EVOLUTIONARY BIOLOGY

Darwinian sex roles confirmed across the animal kingdom

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Since Darwin's conception of sexual selection theory, scientists have struggled to identify the evolutionary forces underlying the pervasive differences between male and female behavior, morphology, and physiology. The Darwin-Bateman paradigm predicts that anisogamy imposes stronger sexual selection on males, which, in turn, drives the evolution of conventional sex roles in terms of female-biased parental care and male-biased sexual dimorphism. Although this paradigm forms the cornerstone of modern sexual selection theory, it still remains untested across the animal tree of life. This lack of evidence has promoted the rise of alternative hypotheses arguing that sex differences are entirely driven by environmental factors or chance. We demonstrate that, across the animal kingdom, sexual selection, as captured by standard Bateman metrics, is indeed stronger in males than in females and that it is evolutionarily tied to sex biases in parental care and sexual dimorphism. Our findings provide the first comprehensive evidence that Darwin's concept of conventional sex roles is accurate and refute recent criticism of sexual selection theory.

INTRODUCTION

Understanding the numerous behavioral, morphological, and physiological differences between the sexes constitutes a central theme in many scientific disciplines, including psychology (*1*), medicine (*2*), and biology (*3*). For more than a century, evolutionary biologists have debated whether males and females are subject to consistently different selection pressures and whether these give rise to the so-called conventional sex roles (*4*). On the basis of observations in fish, birds, reptiles, and mammals, Charles Darwin argued that males are typically eager to copulate, whereas females are choosy about whom to mate with (*5*). However, it took nearly seven decades since these observations before researchers began investigating the ultimate reasons for the proposed sex difference in mating propensity. Inspired by Darwin's sex role concept, Angus John Bateman demonstrated that, in fruit flies, reproductive fitness and mating success are more variable in males compared to females (*6*). Even more importantly, Bateman discovered that fertility increased more steeply with the number of mates for males compared to females, which he interpreted as the primary cause of sex differences in mate competition and thus for Darwinian sex roles. Bateman argued that the observed male bias in the strength of sexual selection arises ultimately from anisogamy and must therefore be inherent to all sexually reproducing animals and plants. These ideas later crystallized in the three Bateman principles predicting that males typically exhibit (i) more variance in reproductive success, (ii) more variance in mating success, and (iii) a stronger dependency of reproductive success on mating success (*7*).

Combining Bateman's principles with Darwin's conception of eager males and discriminating females, the Darwin-Bateman paradigm is now the most commonly invoked concept to explain conventional sex roles (*8*, *9*). Specifically, it provides the conceptual framework to understand two central manifestations of conventional sex roles—female-biased parental care and male-biased sexual dimorphism. First, Trivers predicted that the sex exhibiting greater parental investment (usually the female) becomes a limiting resource for the less caring sex (usually the male) so that the latter competes for access to the former (*10*). However, more recent work proposes that causality here can act both ways (*11*, *12*), where the sex experiencing stronger precopulatory sexual selection is selected to provide less parental care (*13*). Second, sexual selection is considered as one major source driving the tremendous sexual dimorphism observed in behavioral, morphological, physiological, and life history traits (*14*). Many polygamous species show striking elaboration of ornaments and armaments in males relative to the rather inconspicuous appearance of females, which is predicted as a prime outcome of sex biases in sexual selection (*3*).

The evolutionary trajectories linking anisogamy-related investment and male-biased sexual selection to conventional sex roles have recently been formalized as a "sexual cascade," providing a logical imperative for sexual differentiation that back Darwin and Bateman's original insights (*15*). However, despite this well-founded theoretical framework, the Darwin-Bateman paradigm has received substantial criticism. First, Bateman's own study has been questioned on statistical (*16*) and experimental (*17*) grounds, raising doubts whether his data provide evidence for the postulated sex difference in selection. Second, although many empirical studies support stronger sexual selection in males, others convincingly show that both sexes can experience similar levels of sexual selection and that sex roles can be reversed (*18*). Further, it is widely acknowledged that females can also benefit from multiple mating (*19*) and that sperm production entails nontrivial costs for males (*20*). These findings challenge Bateman's restrictive views that female fertility depends primarily on egg production and male fertility on the number of mating partners. Given these issues, it has been argued that, "At best, Bateman's principles should be considered as hypotheses and approached with great care" (*21*). Consequently, as it stands, we are left with a concept that is at the core of sexual selection theory (*13*) but remains highly controversial and untested at a comparative scale. Recently, some researchers even proposed that sexual selection theory as a whole is fundamentally flawed and needs to be replaced by "gender-neutral" models (*22*–*24*). This school of thought predicts that sex roles are driven by stochastic processes or by ecological, social, and demographic conditions. If true, males and females are not expected to show the consistent sex differences in the

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strength of sexual selection, parental care, and sexual dimorphism as predicted by the Darwin-Bateman paradigm (*8*).

