
Sexual size dimorphism in birds

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“The males of many birds are larger than the females, and this no doubt is the result of the advantage gained by the larger and stronger males over their rivals during many generations.”

Darwin (1874)

3.1 Introduction

The difference in body size between males and females has been known by naturalists for hundreds of years. For instance, Charles Darwin (1874) wrote “The male [spider] is generally much smaller than the female, sometimes to an extraordinary degree”, “... the female of almost all fishes is larger than the male”, and “With mammals, when, as is often the case, the sexes differ in size, the males are almost always larger and stronger.”

Birds exhibit a modest range of sexual size dimorphism (SSD) relative to spiders and fishes (see Chapters 1 and 7 in this volume). Nevertheless, they are excellent model organisms to test macroevolutionary patterns for several reasons. There are approximately 9700 bird species, and they inhabit all continents and occupy a variety of niches. Birds are exceptionally well studied in the wild, and data on body sizes, ecology, and behavior are readily accessible for many species. In addition, their taxonomy and phylogeny are reasonably well understood. Males and females can often be easily distinguished, whereas in many invertebrates detailed examination of genitalia is needed to tell sexes apart. Birds have determinate growth so most birds achieve adult size shortly after fledging whereas many invertebrates, fishes, and reptiles keep growing throughout their lives. Birds also exhibit exceptional variation in breeding systems, providing an excellent opportunity to test

Darwin’s assertion about sexual selection and its implication for SSD.

We have three objectives in this chapter. First, we will assess the distribution and pattern of SSD among birds and test whether Darwin’s assertion about male-biased avian dimorphisms are consistent with data. Thus we explore the overall distribution of SSD in five readily measurable morphological traits. We show that SSD in one trait is often only loosely related to SSD in another trait, suggesting different selective forces are acting on different traits. Second, we test an allometric relationship between body size and SSD, termed Rensch’s rule (Abouheif and Fairbairn 1997; Fairbairn 1997). Previous works in several avian taxa demonstrated the existence of such an allometry (Fairbairn 1997; Colwell 2000; Székely *et al.* 2004; Raihani *et al.* 2006). Our objective here is to establish whether this relationship occurs more often than expected by chance among avian families. Finally, we test four major functional explanations of SSD.

Body size and its components are the targets of several selective processes (Andersson 1994; Blanckenhorn 2000). Thus there are advantages of being large (e.g. contests over mates or resources, mate preference by the opposite sex, resilience to temporary food shortage), or small (e.g. early maturation with shorter generation time and more rapid reproduction, higher success in scrambles). SSD is expected to evolve if some of these selective processes are stronger in one sex than in the other, or the outcome of these processes do not cancel out between the sexes. Given that the reproductive physiology and breeding ecology of sexes are often different, we expect extensive SSD in many bird species.

Here we focus on four major functional hypotheses. First, the *mating-competition hypothesis*

predicts increasing SSD, as measured by \log_{10} (male size) – \log_{10} (female size) (see also Chapters 2, 4, and 12 in this volume), with more intense male–male competition. This is because when males compete over females, sheer size is often advantageous. Second, the *display-agility hypothesis* predicts decreasing SSD with more manoeuvrable male displays (Payne 1984; Jehl and Murray 1986; Figuerola 1999). This hypothesis is likely to be relevant if females prefer males with acrobatic displays. Since manoeuvrability in the air increases with small size, selection for producing small males is expected by female choice (Andersson and Norberg 1981). Third, the *resource-division hypothesis* predicts increasing SSD with the potential for overall resource use. Thus to avoid exploiting the same resources when males and females forage together and use the same territory, one may expect enhanced SSD. Since resource division may emerge either via large males and small females or vice versa, we calculated the absolute difference between the sizes of males and females—that is, $|\log_{10}(\text{male size}) - \log_{10}(\text{female size})|$ —and used the absolute difference as a response variable. Finally, the *fecundity hypothesis* predicts increasing female size (relative to male size) with fecundity. We tested the latter prediction by relating SSD to clutch size.

Previous reviews of avian SSD were insightful and thought-provoking (Table 3.1). Our work, however, is distinct from these earlier studies in several respects. First, we use five morphometric

traits whereas most previous studies used only one (or two) *proxies* of body size. Second, our study is the first to test all four fundamental hypotheses of SSD. Whereas the mating-competition hypothesis has been tested extensively, the other three hypotheses were somehow neglected. Finally, we test these hypotheses using the hitherto broadest range of taxa that includes 3767 species (out of 9702 species; Monroe and Sibley 1993) and 125 avian families (out of 146 families).

3.2 Methods

Data were collected from handbooks that included *Birds of the Western Palearctic*, *Birds of Africa*, *Birds of North America Online*, and *Handbook of Birds of New Zealand and Australia* (T. Lislevand *et al.* 2007). Morphometric data of adult birds, preferably taken during breeding season, were compiled. If several data were available for a given species (e.g. from different subspecies), we preferred those with measurements available for more morphological variables, and the ones with larger numbers of individuals for each sex.

