

Sexual selection explains Rensch's rule of size dimorphism in shorebirds

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Sexual size dimorphism shows a remarkably widespread relationship to body size in the animal kingdom: within lineages, it decreases with size when females are the larger sex, but it increases with size when males are the larger sex. Here we demonstrate that this pattern, termed Rensch's rule, exists in shorebirds and allies (Charadriides), and it is determined by two components of sexual selection: the intensity of sexual selection acting on males and the agility of the males' display. These effects are interactive so that the effect of sexual selection on size dimorphism depends on male agility. As a control, we also examine dimorphism in bill length, which is a functionally selected trait. As such, dimorphism in bill length neither exhibits Rensch's rule nor is associated with sexual selection and display. Our results show that variation among taxa in the direction and magnitude of sexual size dimorphism, as manifested as Rensch's rule, can be explained by the interaction between the form and strength of sexual selection acting on each sex in relation to body size.

Male and female animals are rarely the same size, yet the selective processes that create sexual size dimorphism (SSD) are controversial (1). Rensch (2) noted in numerous animal groups that when the male is larger than the female, SSD (measured as the ratio of male to female size) increases with body size, but it decreases with body size in groups in which the male is smaller than the female. Rensch's rule is a pervasive macroecological pattern that has been observed in a wide range of taxa, including mites, water striders, lizards, snakes, turtles, hummingbirds, songbirds, and primates (3–6). To date, the mechanisms producing this pattern remain unclear.

Three forms of selection have been invoked to explain Rensch's rule. First, intrasexual selection may select for large male body size when size is advantageous for fights (1, 7, 8). This hypothesis predicts that male-biased dimorphism should increase with competition between males for access to females in large species, whereas small sex-role-reversed species, in which females compete with each other, should exhibit female-biased dimorphism. Second, intersexual selection may drive the evolution of male size in the opposite direction if small size enhances courtship displays of males, for example, in species where males advertise through acrobatic displays (9, 10). Thus selection on agility of intersexual signaling is expected to produce female-biased dimorphism in small species. This hypothesis predicts female-biased dimorphism if males use agile courtship displays, and male-biased dimorphism if males exhibit nonagile courtship behavior, for instance by displaying from the ground. Third, natural selection through ecological processes may also determine dimorphism. For example, if small species live in resource-poor habitats, then resource limitation could prevent males of small species from responding to sexual selection for large size (6, 11).

Here we assess the relative contributions of these three potential explanations by using phylogenetic comparative analyses of shorebirds and allies including gulls and auks ("shorebirds" henceforward). We distinguish between the effects of sexual competition and male agility on SSD (measured by

differences in mass and wing size between the sexes), and we test for a role of ecological pressures by exploring the effects of habitat productivity on size dimorphism. We show that the combination of inter- and intrasexual competition, and the interaction between them, account for the full range of Rensch's rule, encompassing changes in magnitude of both female- and male-biased dimorphism among species that differ in body size.

Shorebirds are an excellent model system to test these hypotheses. Male body mass ranges from 59% to 169% of female body mass, encompassing nearly the entire range exhibited by the world's 9,700+ species of birds, and the mean body mass varies nearly 80-fold across shorebird species. Shorebirds have diverse mating systems, including social polygyny, social monogamy, and sequential (classical) polyandry (12, 13). Males have diverse displays ranging from ground displays to highly acrobatic aerial displays (9, 14, 15). Finally, they inhabit a wide range of ecological habitats, including tropical, temperate and Arctic wetlands, tundra, forests, and deserts.

Methods

Database. We collated data on the body size, mating behavior, ecology, and life histories of 102 species of shorebirds (see Table 3, which is published as supporting information on the PNAS web site). The body mass (in g) and wing length (in mm) of adult males and females were compiled from published sources by collating data, preferably from the same population during the breeding season. We used the social mating system as an imperfect surrogate of the intensity of sexual competition on a three-point scale: 1, polyandrous; 2, monogamous; 3, polygynous. In socially monogamous shorebirds, extra-pair paternity is low (0–7.8% of chicks, $n = 13$ species; refs. 16 and 17). Agility of males was scored on a three-point scale as follows: 1, ground display; 2, nonacrobatic aerial display; 3, acrobatic aerial display (15). Habitat productivity was scored by five observers blind to species names on a three-point scale: 0, desert and semidesert; 1, dry grassland and tundra, and dry forest; 2, wetland, marsh, seashore, lake, and river. The difference in scores between observers was never more than one, and the median scores were used in the analyses.