We quantitatively contrasted these opposing theories using established metrics of sexual selection: (i) the standardized variance in reproductive success ("opportunity for selection," I), (ii) the standardized variance in mating success ("opportunity for sexual selection," I_s), and (iii) the slope of an ordinary weighted least-squares regression of reproductive success on mating success ("Bateman gradient," β_{ss}). The variance-based estimates I and I_s capture upper limits of selection, whereas the Bateman gradient estimates the average strength and direction of sexual selection (*25*). We synthesized studies reporting these metrics with a random-effects meta-analysis to test (i) the universality of Bateman's claim that sexual selection is typically stronger in males than in females and (ii) the evolutionary link of sexual selection with sex-biased parental care and sexual dimorphism, accounting for phylogenetic nonindependence and for repeated measurements of the same species. We identified 72 studies on 66 animal species, providing estimates of I, I_s, and/or β_{ss} for males and females (Fig. 1). For each reported Bateman metric, we computed an effect size and its variance for the observed sex difference as ΔI, ΔI_s, and $\Delta\beta_{ss}$, with positive values indicating a male bias.

RESULTS

Consistent with Bateman's principles, overall, males showed a higher opportunity for selection (ΔI: lnCVR ± SE: 0.432 ± 0.188; z test: z = 2.291, K = 81, P = 0.022; Fig. 2A) and a steeper Bateman gradient than females ($\Delta\beta_{ss}$: Hedges' d ± SE: 0.344 ± 0.162; z test: z = 2.131, K = 76, P = 0.033; Fig. 2C). The opportunity for sexual selection was slightly, but not significantly, higher in males than in females (ΔI_s: lnCVR ± SE: 0.151 ± 0.156; z test: z = 0.949, K = 88, P = 0.343; Fig. 2B). These findings reveal that sexual selection is typically stronger in males across the sampled taxa.

Between-study variation significantly exceeded pure sampling error for all Bateman metrics (ΔI: Q = 731.063, df = 80, P < 0.001; ΔI_s: Q = 984.471, df = 87, P < 0.001; and $\Delta\beta_{ss}$: Q = 541.216, df = 75, P < 0.001; Fig. 1). Parental care explained a significant fraction of the observed