Explanatory variables were either taken from handbooks (see above), or from specific sources (T. Lislevand *et al.* 2007). Scores of mating competition were taken from Dunn *et al.* (2001), or from handbooks using the following scheme: (1) polyandry, when some females have several social mates; (2) monogamy (<5% of males polygynous); (3) mostly

Table 3.1 Summary of functional analyses of SSD in birds. Only broad-scale studies are listed that used several avian families. N/A indicates that a hypothesis was not tested, and Yes and No show whether a specific hypothesis was supported or not.

Morphometric trait	Functional hypothesis				No. of species (families)	Reference
	Mating competition	Display agility	Resource division	Fecundity		
Wing length	Yes	N/A	N/A	N/A	341 (12)	Payne (1984)
Body mass	Yes	N/A	N/A	N/A	73 (30)	Owens and Hartley (1998)
Body mass, tail length, wing length	Yes	N/A	N/A	No	1031 (91)	Dunn <i>et al.</i> (2001)
Body mass, wing length, tarsus length, bill length, tail length	Yes	Yes	No	No	3767 (125)	This work

monogamy, but occasional polygyny (5–15% of males polygynous); (4) mostly polygyny (>15% of males polygynous), and (5) lek or promiscuous. The latter category includes species in which the male attracts mates to courts or arenas, and he contributes no resource other than sperm to the raising of young (Dunn *et al.* 2001). This scoring reflects the notion that the intensity of male–male competition increases from one to five. Note that cooperative breeders (score 5 in Dunn *et al.* 2001, $n = 103$ species) were merged with monogamous species ($n = 955$ species) to reflect the assumption that sexual selection is weak in many (but not all) cooperative breeders. Excluding the cooperative breeders from the analyses of mating competition does not influence qualitatively our results (not shown). Data for extra-pair paternity are not yet available for vast majority of these species, and this prevented us from using extra-pair paternity in the analyses.

Descriptions of male display behaviors were taken from textbooks (T. Lislvand *et al.* 2007), and these descriptions were scored on a five-point scale: (1) ground displays only, including displays on trees and bushes; (2) ground displays with occasional jumps/leaps into the air; (3) both ground and non-acrobatic flight displays; (4) mainly aerial displays, non-acrobatic; and (5) mainly aerial displays, acrobatic (see further explanations in Raihani *et al.* 2006). A display was considered acrobatic if it included rapid changes in flight direction, twists, rolls, and turns. Three observers scored the descriptions blindly to the identity of species. The scores of the observers were highly consistent (Spearman rank correlations, $r_s = 0.829–0.848$, $n = 1113–1228$ species, $P < 0.001$). To increase the robustness of display scores, we only included species in the analyses that were scored by at least two observers, and the maximum difference between scores was ≤ 2 . We use the median score of observers for each species.

To investigate the influence of resource sharing on the relative sizes of sexes, we collected information on territorial behavior and whether the birds feed on, or away from, their territories. Verbal descriptions of territorial behavior and feeding locations on (or away from) the territory were taken from the literature (T. Lislvand *et al.*

2007), and these descriptions were scored on a three-point scale: (0) males and females do not share resources and they feed away from their breeding territory; (1) males and females share resources on their territory only during the breeding season; and (2) males and females share resources on their territory all year round. As with male displays, three observers scored the descriptions blindly to the identity of species. The scores were consistent among observers ($r_s = 0.628–0.674$, $n = 1454–1629$ species, $P < 0.001$). To increase the robustness of these scores, we only included those species in the analyses that were scored by at least two observers, and the maximum difference between scores was ≤ 1 . We use the median score for a given species. We took clutch size as a measure of fecundity, since data on clutch size are readily available for many species. Other measures, such as the number of clutches produced by females per year, are less universally available for the broad range of species we intended to cover.

In total, we had morphometric data for 3767 species, although due to missing data in one or several morphological measurements, the number of species we used in the analyses varied between 2348 species (tail length) and 2977 species (wing length), and for the explanatory data between 1218 species (display agility) and 2642 species (clutch size).

Comparative evolutionary biologists use a variety of phylogenetic methods to test functional hypotheses (Harvey and Pagel 1991; Martins 1996; Freckleton *et al.* 2002; Blomberg *et al.* 2003). A major constraint of these analyses is that they require a phylogeny. Whereas phylogenies are available for many avian families, they are rarely fully comprehensive, and even comprehensive phylogenies may have uncertain topology and/or branch lengths that may lead to potentially erroneous conclusions. To avoid losing species due to missing phylogenetic information, we decided to carry out the analyses separately for each family using species-level data, and then use the resulting test statistic (for instance, Pearson correlation coefficient, r) as a response variable to assess our working hypotheses. All morphometric data were converted to logarithm base 10 before the analyses.

The dispersion of SSD was compared across traits using Moses test (Daniel 1990) as implemented by the SPSS version 12.0 software package. To be conservative, we did not use 5% trimmed controls in Moses tests and report the two-tailed probabilities.

For testing the existence of Rensch's rule, we fitted a major-axis regression for each family separately. Only families with data from at least five species were used for fitting a major-axis regression between \log_{10} (male size) (dependent variable) and \log_{10} (female size). The distribution of principal axes (β) was tested using Wilcoxon one-sample test against the median of 1.0. Note that we are not concerned with the significance of β for a given family (this may be inflated due to phylogenetic non-independence; Fairbairn 1997). Rather, we took each family as a sampling unit, and test whether the distribution of β is different from 1.0 across avian families. Allometry consistent with the Rensch's rule would be indicated by slopes larger than 1.

