

Darwinian sex roles confirmed across the animal kingdom

Tim Janicke,^{1*} Ines K. Häderer,² Marc J. Lajeunesse,³ Nils Anthes²

2016 © The Authors, some rights reserved; exclusive licensee American Association for the Advancement of Science. Distributed under a Creative Commons Attribution NonCommercial License 4.0 (CC BY-NC). 10.1126/sciadv.1500983

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 pre-copulatory 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

¹Centre d'Écologie Fonctionnelle et Évolutive, UMR 5175, CNRS, Université de Montpellier, Université Paul-Valéry Montpellier, École Pratique des Hautes Études, 1919 Route de Mende, 34293 Montpellier Cedex 05, France. ²Animal Evolutionary Ecology Group, Institute for Evolution and Ecology, University of Tübingen, Auf der Morgenstelle 28, 72076 Tübingen, Germany. ³Department of Integrative Biology, University of South Florida, Tampa, FL 33620, USA. *Corresponding author. E-mail: tim.janicke@cefe.cnrs.fr

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 : $\ln\text{CVR} \pm \text{SE}$: 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’ $d \pm \text{SE}$: 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 : $\ln\text{CVR} \pm \text{SE}$: 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 : $Q = 731.063$, $\text{df} = 80$, $P < 0.001$; ΔI_s : $Q = 984.471$, $\text{df} = 87$, $P < 0.001$; and $\Delta\beta_{ss}$: $Q = 541.216$, $\text{df} = 75$, $P < 0.001$; Fig. 1). Parental care explained a significant fraction of the observed

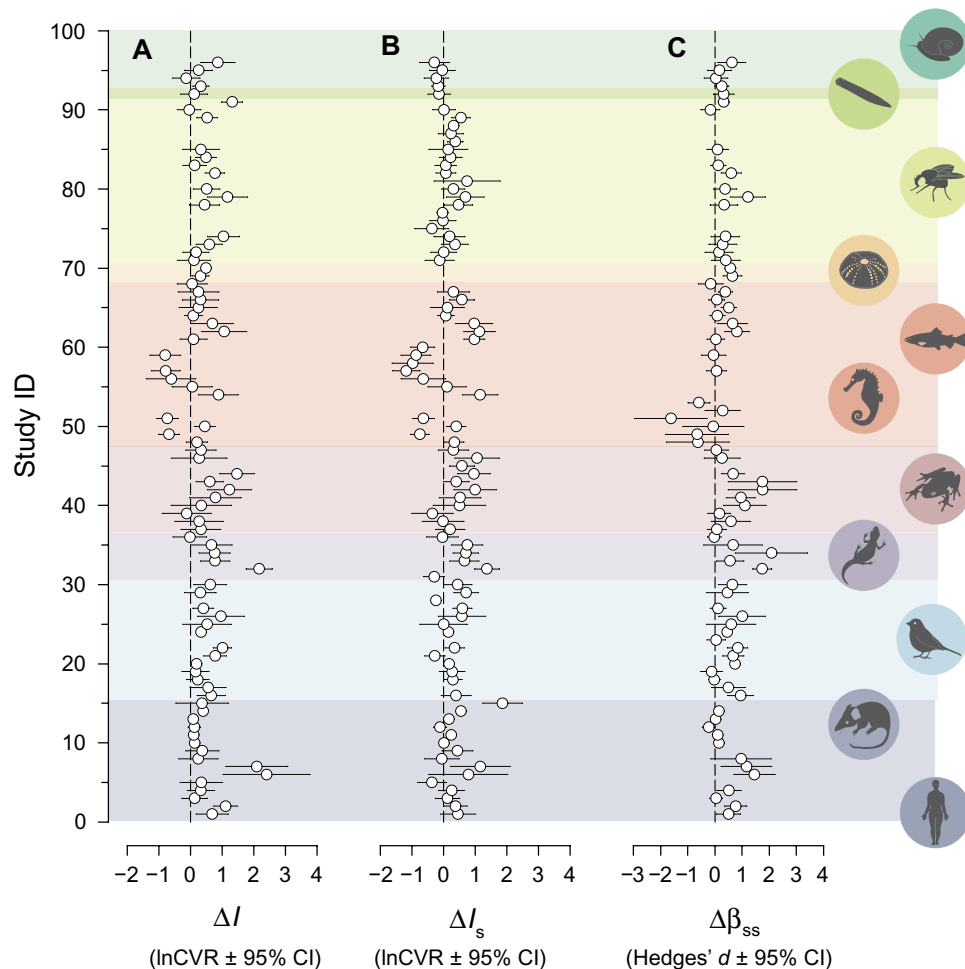


Fig. 1. Sex-biased sexual selection across the animal kingdom. (A to C) Forest plots showing estimates of the sex bias in (A) the opportunity for selection (ΔI), (B) the opportunity for sexual selection (ΔI_s), and (C) the Bateman gradient ($\Delta\beta_{ss}$). Effect sizes ($\ln\text{CVR}$ and Hedges’ 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).