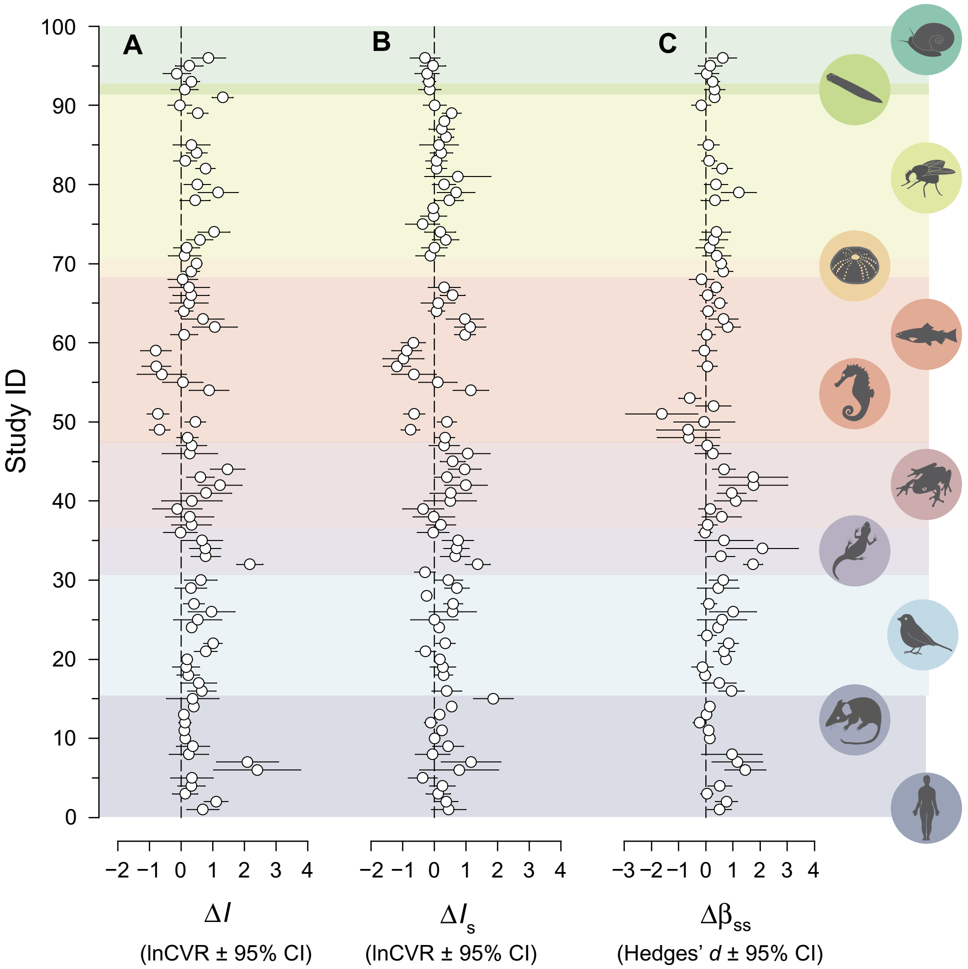

Fig. 1. Sex-biased sexual selection across the animal kingdom. (**A** to **C**) Forest plots showing estimates of the sex bias in (A) the opportunity for selection (ΔI), (B) the opportunity for sexual selection (ΔI_s), and (C) the Bateman gradient ($\Delta\beta_{ss}$). Effect sizes (lnCVR and Hedges' d; see Materials and Methods) are shown with their 95% confidence intervals (CIs). Positive values indicate male-biased sexual selection parameters. Studies are grouped according to taxonomic ranks (color shades and icons).