Functional hypotheses were tested by calculating bivariate Spearman rank correlations (r_s) between morphometric traits (SSD in body mass, and in lengths of wing, tarsus, bill and tail), and explanatory variables (mating competition, display agility, resource division, fecundity). Then we tested the distribution of bivariate rank correlation coefficients (r_s) against a median of 0.0 using Wilcoxon one-sample test. We were unable to use partial rank correlations (Daniel 1990) for testing each explanatory variable while controlling for the other three, because missing data resulted in too few families having enough data with five (or more) degrees of freedom. We use SPSS 12.0 or Minitab 13.31 for statistical analyses, unless otherwise stated. We mostly rely on non-parametric statistics, since SSD—somehow surprisingly—was not normally distributed (see below), and three out of four explanatory variables were scores; that is, measured on the ordinal scale.

3.3 Results

3.3.1 Distribution of SSD

Birds exhibit male-biased SSD in all five morphometric traits (Figure 3.1; Appendix, Table A3.1). This result is consistent between species-level and

family-level analyses. In the latter analyses each family was represented by a single datum, the mean of their species.

The distributions of SSD are not normal at species level (Figure 3.1; Appendix, Table A3.1): the distributions are leptokurtic as there are more species around the mean than predicted by normal distribution. The deviation from normality becomes weaker at family level; nevertheless it remains significant for tail length, and marginally significant for body mass and bill length. These results suggest that strongly dimorphic species (either male-biased or female-biased) are rarer than predicted by a process of random evolution such as Brownian motion.

The dispersion of SSD in body mass is higher than in wing length, tarsus length, and bill length, both at species level (Figure 3.1a; Moses tests, $P < 0.001$) and at family level (Figure 3.1b; Moses tests, all four tests $P < 0.002$). Dispersion of SSD in body mass was not different from dispersion of SSD in tail length at species level, only at family level (Moses tests, $P = 1.000$ and $P < 0.001$, respectively).

Median SSDs are different between the traits: the largest SSD was exhibited in body mass and tail length (Figure 3.1; Appendix, Table A3.1), whereas the smallest SSD was exhibited in tarsus length (Friedman tests using only species (or families) with all five morphometric traits, species level: $\chi^2 = 273.592$, $P < 0.001$, $n = 1366$ species; family level: $\chi^2 = 23.781$, $P < 0.001$, $n = 95$ families).

SSD in one trait only correlates weakly with SSD in the other traits (Figure 3.2a; $r_s = 0.459\text{--}0.685$). This is indicated by a low Kendall's coefficient of concordance ($W = 0.050$, $\chi^2 = 273.592$, $P < 0.001$). The correlation is particularly poor between SSD in tail length and SSD in other traits, suggesting that different selective processes influence tail length and the four other traits. These results remain consistent at family level (Figure 3.2b), and Kendall's coefficient remains low ($W = 0.063$, $\chi^2 = 23.781$, $P < 0.001$).

3.3.2 Species and families exhibiting extreme SSDs

Some of the most male-biased SSDs are exhibited by bustards, grouse, widowbirds, waterfowl,