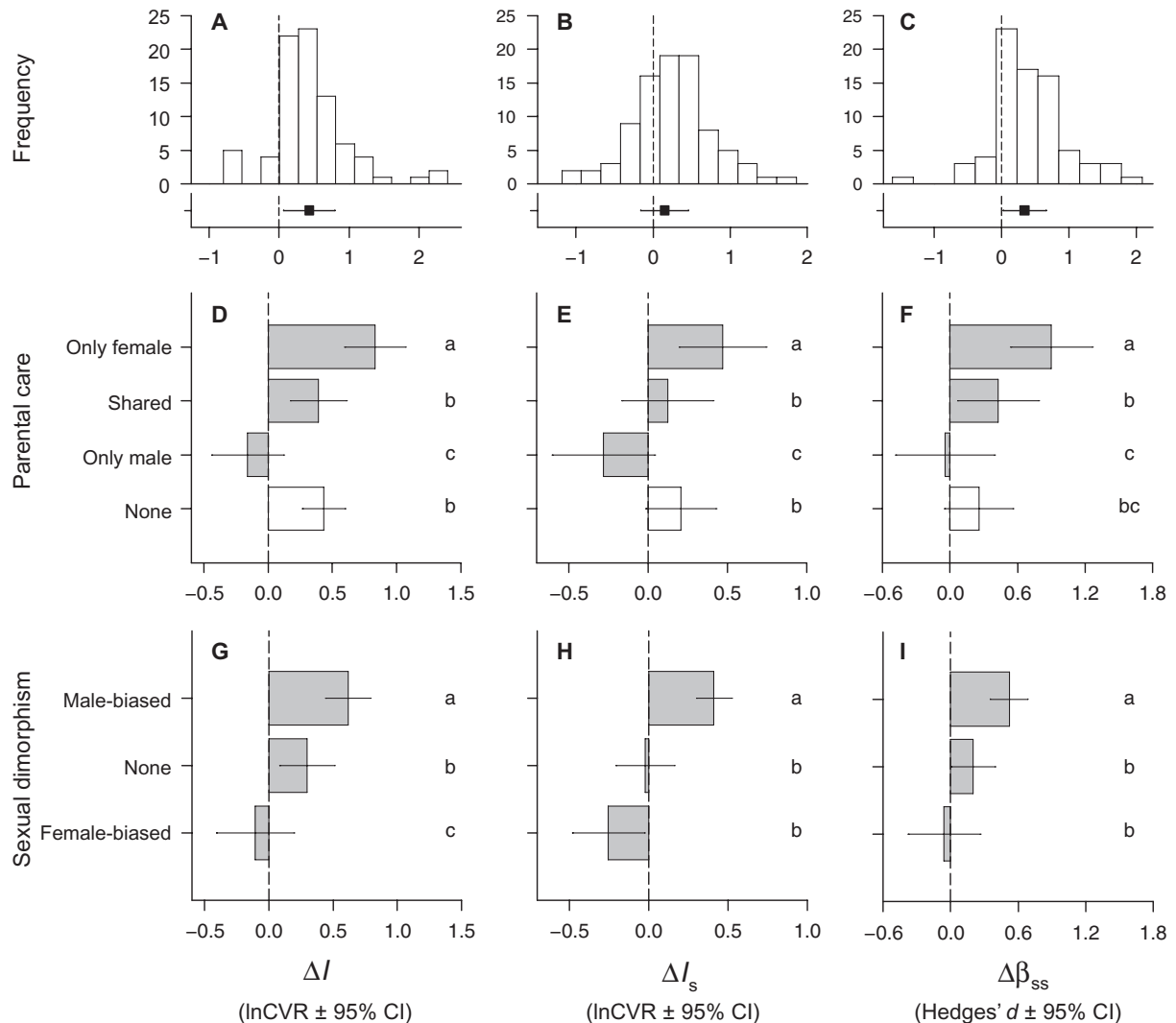


Fig. 2. Sex-biased sexual selection and its evolutionary link to parental care and sexual dimorphism. (A to C) Frequency distributions and global mean effect sizes (filled squares) for sex differences in (A) the opportunity for selection (ΔI), (B) the opportunity for sexual selection (ΔI_s), and (C) 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 $\alpha = 0.05$.

variation in ΔI ($Q_M = 32.667$, $df = 3$, $P < 0.001$, $\text{pseudo-}R^2 = 0.20$), ΔI_s ($Q_M = 19.146$, $df = 3$, $P < 0.001$, $\text{pseudo-}R^2 = 0.15$), and $\Delta \beta_{ss}$ ($Q_M = 31.460$, $df = 3$, $P < 0.001$, $\text{pseudo-}R^2 = 0.32$), 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 : $Q_M = 23.824$, $df = 2$, $P < 0.001$, $\text{pseudo-}R^2 = 0.15$; ΔI_s : $Q_M = 34.943$, $df = 2$, $P < 0.001$, $\text{pseudo-}R^2 = 0.22$; $\Delta \beta_{ss}$: $Q_M = 17.270$, $df = 2$, $P < 0.001$, $\text{pseudo-}R^2 = 0.14$), 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

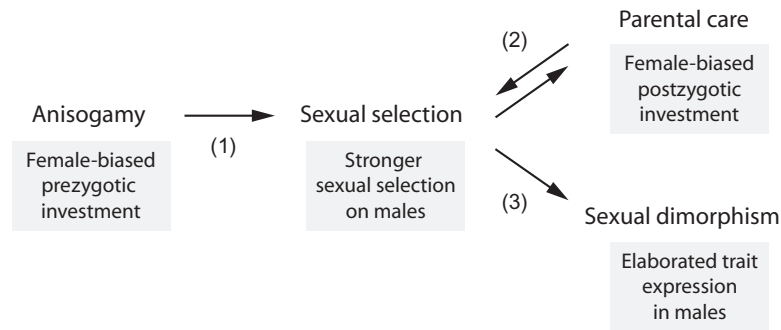


Fig. 3. The sex-role syndrome. Schematic illustration of conventional sex roles summarizing the three main findings of this study: (1) Sexual selection is stronger in males than in females, which must, by definition, be rooted in anisogamy. Stronger sexual selection on males translates in (2) female-biased 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: plathelminthes ($K = 1$), 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.