Phylogeny and Comparative Analyses. The composite phylogeny of sandpipers and plovers (15) was augmented by the morphology-based phylogeny of gulls and auks (18). All species of the Charadriides infraorder for which we have phylogenetic information and data on morphology, behavior, and life history (102 out of 349 species) were included in the study (42/103 for Scolopacida and 60/246 for Charadriida). The phylogeny was fully resolved. Sandgrouse (*Pterocles orientalis*) was used as an outgroup. Branch lengths were not known for several taxa; thus, we used unit branch lengths. Phylogenetic analyses were based on generalized least squares, which is a powerful and compre-

Abbreviation: SSD; sexual size dimorphism.

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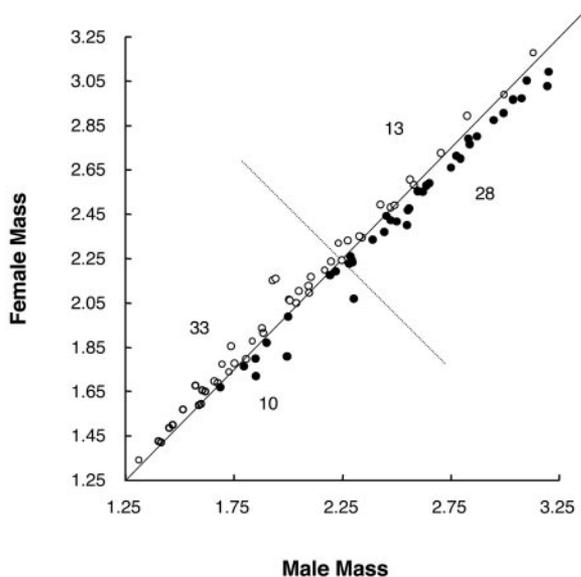


Fig. 1. Rensch's rule in shorebirds and allies. $\log_{10}(\text{female mass})$ is plotted against $\log_{10}(\text{male mass})$: species in which females are larger than males are shown by open circles, and species in which males are larger than females are shown by solid circles. The numbers of species are given in each of the four quadrants delimited by the line of equality and its tangent. If Rensch's rule were false, these numbers would be approximately equal.

hensive approach to the analysis of comparative data (19, 20). Generalized least squares is a modification of generalized linear models in which the phylogeny is used to specify the expected variance and covariance between species under an assumed Brownian model of evolution, and hence it controls for non-independence arising from phylogenetic relationships between species. We checked the adequacy for this model using the test in ref. 21. These methods are identical to weighted generalized least-squares models. We used $\log_{10}(\text{male size}) - \log_{10}(\text{female size})$ as the response, and we regressed it against $\log_{10}(\text{male size})$ and tested for a nonzero slope. Note that this is statistically identical to regressing $\log_{10}(\text{male size})$ against $\log_{10}(\text{female size})$ and testing for a slope different from unity (22). All tests were conducted by using Type III sums of squares.

Because body size is estimated with error, we used major axis regression to estimate the slopes of linear regressions, and we tested the null hypothesis of $b = 1$ using 99.9% confidence intervals. The regression was carried out with \log_{10} transformed body masses and wing length. Following previous work (4, 6), we assigned males to the x axis. Use of female size as the independent variable does not change our results qualitatively. The phylogenetically corrected variance was compared between males and females by using parametric tests (23).