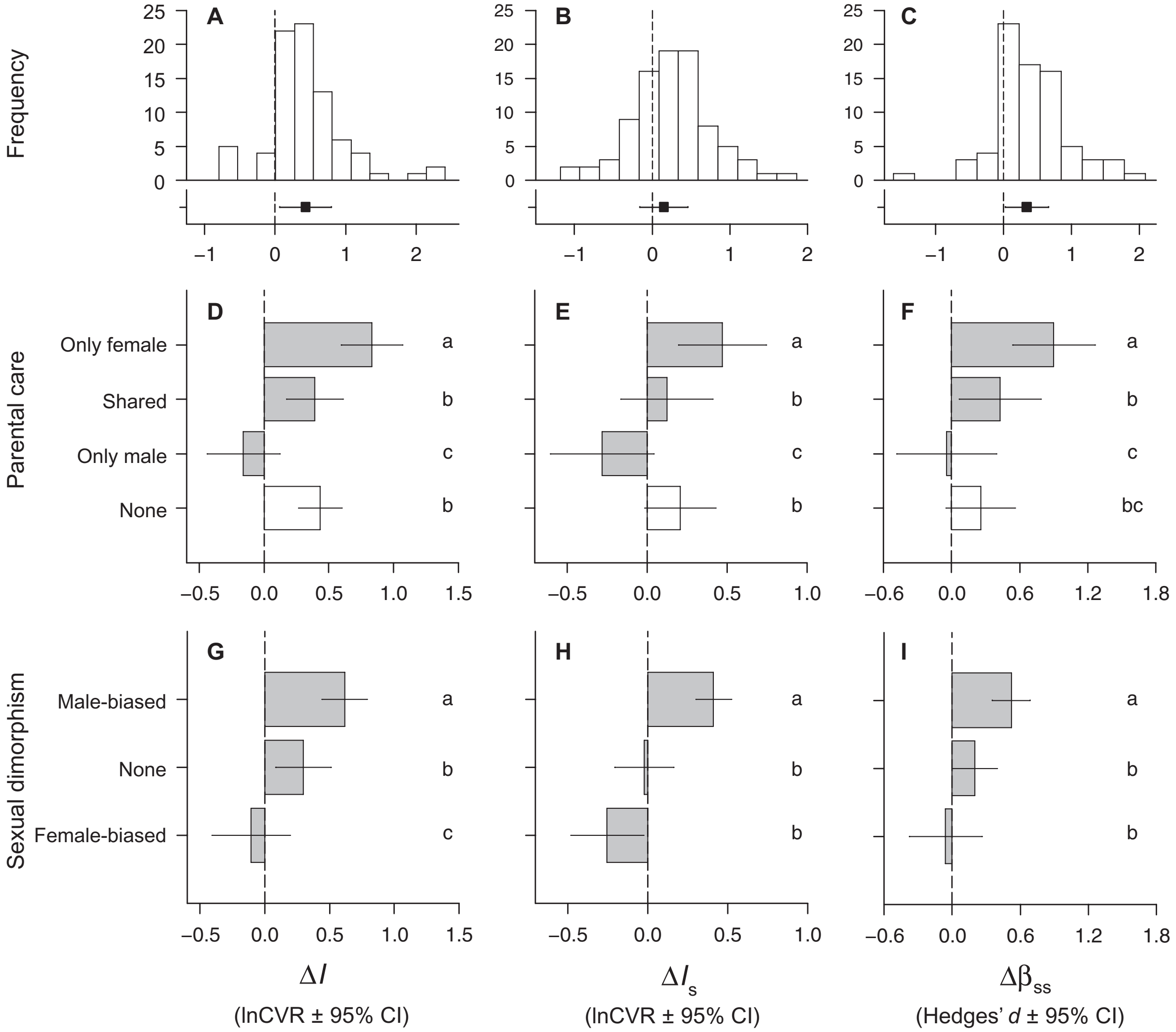

Fig. 2. Sex-biased sexual selection and its evolutionary link to parental care and sexual dimorphism. (**A** to **C**) Frequency distributions and global mean effect sizes (filled squares) for sex differences in (A) the opportunity for selection (ΔI), (B) the opportunity for sexual selection (ΔI_s), and (C) the Bateman gradient ($\Delta\beta_{ss}$). (**D** to **I**) Illustration of how sex differences in Bateman's parameters covary with (D to F) parental care and (G to I) sexual dimorphism, respectively. Error bars are 95% CIs. Different lowercase letters indicate significant differences after stepwise Bonferroni correction at α = 0.05.

variation in ΔI ($Q_M = 32.667$, df = 3, $P < 0.001$, pseudo-$R^2 = 0.20$), ΔI_s ($Q_M = 19.146$, df = 3, $P < 0.001$, pseudo-$R^2 = 0.15$), and $\Delta\beta_{ss}$ ($Q_M = 31.460$, df = 3, $P < 0.001$, pseudo-$R^2 = 0.32$), with stronger sexual selection in males of species with female-biased parental care (Fig. 2, D to F). Sexual dimorphism explained similar magnitudes of interspecific variation in all Bateman metrics of sexual selection (ΔI: $Q_M = 23.824$, df = 2, $P < 0.001$, pseudo-$R^2 = 0.15$; ΔI_s: $Q_M = 34.943$, df = 2, $P < 0.001$, pseudo-$R^2 = 0.22$; $\Delta\beta_{ss}$: $Q_M = 17.270$, df = 2, $P < 0.001$, pseudo-$R^2 = 0.14$), supporting that stronger sexual selection on males translates into male-biased sexual dimorphism.

DISCUSSION

Our findings confirm the generality of conventional sex roles in polygamous animals (Fig. 3). First, the steeper fitness increase with mating success observed for males clearly supports the Darwin-Bateman paradigm. This result is consistent with the hypothesis that sexual selection is typically stronger in the sex that produces the smaller, more abundant, and motile type of gametes (*6*), which is the male by definition. Second, our results confirm that sexual selection is evolutionarily linked to sex-biased parental care and sexual dimorphism. As predicted, stronger sexual selection on males was associated with female-biased parental care and more elaborated trait expression in males.