References (81–222)

REFERENCES AND NOTES

1. A. H. Eagly, W. Wood, The origins of sex differences in human behavior: Evolved dispositions versus social roles. *Am. Psychol.* **54**, 408–423 (1999).
2. E. H. Morrow, The evolution of sex differences in disease. *Biol. Sex Differ.* **6**, 5 (2015).
3. M. Andersson, Sexual selection, in *Monographs in Behavior and Ecology*, J. R. Krebs, T. Clutton-Brock, Eds. (Princeton Univ. Press, Princeton, NJ, 1994).
4. J. Knight, Sexual stereotypes. *Nature* **415**, 254–256 (2002).
5. C. R. Darwin, *The Descent of Man, and Selection in Relation to Sex* (John Murray, London, 1871).
6. A. J. Bateman, Intra-sexual selection in *Drosophila*. *Heredity* **2**, 349–368 (1948).
7. S. J. Arnold, Bateman's principles and the measurement of sexual selection in plants and animals. *Am. Nat.* **144**, S126–S149 (1994).
8. G. A. Parker, T. R. Birkhead, Polyandry: The history of a revolution. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **368**, 20120335 (2013).
9. D. A. Dewsbury, The Darwin-Bateman paradigm in historical context. *Integr. Comp. Biol.* **45**, 831–837 (2005).
10. R. L. Trivers, in *Sexual Selection and the Descent of Man*, B. Campbell, Ed. (Aldine Publishing Company, Chicago, 1972), pp. 136–179.
11. D. C. Queller, Why do females care more than males? *Proc. R. Soc. B Biol. Sci.* **264**, 1555–1557 (1997).
12. H. Kokko, M. D. Jennions, Parental investment, sexual selection and sex ratios. *J. Evol. Biol.* **21**, 919–948 (2008).
13. H. Kokko, H. Klug, M. D. Jennions, Unifying cornerstones of sexual selection: Operational sex ratio, Bateman gradient and the scope for competitive investment. *Ecol. Lett.* **15**, 1340–1351 (2012).
14. A. V. Hedrick, E. J. Temeles, The evolution of sexual dimorphism in animals: Hypotheses and tests. *Trends Ecol. Evol.* **4**, 136–138 (1989).
15. G. A. Parker, The sexual cascade and the rise of pre-ejaculatory (Darwinian) sexual selection, sex roles, and sexual conflict. *Cold Spring Harb. Perspect. Biol.* **6**, a017509 (2014).
16. B. F. Snyder, P. A. Gowaty, A reappraisal of Bateman's classic study of intrasexual selection. *Evolution* **61**, 2457–2468 (2007).
17. P. A. Gowaty, Y.-K. Kim, W. W. Anderson, No evidence of sexual selection in a repetition of Bateman's classic study of *Drosophila melanogaster*. *Proc. Natl. Acad. Sci. U.S.A.* **109**, 11740–11745 (2012).
18. Z. Tang-Martinez, in *Encyclopedia of Animal Behavior*, M. D. Breed, J. Moore, Eds. (Academic Press, Oxford, 2010), pp. 166–176.
19. G. Arnqvist, T. Nilsson, The evolution of polyandry: Multiple mating and female fitness in insects. *Anim. Behav.* **60**, 145–164 (2000).
20. D. A. Dewsbury, Ejaculate cost and male choice. *Am. Nat.* **119**, 601–610 (1982).
21. Z. Tang-Martinez, Repetition of Bateman challenges the paradigm. *Proc. Natl. Acad. Sci. U.S.A.* **109**, 11476–11477 (2012).
22. S. P. Hubbell, L. K. Johnson, Environmental variance in lifetime mating success, mate choice, and sexual selection. *Am. Nat.* **130**, 91–112 (1987).
23. P. A. Gowaty, S. P. Hubbell, Reproductive decisions under ecological constraints: It's about time. *Proc. Natl. Acad. Sci. U.S.A.* **106**, 10017–10024 (2009).
24. J. Roughgarden, in *Current Perspectives on Sexual Selection. What's Left After Darwin?*, T. Hoquet, Ed. (Springer, Dordrecht, 2015), pp. 85–102.
25. K. B. Mobley, in *Animal Behaviour: How and Why Animals Do the Things They Do*, K. Yasukawa, Ed. (Praeger, Santa Barbara, 2014), pp. 99–144.
26. D. J. Hosken, C. M. House, Sexual selection. *Curr. Biol.* **21**, R62–R65 (2011).