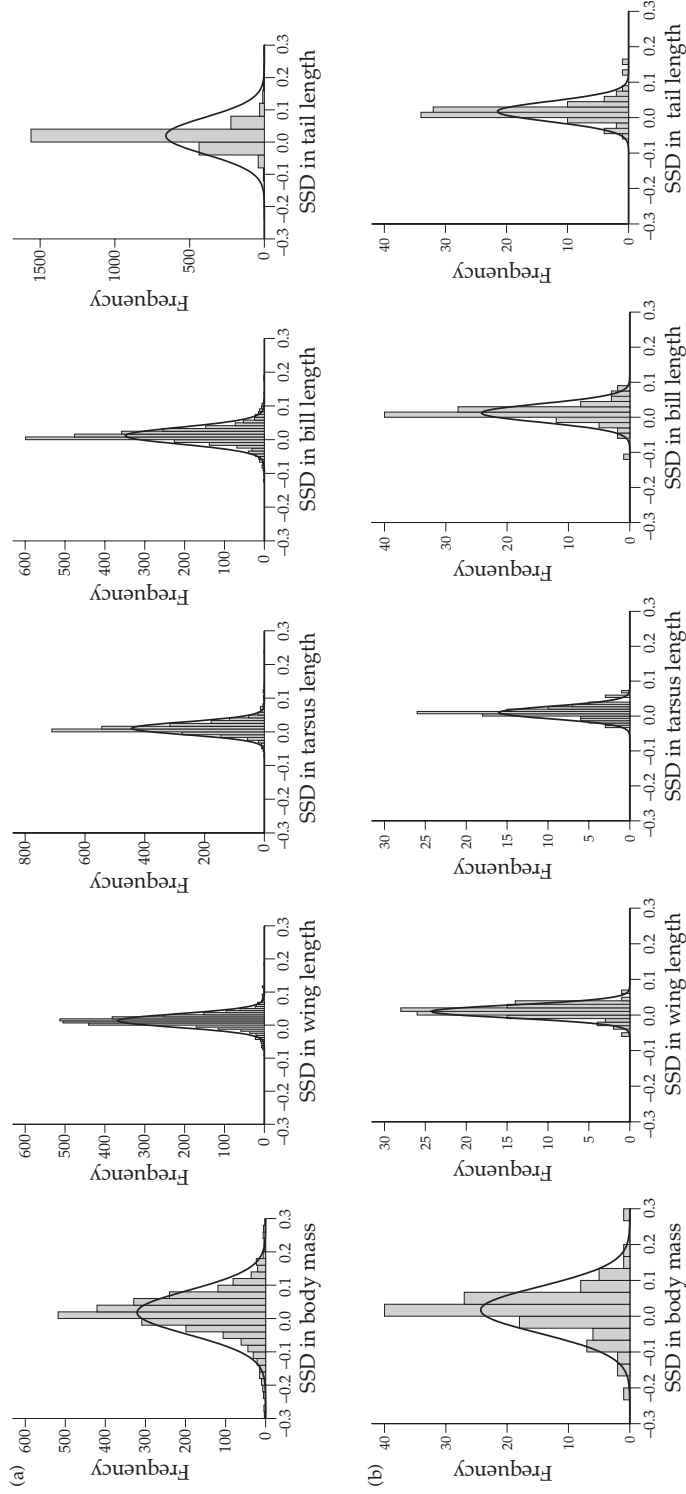


Figure 3.1 Distribution of SSD, calculated as $\log_{10}(\text{male trait}) - \log_{10}(\text{female trait})$ in five morphological traits at (a) species level and (b) family level, using the mean of each species. For sample sizes see Appendix, Table A3.1.

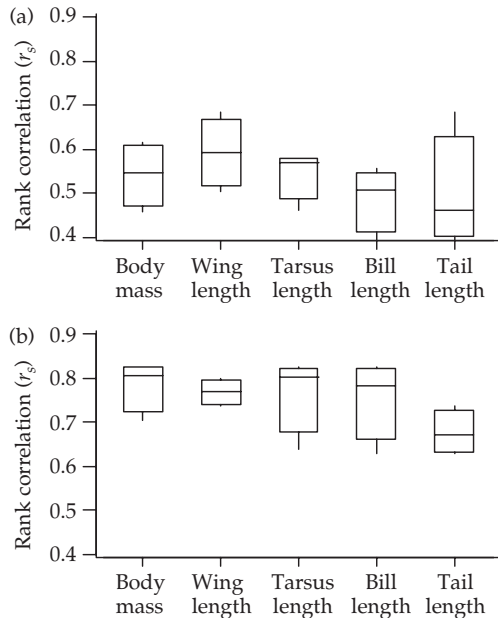


Figure 3.2 Correlations between SSDs of different traits (Spearman rank correlations, r_s). (a) Species level; (b) family level. The line is drawn across the median, and the bottom and the top of the boxes are lower (LQ) and upper quartiles (UQ), respectively. The whiskers extend from LQ and UQ to the lowest and highest observations, respectively, within the range defined by $LQ - 1.5 \cdot (UQ - LQ)$ and $LQ + 1.5 \cdot (UQ - LQ)$.

grackles, and brown songlark (Appendix, Table A3.2), whereas the most female-biased SSDs are exhibited by raptors (Appendix, Table A3.2). Interestingly, the most extreme bill dimorphisms are seen in hornbills (male-biased SSD), kiwis, and long-billed curlew (female-biased SSD). Families showing consistent male-biased SSD are Otididae and Phasianidae (Figure 3.3), whereas families showing consistent female-biased SSD are Accipitridae, Tytonidae, and Turnicidae (Appendix, Table A3.2). The largest ranges of SSD (as measured by the interquartile range) are exhibited by Otididae, Tytonidae, Centropidae, Bombycillidae, Gaviidae (body mass); Tytonidae, Otididae, Trochilidae, Ciconiidae, Falconidae (wing length); Tytonidae, Otididae, Phasianidae, Spheniscidae, Accipitridae (tarsus length); Eurylaimidae, Otididae, Trochilidae, Threskiornithidae, Pelecanidae (bill length); and Nectariniidae, Menuridae, Cerylidae, Spheniscidae, Tytonidae (tail length, Appendix, Table A3.2).

3.3.3 Rensch's rule

The distribution of major-axis slopes (see Methods) is significantly larger than 1.0 for all traits (Figure 3.4). This strongly suggests that most avian families exhibit the allometric relationship between male size and female size, and this relationship occurs in body mass, wing length, tarsus length, bill length, and tail length. The extent of allometry was not different between traits (Friedman test, $\chi^2 = 4.832$, $P = 0.305$, $df = 4$, $n = 50$ families).

Bird families exhibiting the strongest allometry consistent with Rensch's rule are Nectariniidae (mean β of five morphometric traits = 1.231), Otididae (mean $\beta = 1.183$), Passeridae (mean $\beta = 1.179$), Phasianidae (mean $\beta = 1.153$), and Cisticolidae (mean $\beta = 1.148$). Bird families exhibiting the strongest allometry in the opposite direction from the Rensch's rule are Threskiornithidae (mean $\beta = 0.905$), Charadriidae (mean $\beta = 0.962$), Scolopacidae (mean $\beta = 0.977$), Regulidae (mean $\beta = 0.989$), and Columbidae (mean $\beta = 0.992$).

