	0.320

Table A2, continued:

Taxon	% Species male-biased	% Species female-biased	Mean size	SDI
Owls	0	100	583.2 g	0.259
Sandpipers and Allies	9	91	176.4 g	0.150
Insects				
Waterstriders	0	100	11.5 mm	0.121
Arachnids				
True Spiders - excluding Orbweavers	2	84	6.6 mm	0.220
Reptiles				
Snakes				
Colubrids - Watersnakes and Allies	0	100	50.7 mm	0.200
Australian Elapids - Division A	11	184	30.8 mm	0.149

[1] This size dimorphism index was calculated according to Gibbons and Lovich (1992): SDI {(Size of the largest sex/ Size of the smallest sex) - 1}. If males are the larger sex, the ratio is arbitrarily negative. If females are the larger sex the ratio is arbitrarily positive.

[2] Taxa that contain species that are male-biased in size and species that are female-biased in size. A taxon was placed in this group if the frequency of bias in each direction was less than 80% (e.g. 30% female biased and 70% male-biased).

Table A2, continued:

[3] Taxa in which males are the larger sex. A taxon was placed in this group males were the larger sex in more than 80% of the species.

[4] Taxa in which females are the larger sex. A taxon was placed in this group if females were the larger sex in more than 80% of the species.