Larger variances in reproductive success (I) in males than in females imply that males generally exhibit larger opportunities for net selection, defined as the sum of natural selection and sexual selection (*26*). Our results support the idea that this sex bias in net selection is at least partially driven by stronger sexual selection on males as indicated by an overall steeper male β_{ss}. Estimates of β_{ss} (and I_s) capture primarily precopulatory sexual selection (*27*), and we suspect that, in terms of sperm competition and cryptic female choice (*28*), stronger

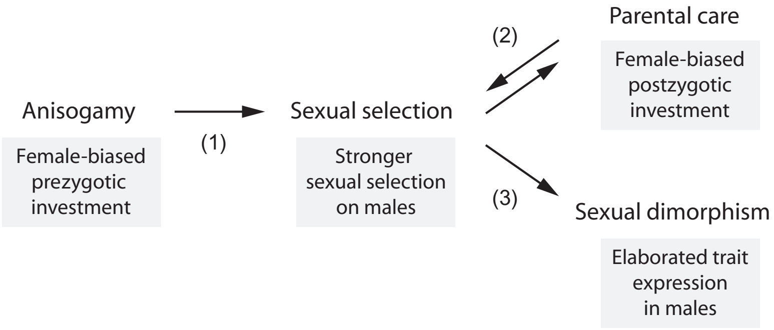

Fig. 3. The sex-role syndrome. Schematic illustration of conventional sex roles summarizing the three main findings of this study: (1) Sexual selection is stronger in males than in females, which must, by definition, be rooted in anisogamy. Stronger sexual selection on males translates in (2) female-biased parental care and (3) male-biased elaboration of traits. Arrowheads indicate direction of causality on the basis of current theory.

postcopulatory sexual selection on males represents an additional selective force, promoting stronger net selection on males. Despite these observed sex biases in I and β_{ss}, we did not detect an overall sex difference in the variance of mating success (I_s), which only showed a weak and statistically nonsignificant tendency for being larger in males. However, this lack of evidence should be interpreted with caution because the explanatory power of I_s for actual sexual selection is controversial and subject to a long-lasting debate (*29*–*31*). Overall, we believe that our analysis provides a rather conservative test for male-biased sexual selection because studies estimating Bateman's parameters in sex role–reversed species are presumably overrepresented in our data set. This is mainly because tests of theory-predicted "exceptions to the rule" are often considered as especially powerful assessments of Bateman's principles—which can motivate exploratory research in species with male-biased parental care and female-biased sexual dimorphism (*32*, *33*).

Although the here-depicted "sex role syndrome" (Fig. 3) appears generally valid for the animal kingdom, there are many exceptions emphasizing that the realized sex biases in sexual selection can still diverge from the primordial contribution of anisogamy (*34*). In many species, the sexes do not differ in the strength of sexual selection because females—just as males—benefit from multiple mating (*35*). Moreover, some taxa, for example, birds and fish, show sex role reversal with stronger sexual selection in females, male-biased parental care, and female ornaments (*36*). Other departures from the sex role syndrome include species with male-biased sexual selection in which neither sex provides parental care, suggesting that asymmetries in the strength of sexual selection do not necessarily promote, or originate from, sex biases in parental care. Finally, sex differences in sexual selection do not inevitably result in sexually dimorphic ornamentation, behavior, or morphology but may instead elicit the evolution of traits affecting post- rather than precopulatory mating success (*15*). This is especially likely for simultaneous hermaphrodites, where a sex-specific expression of secondary sexual traits is intrinsically impossible (*37*). These exceptions to the rule highlight the importance of incorporating environmental conditions when interpreting animal mating systems. There is increasing evidence that sexual selection varies not only between but also within species as a function of demographic and ecological factors (*38*, *39*), as also emphasized by gender-neutral models (*36*). However, our synthesis of current knowledge clearly rejects the hypothesis that stochasticity and environmental conditions alone can explain the observed variation in sex roles across the animal kingdom.

In conclusion, our study confirms conventional sex roles for polygamous species in accordance with the pioneering ideas by Darwin, Bateman, and Trivers. Sexual selection research over the last 150 years has not been carried out under false premises but instead is valid and provides a powerful explanation for differences between males and females. Joint efforts of empiricists and theoreticians are now needed to better understand how and to what extent the environment is modifying the evolution of sex roles beyond the intrinsic sex difference documented here.