Results

Rensch's Rule. Shorebirds exhibit the full range of Rensch's rule: in large shorebirds males are generally larger than females and SSD increases with male size, whereas in small species females are generally larger than males and SSD decreases with size (Fig. 1). As predicted by Rensch's rule, the slope of major axis regression of $\log_{10}(\text{female})$ on $\log_{10}(\text{male})$ is significantly different from 1.0 both in body mass ($b = 0.935$, $P = 0.001$, $n = 87$ species) and wing length ($b = 0.949$, $P = 0.001$, $n = 103$ species). Although major axis regression of log female size on log male size is the conventional way of testing for the existence of Rensch's rule, this test is not corrected for phylogenetic confounding. However, phylogenetically corrected analyses confirm the existence of Rensch's rule comparing the variance of

matched pairs: variance in male size is greater than variance in female size (body mass: $t_{82} = 2.755$, $P < 0.001$; wing length: $t_{99} = 2.527$, $P < 0.01$).

Sexual Selection. We tested for the effects of sexual competition and male agility on dimorphism using phylogenetic generalized least squares. As predicted, more intense male–male competition is associated with increasing male-biased dimorphism (model 1, Table 1), and more agile male displays are associated with increasing female-biased dimorphism (model 2, Table 1). However, the highly significant interaction between sexual competition and agility ($P < 0.0001$, model 3, Table 1) indicates that species with intense male–male competition exhibit female-biased dimorphism if males are agile, whereas they exhibit male-biased dimorphism if males are nonagile (Fig. 2). In contrast, species with low intensity of male–male competition show female-biased dimorphism regardless of male agility (Fig. 2).

Sexual competition, male agility, and their interaction each have a highly significant influence on dimorphism (model 3, Table 1). Once these effects are included in the phylogenetically controlled regression, the predictive power (r^2) of the model nearly doubles (from 0.246–0.258 to 0.454–0.476), and the characteristic relationship between body size and SSD of Rensch's rule is no longer significant (model 3, Table 1).

It is unlikely that our results are confounded by life-history traits such as fecundity, breeding latitude, and migratory behavior. First, small shorebirds may be more fecund than large ones, and thus fecundity selection may favor dimorphism consistent with Rensch's rule. However, including clutch size in model 3 does not change our conclusion, because sexual competition, male agility type, and their interaction remain highly significant ($P < 0.001$), whereas clutch size is nonsignificant (body mass: $F_{1,48} = 0.012$, $P = 0.912$; wing length: $F_{1,48} = 0.001$, $P = 0.972$). Second, shorebirds that breed near the equator may be more dimorphic than species breeding at higher latitudes. Nevertheless, when breeding latitude is included in model 3, sexual competition, male agility, and their interaction remain highly significant ($P < 0.001$), whereas breeding latitude is nonsignificant (body mass: $F_{1,48} = 2.747$, $P = 0.104$) or marginally significant (wing length: $F_{1,48} = 3.662$, $P = 0.062$). Finally, by including migratory distance in model 3, sexual competition, male agility, and their interaction remain highly significant ($P < 0.001$), whereas migratory distance is nonsignificant (body mass: $F_{1,48} = 2.963$, $P = 0.09$; wing length: $F_{1,48} = 0.012$, $P = 0.912$).

Habitat Productivity. We found no evidence that an index of habitat productivity relates to dimorphism in body size, and, importantly, Rensch's rule remains significant when this variable is included (model 4, Table 1). Habitat productivity remains nonsignificantly related to dimorphism when habitat is treated as a categorical variable (phylogenetically controlled regression, body mass: $F_{1,68} = 1.710$, $P = 0.199$). A full model that includes all three hypothesized explanatory variables (sexual competition, male agility, and habitat productivity) confirms that sexual competition, male agility, and their interaction remain highly significant ($P < 0.001$), whereas habitat productivity remains nonsignificant (body mass: $P = 0.604$; wing length: $P = 0.316$). Thus, adding habitat productivity to model 3 only marginally increases the explanatory power (body mass: $r^2 = 0.478$; wing length: $r^2 = 0.462$).