27. A. G. Jones, On the opportunity for sexual selection, the Bateman gradient and the maximum intensity of sexual selection. *Evolution* **63**, 1673–1684 (2009).
28. T. R. Birkhead, T. Pizzari, Postcopulatory sexual selection. *Nat. Rev. Genet.* **3**, 262–273 (2002).
29. W. J. Sutherland, Chance can produce a sex difference in variance in mating success and explain Bateman's data. *Anim. Behav.* **33**, 1349–1352 (1985).
30. H. Klug, J. Heuschele, M. D. Jennions, H. Kokko, The mismeasurement of sexual selection. *J. Evol. Biol.* **23**, 447–462 (2010).
31. A. H. Krakauer, M. S. Webster, E. H. Duval, A. G. Jones, S. M. Shuster, The opportunity for sexual selection: Not mismeasured, just misunderstood. *J. Evol. Biol.* **24**, 2064–2071 (2011).
32. A. G. Jones, G. Rosenqvist, A. Berglund, S. J. Arnold, J. C. Avise, The Bateman gradient and the cause of sexual selection in a sex–role–reversed pipefish. *Proc. Biol. Sci.* **267**, 677–680 (2000).
33. S. T. Emlen, P. H. Wrege, Size dimorphism, intrasexual competition, and sexual selection in Wattled Jacana (*Jacana jacana*), a sex-role-reversed shorebird in Panama. *Auk* **121**, 391–403 (2004).
34. L. Schärer, L. Rowe, G. Arnqvist, Anisogamy, chance and the evolution of sex roles. *Trends Ecol. Evol.* **27**, 260–264 (2012).
35. T. Clutton-Brock, Sexual selection in females. *Anim. Behav.* **77**, 3–11 (2009).
36. M. Ah-King, S. Nylin, Sex in an evolutionary perspective: Just another reaction norm. *Evol. Biol.* **37**, 234–246 (2010).
37. L. Schärer, T. Janicke, S. A. Ramm, Sexual conflict in hermaphrodites. *Cold Spring Harb. Perspect. Biol.* **7**, a017673 (2015).
38. T. Janicke, P. David, E. Chapuis, Environment-dependent sexual selection: Bateman's parameters under varying levels of food availability. *Am. Nat.* **185**, 756–768 (2015).
39. S. C. Mills, A. Grapputo, E. Koskela, T. Mappes, Quantitative measure of sexual selection with respect to the operational sex ratio: A comparison of selection indices. *Proc. Biol. Sci.* **274**, 143–150 (2007).
40. M. D. Jennions, H. Kokko, H. Klug, The opportunity to be misled in studies of sexual selection. *J. Evol. Biol.* **25**, 591–598 (2012).
41. E. D. Ketterson, P. G. Parker, S. A. Raouf, V. Nolan Jr., C. Ziegenfuss, C. H. Chandler, in *Avian Reproductive Tactics: Female and Male Perspectives*, P. G. Parker, N. T. Burley, Eds. (Allen Press, Lawrence, KS, 1998), pp. 81–101.
42. N. M. Gerlach, J. W. McGlothlin, P. G. Parker, E. D. Ketterson, Reinterpreting Bateman gradients: Multiple mating and selection in both sexes of a songbird species. *Behav. Ecol.* **23**, 1078–1088 (2012).
43. M. D. Jennions, H. Kokko, in *Evolutionary Behavioural Ecology*, D. F. Westneat, C. W. Fox, Eds. (Oxford Univ. Press, Oxford, 2010), pp. 343–364.
44. D. Moher, A. Liberati, J. Tetzlaff, D. G. Altman; PRISMA Group, Preferred reporting items for systematic reviews and meta-analyses: The PRISMA Statement. *PLoS Med.* **6**, e1000097 (2009).
45. H. Kokko, M. D. Jennions, Describing mate choice in a biased world: Comments on Edward and Dougherty & Shuker. *Behav. Ecol.* **26**, 320–321 (2015).
46. L. R. Dougherty, D. M. Shuker, The effect of experimental design on the measurement of mate choice: A meta-analysis. *Behav. Ecol.* **26**, 311–319 (2015).
47. P. D. Lorch, Using upper limits of “Bateman gradients” to estimate the opportunity for sexual selection. *Integr. Comp. Biol.* **45**, 924–930 (2005).
48. M. E. Hauber, Fame, fortune, and fitness at the Academy Awards. *J. Ethol.* **25**, 201–204 (2007).
49. J. M. Collet, R. F. Dean, K. Worley, D. S. Richardson, T. Pizzari, The measure and significance of Bateman's principles. *Proc. Biol. Sci.* **281**, 20132973 (2014).
50. B. Péliissié, P. Jarne, P. David, Sexual selection without sexual dimorphism: Bateman gradients in a simultaneous hermaphrodite. *Evolution* **66**, 66–81 (2012).
51. K. B. Mobley, A. G. Jones, Overcoming statistical bias to estimate genetic mating systems in open populations: A comparison of Bateman's principles between the sexes in a sex-role-reversed pipefish. *Evolution* **67**, 646–660 (2013).
52. A. G. Jones, BATEMANATER: A computer program to estimate and bootstrap mating system variables based on Bateman's principles. *Mol. Ecol. Resour.* **15**, 1396–1402 (2015).
53. B. A. Levine, C. F. Smith, G. W. Schuett, M. R. Douglas, M. A. Davis, M. E. Douglas, Bateman-Trivers in the 21st century: Sexual selection in a North American pitvip. *Biol. J. Linn. Soc.* **114**, 436–445 (2015).
54. A. Cockburn, Prevalence of different modes of parental care in birds. *Proc. Biol. Sci.* **273**, 1375–1383 (2006).
55. R. Shine, Ecological causes for the evolution of sexual dimorphism: A review of the evidence. *Q. Rev. Biol.* **64**, 419–461 (1989).
56. R. M. Cox, S. L. Skelly, H. B. John-Alder, A comparative test of adaptive hypotheses for sexual size dimorphism in lizards. *Evolution* **57**, 1653–1669 (2003).
57. S. Nakagawa, R. Poulin, K. Mengersen, K. Reinhold, L. Engqvist, M. Lagisz, A. M. Senior, Meta-analysis of variation: Ecological and evolutionary applications and beyond. *Methods Ecol. Evol.* **6**, 143–152 (2015).
58. L. Hedges, I. Olkin, *Statistical Methods for Meta-Analysis* (Academic Press, New York, 1985).