3.3.4 Functional explanations of SSD

We tested four major hypotheses of SSD by calculating Spearman rank correlations for each family separately (see Methods). Then we tested whether the distribution of rank correlation coefficients is different from 0. Medians of correlation coefficients between mating competition and all five morphometric traits were significantly larger than 0 (Table 3.2). SSDs in body mass and bill length were strongly associated with mating competition. These results suggest that increasing male-biased SSD is strongly associated with intense mating competition.

The median correlation coefficients were less than 0 between display agility and SSD in morphometric traits, although the deviation from 0 was only significant in body mass (Table 3.2). To test whether the relationships between display agility and SSDs are consistent with the prediction, we combined the probability of five tests into a single value (see Sokal and Rohlf 1981). The combined probability test revealed $P < 0.05$ for display agility and SSD ($\chi^2 = 18.984$, $df = 10$), consistent with the display-agility hypothesis. Thus support for the

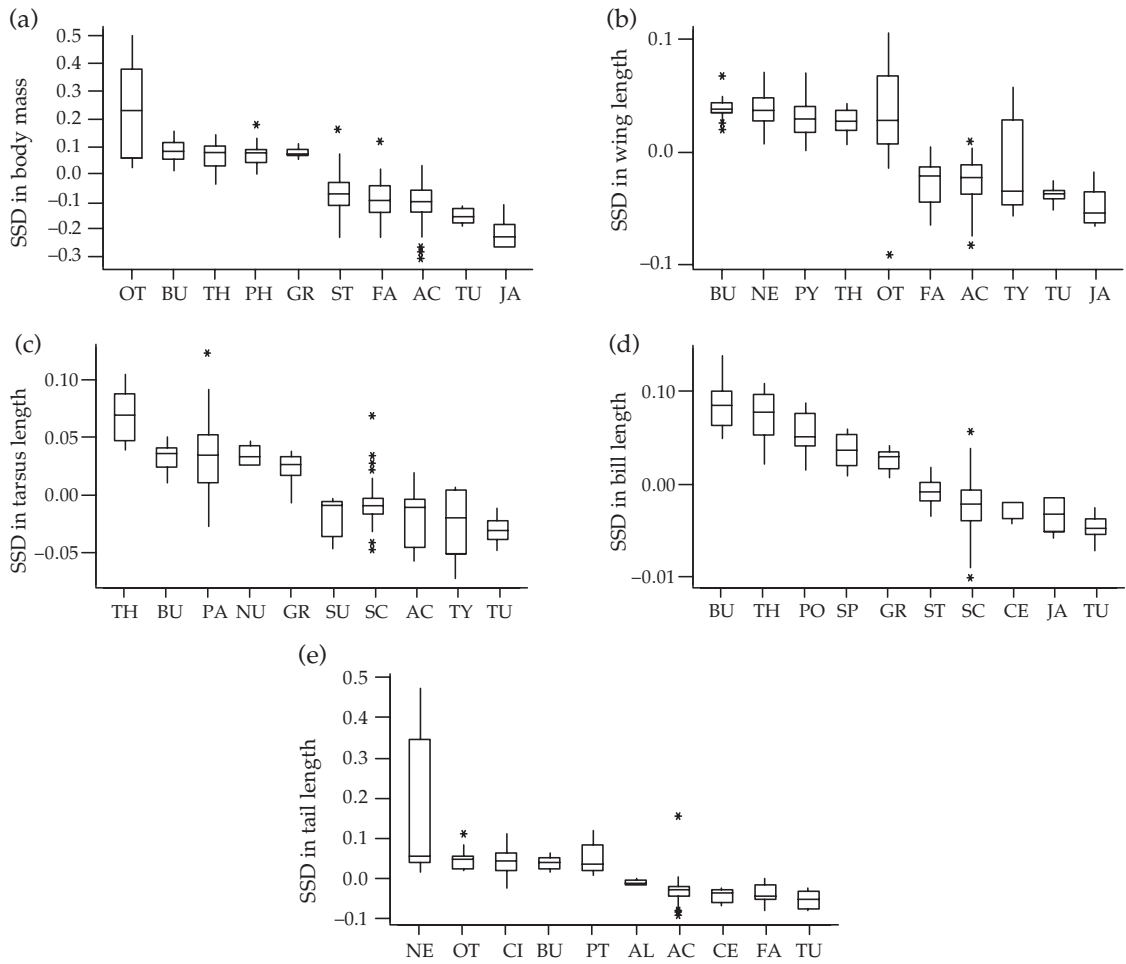


Figure 3.3 Families representing the most extreme male-biased and female-biased SSDs in body mass (a), wing length (b), tarsus length (c), bill length (d), and tail length (e). Only families with at least five data points are included. Shown are the families Accipitridae (AC), Alcedinidae (AL), Bucerotidae (BU), Centropidae (CE), Cisticolidae (CI), Falconidae (FA), Gruidae (GR), Jacanidae (JA), Nectariniidae (NE), Numididae (NU), Otididae (OT), Phasianidae (PA), Phalacrocoracidae (PH), Podicipedidae (PO), Pteroclididae (PT), Pycnonotidae (PY), Scolopacidae (SC); Spheniscidae (SP), Strigidae (ST), Sulidae (SU), Threskiornithidae (TH), Turnicidae (TU), Tytonidae (TY). Asterisks indicate outliers (see Figure 3.2 legend). For details of the boxplots see Figure 3.2. SSDs were calculated as $\log_{10}(\text{male trait}) - \log_{10}(\text{female trait})$.