SSD is unlikely to be the result of selection imposed directly by ecological factors, because selection operating on an ecological trait, bill length (measured as the length of the culmen, the dorsal ridge of the upper mandible, from the forehead to the tip), has been fundamentally different from selection operating on other aspects of body size. The phylogenetically corrected variance in bill length does not differ between males and females (t_{99}

Table 1. Associations among SSD, sexual selection, and habitat productivity determined by phylogenetically corrected linear models

Model (covariate df, error df)	Body mass	Wing length
Model 1 (1, 72)		
Sexual competition	0.037 ± 0.013 (0.006)	0.014 ± 0.004 (0.0009)
Male size	0.019 ± 0.009 (0.033)	0.0207 ± 0.019 (0.271)
<i>r</i> ²	0.258	0.246
Model 2 (1, 72)		
Male agility	-0.031 ± 0.008 (0.0002)	-0.009 ± 0.003 (0.0015)
Male size	0.025 ± 0.008 (0.0024)	0.051 ± 0.017 (0.0037)
<i>r</i> ²	0.258	0.204
Model 3 (1, 70)		
Sexual competition	0.135 ± 0.026 (not tested)	0.045 ± 0.009 (not tested)
Male agility	-0.119 ± 0.023 (not tested)	-0.036 ± 0.007 (not tested)
Sexual competition * male agility	0.048 ± 0.012 (0.0001)	0.015 ± 0.004 (0.0001)
Male size	0.013 ± 0.007 (0.075)	0.011 ± 0.016 (0.498)
<i>r</i> ²	0.476	0.454
Model 4 (1, 72)		
Habitat productivity	-0.0076 ± 0.013 (0.552)	-0.001 ± 0.004 (0.864)
Male size	0.0279 ± 0.0087 (0.002)	0.047 ± 0.018 (0.012)
<i>r</i> ²	0.126	0.085

SSD (response variable) is given in all models as $\log_{10}(\text{male mass or wing length}) - \log_{10}(\text{female mass or wing length})$. Male size is given as $\log_{10}(\text{male body mass})$ or $\log_{10}(\text{male wing length})$, as appropriate. For each model, regression coefficients ± SE are given together with *r*², the total proportion of variance explained. Numbers in brackets are probability levels, except in the case of terms that are included in an interaction and are therefore not tested.

= 0.0015, *P* = 0.90), and Rensch's rule does not apply to dimorphism in bill length (model 1, Table 2). In common with the analyses based on body size, there are associations between dimorphism in bill length and the strength of intersexual selection and male agility (model 2, Table 2). However, bill length correlates with male size in males, and female size in females, with the consequence that there is a correlation between dimorphism in bill length and body size dimorphism. When male size and female size are controlled statistically, the association of bill size dimorphism with agility and the strength of intersexual selection no longer remain significant (model 3, Table 2), indicating that bill size dimorphism is not explained by these variables. Given this finding, as well as the lack of support for

Rensch's rule for bill size dimorphism, it appears that the selective pressures operating on dimorphism in bill length are different from those operating on dimorphism in body size.

Discussion

Shorebirds, which were previously thought to exhibit no allometric trend (3), have a significant allometry consistent with Rensch's rule. Our results are consistent between two measures of size: body mass and wing length. It is unlikely that life history traits and ecology confound the relationships between body size and SSD, because fecundity, migratory behavior, and habitat

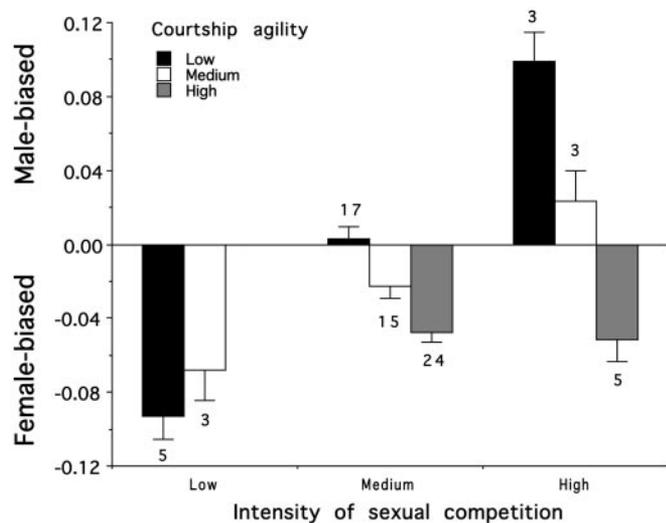


Fig. 2. Sexual dimorphism in body mass [mean ± SE $\log_{10}(\text{male mass}) - \log_{10}(\text{female mass})$] in relation to the intensity of sexual competition and male agility. The numbers of species are given below (or above) each bar.