MATERIALS AND METHODS

General approach

We performed a meta-analysis to test the generality of Bateman's principles across the animal kingdom and to explore how between-study variation in the three tested Bateman parameters translates into differences in parental care and sexual dimorphism. For this synthesis, we extracted estimates of Bateman's three parameters from the primary literature, notably the standardized variance in reproductive success (opportunity for selection, I), the standardized variance in mating success (opportunity for sexual selection, I_s), and/or the slope of an ordinary least-squares regression of reproductive success on mating success (Bateman gradient, β_{ss}) (*27*). These metrics quantify the maximum strength of selection on offspring production (I), the maximum strength of selection on mating success (I_s), and linear phenotypic selection on mating success (β_{ss}), allowing comparisons of the opportunity and strength of (sexual) selection among and within species (*25*, *27*, *40*). The potential limitations of interpretations of these measures must be kept in mind. First, both I and I_s describe upper limits to, rather than actual, (sexual) selection. Second, I_s can confound variance in mating success caused by sexual selection with variance caused by chance or sampling error, which may complicate direct comparisons between environments or species (*30*, *40*). Finally, previous quantifications of β_{ss} did not experimentally manipulate the predictor variable, mating success. Thus, β_{ss} may signify not only the strength of selection on mating success but also the effect of individual quality (in terms of reproductive output) on mating success, which has been argued to be particularly likely for females (*41*, *42*). Despite these limitations, Bateman's parameters are considered as powerful standardized metrics that are widely used to quantify sexual selection, with β_{ss} providing a particularly direct estimate of the direction and strength of sexual selection (*27*, *31*, *43*). Given their definition, all three parameters are statistically and logically intertwined so that they are expected to be correlated (*27*). We report all three parameters because they provide complementary information regarding the putative origin, strength, and consequence of sexual selection (*27*).

Literature search

The systematic literature search largely followed the PRISMA (Preferred Reporting Items for Systematic Reviews and Meta-Analyses) statement (*44*). We first identified relevant studies from ISI Web of Knowledge (Web of Science Core Collection, from 1900 to 2014) with the "topic" search terms defined as ("Bateman*" OR "opportunit* for selection" OR "opportunit* for sexual selection" OR "selection gradient*"). This literature search was initiated on 6 December 2012 and repeated on 25 April 2015. Further, we posted a request for "gray" literature and unpublished data sets on the "EvolDir" mailing list (http://evol.mcmaster.ca/evoldir.html) on 4 December 2012.

This search protocol identified 2159 candidate studies (database search: 2159 candidates; gray literature and unpublished data: 0 candidates). We added 22 studies to this candidate pool based on downward citation searches using the candidates identified with ISI Web of Knowledge (fig. S1). All studies (n = 2181) were then screened and assessed for eligibility to comply with two inclusion criteria. First, we considered only studies reporting estimates of I_s and/or β_{ss}. Studies exclusively providing estimates of I, and thus the opportunity for net selection rather than sexual selection, were excluded (n = 42). Second, given our focus on the sex differences in Bateman metrics, we excluded studies reporting estimates for only one sex (n = 53). Restricting our analysis to paired comparisons minimizes problems associated with potential publication biases resulting from a tendency for studying only the sex of a given species for which there is at least circumstantial evidence for mate choice—an issue that has been raised recently (*45*) in response to a meta-analysis providing no support for a sex-biased strength of mate choice (*46*).

We excluded three studies because of specificities of the experimental design questioning the reliability or the comparability of the provided Bateman's parameters (*6*, *47*, *48*). This includes Bateman's original study for reasons reported elsewhere (*17*). We retained a sample of n = 72 studies, covering 66 species and providing 81, 88, and 76 estimates (hereafter K) for male and female I, I_s, and β_{ss}, respectively (table S1). For 43 of these studies, we were unable to compute effect sizes based on the information reported in a given article. We then either ran additional analysis based on raw data presented in tables or extracted them from graphs using the imaging software GraphClick version 3.0.2 (www.arizona-software.ch) (K = 25), or we requested additional information directly from the authors (K = 18).