Table 3.2 The distribution of Spearman rank correlations (r_s) between SSD traits and functional explanations. r_s was only calculated for families with data from at least five species. The median of rank correlations, the probability of Wilcoxon one-sample test (P) of difference from median = 0, and number of avian families (n) are given. P values of less than 0.05 are shown in *italic*.

Trait	Mating competition		Display agility		Resource division		Fecundity	
	Median	<i>P</i> (<i>n</i>)	Median	<i>P</i> (<i>n</i>)	Median	<i>P</i> (<i>n</i>)	Median	<i>P</i> (<i>n</i>)
Body mass	0.2481	<i>0.003</i> (18)	-0.1222	<i>0.016</i> (34)	0.0393	0.504 (36)	-0.0428	0.379 (61)
Wing length	0.1933	<i>0.013</i> (15)	-0.0618	0.237 (39)	0.0329	0.548 (44)	-0.0314	0.527 (63)
Tarsus length	0.1497	<i>0.038</i> (12)	-0.0511	0.442 (34)	0.0044	0.950 (39)	-0.0177	0.669 (55)
Bill length	0.2816	<i>0.001</i> (15)	-0.0658	0.200 (35)	0.0302	0.526 (38)	-0.0164	0.757 (57)
Tail length	0.2310	<i>0.008</i> (13)	-0.0566	0.225 (34)	0.0927	0.078 (39)	-0.0253	0.601 (55)

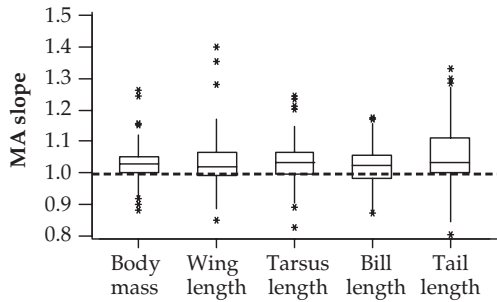


Figure 3.4 Rensch's rule in birds. The principal axis of major-axis (MA) regression $\log_{10}(\text{male size}) : \log_{10}(\text{female size})$ was calculated separately for each family with data from at least five species. The median slope is significantly larger than 1.0 in all traits (Wilcoxon one-sample tests, body mass $W = 1596$, $P < 0.001$, $n = 64$ families; wing length $W = 1729$, $P < 0.002$, $n = 69$ families; tarsus length $W = 1411$, $P < 0.001$, $n = 59$ families; bill length $W = 1363$, $P < 0.003$, $n = 61$ families; tail length $W = 1546$, $P < 0.001$, $n = 61$ families). Asterisks indicate outliers (see Figure 3.2); two outliers in tail length are not shown, Nectariniidae (1.787) and Passeridae (1.697).

display-agility hypothesis is weaker than for the mating-competition hypothesis (combined probability test of mating competition and morphometric traits, $\chi^2 = 50.316$, $df = 10$, $P < 0.001$).

There is no clear pattern in Spearman rank correlations between SSD, resource use, and fecundity (Table 3.2). This is indicated by the non-significant combined probability values of resource use ($\chi^2 = 9.062$, $df = 10$, $P > 0.5$) and fecundity ($\chi^2 = 5.600$, $df = 10$, $P > 0.5$).

Avian families exhibiting the strongest relationship with SSD in the predicted direction are Trochilidae, Hirundinidae, Phasianidae, Passeridae, Anatidae (mating competition); Falconidae, Trochilidae, Musophagidae, Strigidae, Pardalotidae (display agility); Tytonidae, Falconidae, Pycnonotidae, Hirundinidae, Pardalotidae (resource division); and Jacanidae, Dendrocygnidae, Burhinidae, Maluridae, Petroicidae (fecundity). Families showing the strongest relationship with SSD in the opposite direction to the predicted directions are Tyrannidae, Muscicapidae, Sylviidae, Accipitridae, Meliphagidae (mating competition); Laniidae, Sturnidae, Cuculidae, Phasianidae (display agility); Centropidae, Threskiornithidae, Cuculidae, Otidae, Podicipedidae (resource division); and Tytonidae, Odontophoridae, Glareolidae, Ciconiidae (fecundity).