Table 2. Associations between SSD in bill length as $\log_{10}(\text{male bill length}) - \log_{10}(\text{female bill length})$ and measures of sexual selection and display agility of males

Model (covariate df, error df)	Bill length
Model 1 (1, 72)	
Male size	0.002 ± 0.004 (0.56)
<i>r</i> ²	0.005
Model 2 (1, 70)	
Sexual competition	-0.033 ± 0.011 (not tested)
Male agility	-0.039 ± 0.010 (not tested)
Sexual competition * male agility	0.011 ± 0.005 (0.034)
Male size	-0.002 ± 0.003 (0.522)
<i>r</i> ²	0.348
Model 3 (1, 69)	
Sexual competition	0.008 ± 0.01 (not tested)
Male agility	-0.003 ± 0.009 (not tested)
Sexual competition * male agility	-0.003 ± 0.004 (0.51)
Male size	0.293 ± 0.04 (<0.0001)
Female Size	-0.299 ± 0.04 (<0.0001)
<i>r</i> ²	0.633

Male size is given as $\log_{10}(\text{male body mass})$.

productivity are all unrelated to SSD. We also tested and rejected habitat productivity as an explanation for Rensch's rule. The latter result was consistent with the analyses of a morphological indicator of feeding ecology, bill length.

Our results suggest that Rensch's rule is determined by a combination of sexual competition and male agility, and they are consistent with the following scenario. First, male-biased dimorphism increases with male size because directional sexual selection favors large males, and these males typically exhibit nonagile displays. Thus divergence in SSD is due to strong directional selection on males, with a weaker correlational selection on females (3). Second, female-biased dimorphism increases with decreasing male size for two reasons. (i) The intensity of male-male competition increases, and directional selection favors small males that exhibit agile displays. (ii) Directional selection between females favors large females in sex-role-reversed species. The correlation between male size and SSD across shorebirds, which is diagnostic of Rensch's rule, is thus indirect and mediated by sexual selection acting on both males and females. Our analyses indicate no independent effect of body size on dimorphism; i.e., Rensch's rule appears to be entirely the result of this indirect interaction.

Empirical studies are scanty, although they tend to support these inferences. First, in acrobatic shorebirds, the frequency of energetically demanding song-flights by males correlates with the number of mates (Northern lapwing; ref. 24), and small males exhibit more aerial displays than large ones (dunlin; ref. 10). Second, in the nonacrobatic bronze-winged jacana, heavy females have larger harems than light ones have (25).

The interaction between forms and intensity of sexual selection may explain why other taxa with intense male-male competition exhibit a range of dimorphisms including both male-biased and female-biased dimorphisms (e.g., fruit flies,

pinnipeds, and primates; refs. 26–28). Our analyses predict that sexual selection should favor large males in relatively large species among closely related taxa, and these males should exhibit nonagile displays, whereas in relatively small species, sexual selection should favor agile displays and small males.

A review of 42 taxa showed that in 18 cases, there was statistically significant allometry in body size consistent with Rensch's rule, whereas only 2 taxa are statistically inconsistent with the pattern (3–6). Likewise, 30 slopes of the major axis regression out of 38 are consistent with Rensch's rule, whereas 8 slopes are not. Exceptions to the rule are therefore rare and occur particularly in taxa in which females are the larger sex (29, 30). We suggest that in those taxa that contradict Rensch's rule, strong fertility selection acts on females. Consistent with this suggestion, two taxa that deviate significantly from Rensch's rule (owls and stick insects) have female-biased dimorphism and fecundity selection has been proposed to favor large females (1, 31).

SSD is often used as an indicator of the intensity of sexual selection (32, 33). Our analyses show that this assumption is not straightforward, because intense sexual selection acting on males may produce female-biased dimorphism if male agility is under selection. Taken together, new phylogenetic comparative analyses of the intensity and form of sexual selection acting on males, and fecundity selection acting on females are needed to reveal why some animal taxa exhibit Rensch's rule whereas others do not.

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