The majority of the extracted estimates of mating success relied on molecular parentage assignment and reflected the number of genetic partners (that is, the number of individuals in the population that share at least one offspring with a given focal individual; K = 64) rather than the actual number of copulation partners (K = 13) or the number of copulations (K = 19). Using the number of genetic partners as an estimate of mating success bears the risk of biasing I, I_s, and β_{ss} for males and females. Specifically, in cases where males mate often and sperm usage skewed toward few males in the population (for example, because of variation in sperm competitiveness among males and/or cryptic female choice), both males and females obtain lower fitness returns per actual mating partner compared to the return per genetic mating partner, leading to an overestimation of β_{ss} when it is estimated using genetic mating success. However, this source of overestimation is likely to apply to both sexes and therefore does not necessarily translate into a systematic bias in the sex difference of I, I_s, and β_{ss} (*49*, *50*), which are the target variables of this study (see below). A more serious problem arises from studies in which reproductive success of one sex (typically the male) is estimated with larger measurement error than the one of the other sex. For instance, if paternity assignment is based on a fraction of actually sired offspring, then the variance in male reproductive success suffers from a binomial sampling error, which may affect the sex bias in I, I_s, and β_{ss}. This issue has been addressed in more recent empirical tests of Bateman's principles (*50*–*53*), suggesting that it can affect the magnitude but not the direction of the sex difference in I, I_s, and β_{ss}.

Moderator variables: Parental care and sexual dimorphism

For all species, we classified sex biases in parental care and sexual dimorphism on the basis of published data (table S1). Specifically, we assigned species to four categories of postzygotic parental investment including "no care" (neither sex provides care; K = 36), "male-only care" (only males provide care; K = 16), "biparental care" (both sexes provide care; K = 21), and "female-only care" (only females provide care; K = 23) (*54*). Sexual dimorphism was classified for all species using three categories: "male-biased" (K = 61), "none" (K = 20), and "female-biased" (K = 15) sexual dimorphism. This classification accounts for dimorphism in secondary sexually selected characters encompassing behavior (for example, courtship and acoustic signals), ornamentation (for example, pigmentation), and morphology (for example, armaments). We excluded sexual size dimorphism because it often results from fecundity selection and therefore lacks a predictable overall directionality in response to sexual selection (*55*, *56*). More precisely, we first scored the sex bias in behavior, ornamentation, and morphology separately on the basis of primary literature, coded as male-biased = 1, unbiased = 0, and female-biased = −1. We then computed average scores and classified positive values as male-biased and negative values as female-biased. Species with an average score of zero were rated as nonsexually dimorphic.

Computation of effect sizes

We defined effect sizes for the sex bias in I, I_s, and β_{ss} as ΔI, ΔI_s, and $\Delta\beta_{ss}$, respectively, with positive values indicating a male bias. ΔI and ΔI_s were assessed using the coefficient of variation ratio "lnCVR," defined as the natural logarithm of the ratio between the coefficients of variation from two groups (*57*). The effect size $\Delta\beta_{ss}$ was computed as Hedges' d (*58*), which we converted from t or F statistics used to compare male and female Bateman gradients in the primary studies (*59*). Variances of lnCVR and Hedges' d were computed as described elsewhere (*57*, *59*). All effect sizes were highly correlated with each other (Spearman correlation: ΔI versus ΔI_s: $\rho = 0.661$, $P < 0.001$, $K = 76$; ΔI versus $\Delta\beta_{ss}$: $\rho = 0.768$, $K = 73$, $P < 0.001$; $\Delta\beta_{ss}$ versus ΔI_s: $\rho = 0.484$, $K = 68$, $P < 0.001$; fig. S2).

Phylogenetic affinities

Traditional meta-analysis revealed that higher-order taxonomic groups differed in ΔI ($Q_M = 18.950$, df = 5, $P = 0.002$, $R^2 = 0.24$; taxa with fewer than five species excluded from all analyses) and $\Delta\beta_{ss}$ ($Q_M = 13.460$, df = 5, $P = 0.019$, $R^2 = 0.06$) but not in ΔI_s ($Q_M = 8.001$, df = 5, $P = 0.156$, $R^2 = 0.04$). These differences among taxa were largely driven by the near-zero estimates for ΔI and $\Delta\beta_{ss}$ in bony fishes (fig. S3). To account for phylogenetic nonindependence (that is, phylogenetic signals of higher- and lower-order taxa) and for multiple estimates obtained from a single species, we reconstructed the phylogeny of all included species and ran a phylogenetically independent meta-analysis (*60*). For this, we reconstructed a phylogeny (fig. S4) based on divergence times retrieved from the TimeTree database (*61*) (expert results) complemented with information from additional primary studies [that is, Pulmonata (*62*), Coenagrionidae (*63*), Heteroptera (*64*), Bruchinae (*65*), Strongylocentrotidae (*66*), Osteichthyes (*67*–*69*), Anura (*70*), Lacertidae (*71*), and Rodentia (*72*, *73*)]. We aged undated nodes on the basis of the divergence dates of neighboring nodes using the Branch Length Adjuster (BLADJ) algorithm (*74*). Using a phylogenetically controlled meta-analysis allows testing of the hypothesis of sex-specific sexual selection based on our current knowledge while correcting for potential publication biases toward taxa showing a particular form of sex-specific sexual selection (that is, taxa with particularly strong male- or female-biased sexual selection such as fruit flies of the genus *Drosophila* or pipefishes of the genus *Syngnathus*, respectively).