3.4 Discussion

Our work has confirmed Darwin's assertion that most birds exhibit male-biased SSD. This result was consistent between species and families, and among five morphometric traits. The frequency distribution of SSD, however, was significantly leptokurtic: more species were monomorphic than predicted by normal distribution. At family level the frequency distributions remained leptokurtic; nevertheless the deviation from normal was statistically weaker or non-significant. We consider three explanations for the non-normal distributions of SSD. First, the non-normality is a statistical artifact due to measurement error, or bias due to variable number of specimens measured for males and females. However, measurement error for a given sex should not produce bias toward more monomorphic species. Also, if only a few males and females are measured from a given species, this is likely to inflate SSD and thus produce strongly male-biased (or female-biased) SSDs, the opposite pattern to Figure 3.1. Second, non-normal distributions of SSD may be real biological features. For instance, genetic correlations between the sizes of males and females may pull the sexes toward the same mean (Merilä *et al.* 1999; see also Chapter 18 in this volume). Also, strong stabilizing selection may act on the sizes of males and females (Price and Grant 1985). The latter explanation appears to be relevant, since males and females spend much of their lives living in proximity to each other in many birds, so that using similar niches may require similar body sizes in males and females. Third, the extent of SSD is often related to sexual selection, and intense sexual selection in turn facilitates species diversification and may elevate the risk of extinction (Owens *et al.* 1999; Morrow and Pitcher 2003). Consequently, the deviations from normal distribution may be due to heterogeneous rates of extinction and/or speciation in regards to SSD.

SSD in body mass exhibited the widest range of values of all five morphometric traits. On the one hand, since the body masses of many birds change spectacularly between breeding and non-breeding seasons, and over a single day (Cuthill and Houston 1997), the different dates and/or times of

measurements may inflate the extent of SSD in body mass. Female mass may also change from before to after egg laying. Given, however, that our data-set preferentially included measurements taken during the breeding season, these effects are likely to be minor. On the other hand, body mass is a three-dimensional trait whereas the lengths of wing, tarsus, bill, and tail are single-dimensional. Thus SSD as calculated from a three-dimensional trait may amplify the SSDs exhibited by single-dimensional traits (see Chapter 1 in this volume).

Interestingly, the correlations between the five measures of SSD were weak, particularly those between tail length and the other traits. The low correlations may have important implications. First, the ancestral patterns of integration between various morphometric traits may persist over considerable time, thus constraining possible evolutionary patterns (Arnold 1981). The apparent low correlations we report suggest that tail length responds to different selective forces than the other traits. A nested analysis of variance using taxonomic hierarchy (species, genera, family, and order) as a random factor suggests that different evolutionary processes are operating on SSD in tail length. Whereas for the other four morphological variables over 50% of variance is concentrated at family or order levels (50.8, 51.1, 51.3, and 66.3% variance in SSD of body mass, wing length, tarsus length, and bill length, respectively), in tail-length SSD the corresponding value was low (14.50%) and most variance occurred at species and genus levels (55.60 and 29.9%, respectively). Our results are thus consistent with those of Björklund (1990), who argued that different forces (or constraints) operate on different morphological characters (for examples from other taxa, see Chapters 9 and 11 in this volume).

Second, tail length is more variable than the other traits in Palearctic birds (Fitzpatrick 1997), an observation that is probably related to the implication of this trait in sexual selection. Møller and Cuervo (1998) identified 70 independent events in the evolution of ornamental tail feathers. The extreme elongation of tails has been related to sexual selection in several birds (Andersson 1982; Andersson and Andersson 1994; Winquist and Lemon 1994; Regosin and Pruett-Jones 2001;

Møller *et al.* 2006). Third, low interspecific variation in wing length in comparison to tail length has been found in different bird taxa, and this low variation is considered to be the result of stabilizing selection on wing morphology (Alatalo 1988; Balmford *et al.* 1993; Thomas 1993; Fitzpatrick 1997; Groombridge *et al.* 2004). In comparison, tail length appears to be a compromise between aerodynamics and sexual selection. Thus further work is essential to evaluate how sexual selection and utilitarian processes such as aerodynamics, migratory behavior, and flight capacity influence each morphological trait.

Our analyses strongly suggest that Rensch's rule occurs in a broad range of avian taxa, and the rule appears to be exhibited by all five morphometric traits. These results expand on previous work that shows the existence of Rensch's rule among Passeriformes, Pelecaniformes, Procellariiformes (Fairbairn 1997), Galliformes (Sæther and Andersen 1988; Fairbairn 1997), hummingbirds (Fairbairn 1997; Colwell 2000), bustards (Payne 1984; Rainahi *et al.* 2006), grouse (Payne 1984; T. Lislevand *et al.* 2007), and shorebirds (Székely *et al.* 2004). No evidence of allometry consistent with the Rensch's rule was found in Falconiformes, Strigiformes, Anseriformes, Charadriiformes (Fairbairn 1997), and seabirds (Serrano-Meneses and Székely 2006).

The discrepancy between some of the previous studies of Rensch's rule raises two important questions. First, what is the correct way of testing Rensch's rule? As Fairbairn (1997) argues, major-axis regression using phylogenetic control is desirable. Phylogenetic correction, however, can be carried out in a variety of ways (Freckleton *et al.* 2002), and the phylogenies themselves are prone to errors. Second, what is the correct taxonomic level of analysis: species, genera, or families? Rensch (1959, p. 159) suggested that "This rule, however, applies only to subspecies of a species, to related species of a genus, or to related genera of a family". Note that Rensch himself is inconsistent, illustrating his rule using three species of Scarabaeidae that represent three different genera (Rensch 1959, Figure 50, p. 160). In our view, the answer to both issues requires simulation studies to explore the sensitivity of the allometric

relationship to phylogeny, comparative methods, and the taxonomic level of analyses.