59. M. J. Lajeunesse, in *Handbook of Meta-analysis in Ecology and Evolution*, J. Koricheva, J. Gurevitch, K. Mengersen, Eds. (Princeton Univ. Press, Princeton, NJ, 2013), pp. 195–206.
60. M. J. Lajeunesse, M. S. Rosenberg, M. D. Jennions, in *Handbook of Meta-analysis in Ecology and Evolution*, J. Koricheva, J. Gurevitch, K. Mengersen, Eds. (Princeton Univ. Press, Princeton, NJ, 2013), pp. 284–299.
61. S. B. Hedges, J. Dudley, S. Kumar, TimeTree: A public knowledge-base of divergence times among organisms. *Bioinformatics* **22**, 2971–2972 (2006).
62. P. Jarne, P. David, J.-P. Pointier, J. M. Koene, in *The Evolution of Primary Sexual Characters in Animals*, J. L. Leonard, A. Córdoba-Aguilar, Eds. (Oxford Univ. Press, New York, 2010), pp. 173–196.
63. J. Swaegers, S. B. Janssens, S. Ferreira, P. C. Watts, J. Mergeay, M. A. McPeck, R. Stoks, Ecological and evolutionary drivers of range size in *Coenagrion* damselflies. *J. Evol. Biol.* **27**, 2386–2395 (2014).
64. M. Li, Y. Tian, Y. Zhao, W. Bu, Higher level phylogeny and the first divergence time estimation of heteroptera (Insecta: Hemiptera) based on multiple genes. *PLOS One* **7**, e32152 (2012).
65. G. J. Kerfoot, B. P. Le Ru, G. Genson, C. Cruaud, A. Couloux, A. Delobel, Phylogenetics, species boundaries and timing of resource tracking in a highly specialized group of seed beetles (Coleoptera: Chrysomelidae: Bruchinae). *Mol. Phylogenet. Evol.* **59**, 746–760 (2011).
66. Y.-H. Lee, Molecular phylogenies and divergence times of sea urchin species of Strongylocentrotidae. *Mol. Biol. Evol.* **20**, 1211–1221 (2003).
67. R. Betancur-R, R. E. Broughton, E. O. Wiley, K. Carpenter, J. A. López, C. Li, N. I. Holcroft, D. Arcila, M. Sanciangco, J. C. Cureton II, F. Zhang, T. Buser, M. A. Campbell, J. A. Ballesteros, A. Roa-Varon, S. Willis, W. C. Borden, T. Rowley, P. C. Reneau, D. J. Hough, G. Lu, T. Grande, G. Arratia, G. Ortí, The tree of life and a new classification of bony fishes. *PLOS Curr.* **5**, ecurrents.tol.53ba26640df0c8ae75bb165c8c26288 (2013).
68. P. R. Teske, L. B. Beheregaray, Evolution of seahorses' upright posture was linked to Oligocene expansion of seagrass habitats. *Biol. Lett.* **5**, 521–523 (2009).
69. S. V. Shedko, I. L. Miroshnichenko, G. A. Nemkova, Phylogeny of salmonids (Salmoniformes: Salmonidae) and its molecular dating: Analysis of nuclear *RAG1* gene. *Russ. J. Genet.* **48**, 575–579 (2012).
70. R. A. Pyron, J. J. Wiens, A large-scale phylogeny of Amphibia including over 2800 species, and a revised classification of extant frogs, salamanders, and caecilians. *Mol. Phylogenet. Evol.* **61**, 543–583 (2011).
71. S. Carranza, E. N. Arnold, F. Amat, DNA phylogeny of *Lacerta* (*Iberolacerta*) and other lacertine lizards (Reptilia: Lacertidae): Did competition cause long-term mountain restriction? *Syst. Biodivers.* **2**, 57–77 (2004).
72. N. Lartillot, F. Delsuc, Joint reconstruction of divergence times and life-history evolution in placental mammals using a phylogenetic covariance model. *Evolution* **66**, 1773–1787 (2012).
73. R. G. Harrison, S. M. Bogdanowicz, R. S. Hoffmann, E. Yensen, P. W. Sherman, Phylogeny and evolutionary history of the ground squirrels (Rodentia: Marmotinae). *J. Mamm. Evol.* **10**, 249–276 (2003).
74. C. O. Webb, D. D. Ackery, S. W. Kembel, Phylocom: Software for the analysis of phylogenetic community structure and trait evolution. *Bioinformatics* **24**, 2098–2100 (2008).
75. W. Viechtbauer, Conducting meta-analyses in R with the metafor package. *J. Stat. Softw.* **36**, 1–48 (2010).
76. M. J. Lajeunesse, Meta-analysis and the comparative phylogenetic method. *Am. Nat.* **174**, 369–381 (2009).
77. M. H. Graham, Confronting multicollinearity in ecological multiple regressions. *Ecology* **84**, 2809–2815 (2003).
78. R. R. Sokal, F. J. Rohlf, *Biometry: The Principles and Practice of Statistics in Biological Research* (W. H. Freeman and Co., New York, ed. 4, 2012), p. 937.
79. C. B. Begg, M. Mazumdar, Operating characteristics of a rank correlation test for publication bias. *Biometrics* **50**, 1088–1101 (1994).
80. S. Nakagawa, E. S. A. Santos, Methodological issues and advances in biological meta-analysis. *Evol. Ecol.* **26**, 1253–1274 (2012).
81. K. E. Munroe, J. L. Koprowski, Sociality, Bateman's gradients, and the polygynandrous genetic mating system of round-tailed ground squirrels (*Xerospermophilus tereticaudus*). *Behav. Ecol. Sociobiol.* **65**, 1811–1824 (2011).
82. K. A. Ernest, M. A. Mares, *Spermophilus tereticaudus*. *Mamm. Species* **274**, 1–9 (1987).
83. P. H. Jones, J. L. Van Zant, F. S. Dobson, Variation in reproductive success of male and female Columbian ground squirrels (*Urociellus columbianus*). *Can. J. Zool.* **90**, 736–743 (2012).
84. C. L. Elliott, J. T. Flinders, *Spermophilus columbianus*. *Mamm. Species* **372**, 1–9 (1991).
85. P. Bergeron, P.-O. Montiglio, D. Réale, M. M. Humphries, D. Garant, Bateman gradients in a promiscuous mating system. *Behav. Ecol. Sociobiol.* **66**, 1125–1130 (2012).
86. L. Elliott, *Social Behavior and Foraging Ecology of the Eastern Chipmunk* (*Tamias striatus*) in the Adirondack Mountains (Smithsonian Contributions in Zoology, Smithsonian Institution Press, Washington, 1978).