Statistical analysis

Multivariate linear mixed-effects models were performed using the R package metafor version 1.9.2 (*75*). Specifically, our phylogenetic meta-analyses incorporated a restricted maximum likelihood–based estimate of the between-study variance (as is typically required for random-effects modeling) as well as species and phylogeny as separate random factors using the rma.mv function. The species random factor modeled multiple effect sizes from the same species, and the phylogeny was treated as an unstructured variance-covariance matrix assuming phylogenetic correlations derived from a Brownian motion model of evolution (*60*, *76*). First, we ran a random-effects model without any moderator variable to test for the overall sex biases in I, I_s, and β_{ss} across all species and for heterogeneity among studies. Second, we explored how sex-biased parental care and sexual dimorphism translate into sex-specific sexual selection. Because these two predictors are correlated (Pearson χ^2 test: $\chi^2 = 63.103$, df = 6, $P < 0.001$), we analyzed the moderator variables parental care and sexual dimorphism in separate models to avoid problems arising from multicollinearity (*77*). We quantified the explained variance of both moderator variables using McFadden's pseudo-R^2 (*78*).

We evaluated publication bias on the basis of visual inspection of funnel plots and Kendall rank correlation tests for funnel plot asymmetry between effect sizes and their SEs (*79*). Rank correlation tests were carried out on raw effect sizes and so-called meta-analytic residuals obtained from models, including parental care or sexual size dimorphism as a moderator variable (*80*). We found no evidence for significant publication bias for ΔI and $\Delta\beta_{ss}$ based on funnel plot asymmetry using raw effect sizes or meta-analytic residuals (rank correlation tests, raw effect sizes: ΔI: Kendall $\tau = 0.035$, $P = 0.652$; β_{ss}: Kendall $\tau = 0.044$, $P = 0.576$; meta-analytic residuals accounting for parental care: ΔI: Kendall $\tau = -0.031$, $P = 0.687$; $\Delta\beta_{ss}$: Kendall $\tau = -0.051$, $P = 0.523$; meta-analytic residuals accounting for sexual dimorphism: ΔI: Kendall $\tau = 0.061$, $P = 0.423$; $\Delta\beta_{ss}$: Kendall $\tau = -0.114$, $P = 0.145$; fig. S5, A to C and G to I). However, ΔI_s was slightly biased toward positive estimates with large SEs, suggesting moderate publication bias (rank correlation tests, raw effect sizes: Kendall $\tau = 0.147$, $P = 0.042$; meta-analytic residuals accounting for parental care: Kendall $\tau = 0.149$, $P = 0.040$; meta-analytic residuals accounting for sexual dimorphism: Kendall $\tau = 0.241$, $P = 0.001$; fig. S5, E to G). Thus, findings regarding ΔI_s need to be considered with caution.

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at http://advances.sciencemag.org/cgi/content/full/2/2/e1500983/DC1

Fig. S1. PRISMA diagram depicting the data flow through the different phases of the meta-analysis.

Fig. S2. Bivariate correlations of the effect sizes for sex differences in the three Bateman metrics, showing (A) ΔI versus ΔI_s, (B) ΔI versus $\Delta\beta_{ss}$, and (C) ΔI_s versus $\Delta\beta_{ss}$.

Fig. S3. Comparison of (A) ΔI, (B) ΔI_s, and (C) $\Delta\beta_{ss}$ between higher-order taxa [taxa with $K < 5$ excluded: platyhelminthes ($K = 1$), molluscs ($K = 4$), and echinoderms ($K = 2$)].

Fig. S4. Phylogenetic tree of all species included in the meta-analysis.

Fig. S5. Funnel plots for (A to C) ΔI, (D to F) ΔI_s, and (G to I) $\Delta\beta_{ss}$.

Table S1. List of all primary studies included in the meta-analysis.

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