We also identified a number of species and families with extreme SSDs and/or with large intra-familial variation in SSD. These taxa will be excellent for comparative analyses across species, and for detailed observational and experimental studies within species. Note that our lists are not exhaustive, since our data-set only included about one-third of all bird species due to restricted data availability and time constraints in data compilation. For instance, display agility of males relates to SSD in a number of taxa (Figuerola 1999; Székely *et al.* 2004; Raihani *et al.* 2006; Serrano-Meneses and Székely 2006). None of these studies, however, used quantitative data on display behavior, because high-resolution comparable data are simply not available for the vast majority of species. Measures of agility (e.g. frequencies of rolls and turns, estimates of descending/ascending height; see Grønstøl 1996) from a range of species would be extremely useful for functional testing of the display-agility hypothesis using comparative methods. Behavior and ecology of many species are gradually better understood, partly due to efforts in the tropics and southern hemispheres where most species live. Also, with the advent of high-throughput sequence analyses that lead to better molecular phylogenies, we anticipate future comparative analyses to become more powerful.

Our results are consistent with the assertion of Darwin (1874) and previous comparative studies that intense mating competition between males predicts male-biased SSD (Table 3.1; Webster 1992; Winquist and Lemon 1994; Raihani *et al.* 2006; but see Björklund 1990; Oakes 1992). We also showed that the relationship between sexual selection and SSD is more complex than usually acknowledged, since display agility, a functional explanation that is often considered of minor importance, was related to reduced size in males relative to females. The latter effect, however, was weaker than the effect of mating competition on SSD. One potential explanation for the different predictive powers of mating competition and display agility may be data quality. Breeding system, a proxy we used for mating competition, is often better described in the literature than display agility, for which we used

scores based upon verbal descriptions. Interestingly, mating competition is not only likely to select for large size in the sex competing more intensively for mates, but can also promote changes toward small size when small size is favored during displays. To what degree these results in birds elucidate the processes in other taxa is not yet known. We conjecture that male agility should influence SSD in many more taxa in which males display to and/or fight over females; for instance bats, primates, and pinnipeds.

We found no support for the fecundity and resource-division hypotheses. There may be good reasons why these hypotheses may only work in certain avian taxa (Selander 1972; Shine 1989; Temeles and Kress 2003). For instance, fecundity selection may only be important in capital breeders—those using resources from their own body to produce offspring—but not in income breeders. In sum, we agree with Andersson (1994) that discounting fecundity selection and resource division would be premature, since differences between species in foraging ecology, parental roles, and demands imposed by egg production may also affect SSD. To advance these hypotheses (and others we have not considered here; see Andersson 1994; Blanckenhorn 2000), one needs further comparative analyses, perhaps using higher-quality data from those groups that exhibit unusually large ranges in SSD.

We propose that future tests of functional hypotheses in avian SSD should use a two-pronged approach. First, we need to select a group of species for detailed quantitative description of selective forces in regards to major functional hypotheses. This may include observational or experimental tests of specific hypotheses. Second, these observational (or experimental) data should be compared among species using standard comparative methods to establish which (if any) hypotheses predict SSD across species and traits (see Chapters 2, 4, and 13 in this volume). Note that functional hypotheses may have integrated effects and there may be statistical interactions between these effects (Székely *et al.* 2004). Powerful statistical analyses of cross-species effects require precise data, a good number of species and sound phylogenetic hypotheses. Thus integrating the

results of within-species and across-species approaches are likely to provide comprehensive functional explanations of SSD.

3.5 Summary

Birds are excellent model organisms for testing functional explanations of SSD, since many species are exceptionally well studied in nature. We review four major functional hypotheses of SSD, and test these using data on five morphometric traits from over 2500 bird species. We show that SSD is male-biased in most avian species and families. We also report that allometry consistent with Rensch's rule occurs in significantly more avian families than expected by chance. Finally, using cross-species analyses we show that SSDs are most consistent with sexual selection, specifically with the mating competition and the display agility hypotheses. Sexual selection, however, is unlikely to explain all variation in SSD, and further work is essential to test how ecological use of resources and fecundity selection may trigger, or amplify, changes in SSD. Further work is also essential to establish the interactive effects of these selective processes, and evaluate their significance in major avian lineages. We argue that these challenging projects are timely given rapid accumulation of data on natural history, improved estimates of phylogenetic relationships and recent advances in statistical analyses of cross-species data.

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3.7 Suggested readings

- Andersson, M. (1994) *Sexual Selection*. Princeton University Press, Princeton, NJ.
- Fairbairn, D.J. (1997) Allometry for sexual size dimorphism: pattern and process in the coevolution of body size in males and females. *Annual Review of Ecology and Systematics* **28**, 659–687.
- Székely, T., Freckleton, R.P., and Reynolds, J.D. (2004) Sexual selection explains Rensch's rule of size dimorphism in shorebirds. *Proceedings of the National Academy of Sciences USA* **101**, 12224–12227.