87. D. P. Snyder, *Tamias striatus*. *Mamm. Species* **168**, 1–8 (1982).
88. A. I. Schulte–Hostedde, J. S. Millar, H. L. Gibbs, Sexual selection and mating patterns in a mammal with female-biased sexual size dimorphism. *Behav. Ecol.* **15**, 351–356 (2004).
89. D. A. Sutton, *Tamias amoenus*. *Mamm. Species* **390**, 1–8 (1992).
90. D. O. Ribble, Lifetime reproductive success and its correlates in the monogamous rodent, *Peromyscus californicus*. *J. Anim. Ecol.* **61**, 457–468 (1992).
91. D. J. Gubernick, J. R. Alberts, The biparental care system of the California mouse, *Peromyscus californicus*. *J. Comp. Psychol.* **101**, 169–177 (1987).
92. J. F. Merritt, *Peromyscus californicus*. *Mamm. Species* **85**, 1–6 (1978).
93. T. J. Horne, H. Ylonen, Female bank voles (*Clethrionomys glareolus*) prefer dominant males; but what if there is no choice? *Behav. Ecol. Sociobiol.* **38**, 401–405 (1996).
94. K. J. Nutt, Genetic reconstruction of breeding patterns in gundis (Rodentia: Ctenodactylidae). *Behav. Ecol. Sociobiol.* **61**, 1651–1663 (2007).
95. K. J. Nutt, Philopatry of both sexes leads to the formation of multimale, multifemale groups in *Ctenodactylus gundi* (Rodentia: Ctenodactylidae). *J. Mammal.* **86**, 961–968 (2005).
96. M. Jokela, A. Rotkirch, I. J. Rickard, J. Pettay, V. Lummaa, Serial monogamy increases reproductive success in men but not in women. *Behav. Ecol.* **21**, 906–912 (2010).
97. A. F. Dixon, *Sexual Selection and the Origins of Human Mating Systems* (Oxford Univ. Press, Oxford, 2009).
98. A. Courtiol, J. E. Pettay, M. Jokela, A. Rotkirch, V. Lummaa, Natural and sexual selection in a monogamous historical human population. *Proc. Natl. Acad. Sci. U.S.A.* **109**, 8044–8049 (2012).
99. M. Borgerhoff Mulder, Serial monogamy as polygyny or polyandry?: Marriage in the Tanzanian Pimbwe. *Hum. Nat.* **20**, 130–150 (2009).
100. J. A. Moorad, D. E. L. Promislow, K. R. Smith, M. J. Wade, Mating system change reduces the strength of sexual selection in an American frontier population of the 19th century. *Evol. Hum. Behav.* **32**, 147–155 (2011).
101. J. Byers, S. Dunn, Bateman in nature: Predation on offspring reduces the potential for sexual selection. *Science* **338**, 802–804 (2012).
102. B. W. O’Gara, *Antilocapra americana*. *Mamm. Species* **90**, 1–7 (1987).
103. B. E. Byers, H. L. Mays Jr., I. R. K. Stewart, D. F. Westneat, Extrapair paternity increases variability in male reproductive success in the chestnut-sided warbler (*Dendroica pensylvanica*), a socially monogamous songbird. *Auk* **121**, 788–795 (2004).
104. L. A. Whittingham, P. O. Dunn, Effects of extra-pair and within-pair reproductive success on the opportunity for selection in birds. *Behav. Ecol.* **16**, 138–144 (2005).
105. K. A. Peterson, K. J. Thusius, L. A. Whittingham, P. O. Dunn, Allocation of male parental care in relation to paternity within and among broods of the common yellowthroat (*Geothlypis trichas*). *Ethology* **107**, 573–586 (2001).
106. G. Ritchison, The flight songs of common yellowthroats: Description and causation. *Condor* **93**, 12–18 (1991).
107. B. E. Woolfenden, L. H. Gibbs, S. G. Sealy, High opportunity for sexual selection in both sexes of an obligate brood parasitic bird, the brown-headed cowbird (*Molothrus ater*). *Behav. Ecol. Sociobiol.* **52**, 417–425 (2002).
108. K. J. McGraw, E. A. Mackillop, J. Dale, M. E. Hauber, Different colors reveal different information: How nutritional stress affects the expression of melanin- and structurally based ornamental plumage. *J. Exp. Biol.* **205**, 3747–3755 (2002).
109. M. J. West, A. P. King, D. H. Eastzer, Validating the female bioassay of cowbird song: Relating differences in song potency to mating success. *Anim. Behav.* **29**, 490–501 (1981).
110. D. M. O’Neal, D. G. Reichard, K. Pavlis, E. D. Ketterson, Experimentally-elevated testosterone, female parental care, and reproductive success in a songbird, the Dark-eyed Junco (*Junco hyemalis*). *Horm. Behav.* **54**, 571–578 (2008).
111. J. A. Hill, D. A. Enstrom, E. D. Ketterson, V. Nolan Jr., C. Ziegenfuss, Mate choice based on static versus dynamic secondary sexual traits in the dark-eyed junco. *Behav. Ecol.* **10**, 91–96 (1999).
112. A. Poesel, H. L. Gibbs, D. A. Nelson, Extrapair fertilizations and the potential for sexual selection in a socially monogamous songbird. *Auk* **128**, 770–776 (2011).
113. C. J. Norment, Patterns of nestling feeding in Harris’s Sparrows, *Zonotrichia querula* and White-crowned Sparrows, *Z. leucophrys*, in the Northwest Territories, Canada. *Can. Field Nat.* **117**, 203–208 (2003).
114. S. L. Balenger, L. S. Johnson, H. L. Mays Jr., B. S. Masters, Extra-pair paternity in the socially monogamous mountain bluebird *Sialia currucoides* and its effect on the potential for sexual selection. *J. Avian Biol.* **40**, 173–180 (2009).
115. L. S. Johnson, J. L. Brubaker, E. Ostlind, S. L. Balenger, Effect of altitude on male parental expenditure in Mountain Bluebirds (*Sialia currucoides*): Are higher-altitude males more attentive fathers? *J. Ornithol.* **148**, 9–16 (2007).
116. V. García-Navas, E. S. Ferrer, J. Bueno-Enciso, R. Barrientos, J. José Sanz, J. Ortego, Extrapair paternity in Mediterranean blue tits: Socioecological factors and the opportunity for sexual selection. *Behav. Ecol.* **25**, 228–238 (2014).
117. E. Schlicht, B. Kempenaers, Extrapair paternity in the blue tit (*Parus caeruleus*): Female choice, male characteristics, and offspring quality. *Evolution* **67**, 1420–1434 (2013).
118. S. Andersson, J. Örnberg, M. Andersson, Ultraviolet sexual dimorphism and assortative mating in blue tits. *Proc. R. Soc. B Biol. Sci.* **265**, 445–450 (1998).
119. V. Amrhein, L. E. Johannessen, L. Kristiansen, T. Slagsvold, Reproductive strategy and singing activity: Blue tit and great tit compared. *Behav. Ecol. Sociobiol.* **62**, 1633–1641 (2008).
120. U. Glutz von Blotzheim, K. Bauer, *Handbuch der Vögel Mitteleuropas. Band 13/1* (Aula-Verlag, Wiesbaden, 1993).
121. L. A. Whittingham, J. T. Lifjeld, Extra-pair fertilizations increase the opportunity for sexual selection in the monogamous House Martin *Delichon urbica*. *J. Avian Biol.* **26**, 283–288 (1995).
122. U. Glutz von Blotzheim, K. Bauer, *Handbuch der Vögel Mitteleuropas. Band 10/1* (Aula-Verlag, Wiesbaden, 1985).
123. L. K. Walker, J. G. Ewen, P. Brekke, R. M. Kilner, Sexually selected dichromatism in the hihi *Notiomystis cincta*: Multiple colours for multiple receivers. *J. Evol. Biol.* **27**, 1522–1535 (2014).
124. M. Low, The energetic cost of mate guarding is correlated with territorial intrusions in the New Zealand stitchbird. *Behav. Ecol.* **17**, 270–276 (2006).
125. J. Collet, D. S. Richardson, K. Worley, T. Pizzari, Sexual selection and the differential effect of polyandry. *Proc. Natl. Acad. Sci. U.S.A.* **109**, 8641–8645 (2012).
126. T. Pizzari, Food, vigilance, and sperm: The role of male direct benefits in the evolution of female preference in a polygamous bird. *Behav. Ecol.* **14**, 593–601 (2003).
127. J. D. Ligon, R. Kimball, M. Merola-Zwartjes, Mate choice by female red junglefowl: The issues of multiple ornaments and fluctuating asymmetry. *Anim. Behav.* **55**, 41–50 (1998).
128. A. H. Krakauer, Sexual selection and the genetic mating system of Wild Turkeys. *Condor* **110**, 1–12 (2008).
129. S. J. Arnold, M. J. Wade, On the measurement of natural and sexual selection: Applications. *Evolution* **38**, 720–734 (1984).
130. R. L. Trivers, Sexual selection and resource-acquiring abilities in *Anolis garmani*. *Evolution* **30**, 253–269 (1976).
131. M. R. Prosser, P. J. Weatherhead, H. L. Gibbs, G. P. Brown, Genetic analysis of the mating system and opportunity for sexual selection in northern water snakes (*Nerodia sipedon*). *Behav. Ecol.* **13**, 800–807 (2002).
132. K. J. Kissner, P. J. Weatherhead, H. L. Gibbs, Experimental assessment of ecological and phenotypic factors affecting male mating success and polyandry in northern watersnakes, *Nerodia sipedon*. *Behav. Ecol. Sociobiol.* **59**, 207–214 (2005).
133. R. C. Stebbins, *A Field Guide to Western Reptiles and Amphibians* (Houghton Mifflin Harcourt, Boston, 2003), p. 560.
134. P. J. Weatherhead, F. E. Barry, G. P. Brown, M. R. L. Forbes, Sex ratios, mating behavior and sexual size dimorphism of the northern water snake, *Nerodia sipedon*. *Behav. Ecol. Sociobiol.* **36**, 301–311 (1995).
135. G. W. Schuett, Fighting dynamics of male copperheads, *Agkistrodon contortrix* (Serpentes, Viperidae): Stress-induced inhibition of sexual behavior in losers. *Zoo Biol.* **15**, 209–221 (1996).
136. G. W. Schuett, J. C. Gillingham, Courtship and mating of the copperhead, *Agkistrodon contortrix*. *Copeia*, 374–381 (1988).
137. P. S. Fitze, J.-F. Le Galliard, Inconsistency between different measures of sexual selection. *Am. Nat.* **178**, 256–268 (2011).
138. E. Vercken, J. Clobert, Ventral colour polymorphism correlates with alternative behavioural patterns in female common lizards (*Lacerta vivipara*). *Ecoscience* **15**, 320–326 (2008).
139. L. Gvozdík, R. Van Damme, Evolutionary maintenance of sexual dimorphism in head size in the lizard *Zootoca vivipara*: A test of two hypotheses. *J. Zool.* **259**, 7–13 (2003).
140. K. Huyghe, R. Van Damme, K. Breugelmans, A. Herrel, B. Vanhooydonck, Z. Tadić, T. Backeljau, Parentage analyses suggest female promiscuity and a disadvantage for athletic males in the colour-polymorphic lizard *Podarcis melisellensis*. *Behav. Ecol. Sociobiol.* **68**, 1357–1366 (2014).
141. R. N. Williams, J. A. DeWoody, Reproductive success and sexual selection in wild eastern tiger salamanders (*Ambystoma t. tigrinum*). *Evol. Biol.* **36**, 201–213 (2009).
142. R. A. Nussbaum, E. D. J. Brodie, R. M. Storm, *Amphibians and Reptiles of the Pacific Northwest* (University Press of Idaho, Moscow, ID, 1983).
143. R. N. Williams, D. Gopurenko, K. R. Kemp, B. Williams, J. A. DeWoody, Breeding chronology, sexual dimorphism, and genetic diversity of congeneric ambystomatid salamanders. *J. Herpetol.* **43**, 438–449 (2009).
144. D. Gopurenko, R. N. Williams, C. R. McCormick, J. A. DeWoody, Insights into the mating habits of the tiger salamander (*Ambystoma tigrinum tigrinum*) as revealed by genetic parentage analyses. *Mol. Ecol.* **15**, 1917–1928 (2006).
145. D. Gopurenko, R. N. Williams, J. A. DeWoody, Reproductive and mating success in the small-mouthed salamander (*Ambystoma texanum*) estimated via microsatellite parentage analysis. *Evol. Biol.* **34**, 130–139 (2007).
146. D. A. Croshaw, Quantifying sexual selection: A comparison of competing indices with mating system data from a terrestrially breeding salamander. *Biol. J. Linn. Soc.* **99**, 73–83 (2010).
147. A. G. Jones, J. R. Arguello, S. J. Arnold, Molecular parentage analysis in experimental newt populations: The response of mating system measures to variation in the operational sex ratio. *Am. Nat.* **164**, 444–456 (2004).

148. L. R. Pokhrel, I. Karsai, M. K. Hamed, T. F. Laughlin, Dorsal body pigmentation and sexual dimorphism in the marbled salamander (*Ambystoma opacum*). *Ethol. Ecol. Evol.* **25**, 214–226 (2013).
149. A. G. Jones, J. R. Arguello, S. J. Arnold, Validation of Bateman's principles: A genetic study of sexual selection and mating patterns in the rough-skinned newt. *Proc. Biol. Sci.* **269**, 2533–2539 (2002).
150. C. R. Propper, Courtship in the rough-skinned newt *Taricha granulosa*. *Anim. Behav.* **41**, 547–554 (1991).
151. L. D. Houck, S. J. Arnold, R. A. Thisted, A statistical study of mate choice: Sexual selection in a plethodontid salamander (*Desmognathus ochrophaeus*). *Evolution* **39**, 370–386 (1985).
152. D. C. Forester, The adaptiveness of parental care in *Desmognathus ochrophaeus* (Urodela: Plethodontidae). *Copeia* **1979**, 332–341 (1979).
153. T. Broquet, J. Jaquéry, N. Perrin, Opportunity for sexual selection and effective population size in the lek-breeding European treefrog (*Hyla arborea*). *Evolution* **63**, 674–683 (2009).
154. K. D. Wells, *The Ecology and Behavior of Amphibians* (University of Chicago Press, Chicago, 2007).
155. D. Gomez, C. Richardson, T. Lengagne, S. Plenet, P. Joly, J.-P. Léna, M. Théry, The role of nocturnal vision in mate choice: Females prefer conspicuous males in the European tree frog (*Hyla arborea*). *Proc. Biol. Sci.* **276**, 2351–2358 (2009).
156. D. Gomez, C. Richardson, M. Théry, T. Lengagne, J.-P. Léna, S. Plenet, P. Joly, Multimodal signals in male European treefrog (*Hyla arborea*) and the influence of population isolation on signal expression. *Biol. J. Linn. Soc.* **103**, 633–647 (2011).
157. E. Ursprung, M. Ringler, R. Jehle, W. Hödl, Strong male/male competition allows for non-choosy females: High levels of polygyny in a territorial frog with paternal care. *Mol. Ecol.* **20**, 1759–1771 (2011).
158. E. Ringler, M. Ringler, R. Jehle, W. Hödl, The female perspective of mating in *A. femoralis*, a territorial frog with paternal care – a spatial and genetic analysis. *PLoS One* **7**, e40237 (2012).
159. L. O. Rodríguez, W. E. Duellman, *Guide to the Frogs of the Iquitos Region, Amazonian Peru* (University of Kansas, Lawrence, KS, 1994).
160. T. Aronsen, A. Berglund, K. B. Mobley, I. I. Ratikainen, G. Rosenqvist, Sex ratio and density affect sexual selection in a sex-role reversed fish. *Evolution* **67**, 3243–3257 (2013).
161. A. G. Jones, G. Rosenqvist, A. Berglund, J. C. Avise, The measurement of sexual selection using Bateman's principles: An experimental test in the sex-role-reversed pipefish *Syngnathus typhle*. *Integr. Comp. Biol.* **45**, 874–884 (2005).
162. C. Partridge, A. Boettcher, A. G. Jones, The role of courtship behavior and size in mate preference in the sex-role-reversed Gulf pipefish, *Syngnathus scovelli*. *Ethology* **119**, 692–701 (2013).
163. A. Berglund, G. Rosenqvist, Male pipefish prefer ornamented females. *Anim. Behav.* **61**, 345–350 (2001).
164. E. Rose, K. A. Paczolt, A. G. Jones, The contributions of premating and postmating selection episodes to total selection in sex-role-reversed Gulf pipefish. *Am. Nat.* **182**, 410–420 (2013).
165. E. Rose, K. A. Paczolt, A. G. Jones, The effects of synthetic estrogen exposure on premating and postmating episodes of selection in sex-role-reversed Gulf pipefish. *Evol. Appl.* **6**, 1160–1170 (2013).
166. A. G. Jones, J. C. Avise, Mating systems and sexual selection in male-pregnant pipefishes and seahorses: Insights from microsatellite-based studies of maternity. *J. Hered.* **92**, 150–158 (2001).
167. K. B. Mobley, C. M. Small, A. G. Jones, The genetics and genomics of Syngnathidae: Pipefishes, seahorses and seadragons. *J. Fish Biol.* **78**, 1624–1646 (2011).
168. C. Kvarnemo, G. I. Moore, A. G. Jones, Sexually selected females in the monogamous Western Australian seahorse. *Proc. Biol. Sci.* **274**, 521–525 (2007).
169. C. Kvarnemo, G. I. Moore, A. G. Jones, W. S. Nelson, J. C. Avise, Monogamous pair bonds and mate switching in the Western Australian seahorse *Hippocampus subelongatus*. *J. Evol. Biol.* **13**, 882–888 (2000).
170. O. Rios-Cardenas, Patterns of parental investment and sexual selection in teleost fishes: Do they support Bateman's principles? *Integr. Comp. Biol.* **45**, 885–894 (2005).
171. A. Tatarenkov, C. I. M. Healey, G. F. Grether, J. C. Avise, Pronounced reproductive skew in a natural population of green swordtails, *Xiphophorus helleri*. *Mol. Ecol.* **17**, 4522–4534 (2008).
172. L. S. Blumer, A bibliography and categorization of bony fishes exhibiting parental care. *Zool. J. Linn. Soc.* **75**, 1–22 (1982).
173. A. L. Basolo, B. C. Trainor, The conformation of a female preference for a composite male trait in green swordtails. *Anim. Behav.* **63**, 469–474 (2002).
174. S. A. Becher, A. E. Magurran, Multiple mating and reproductive skew in Trinidadian guppies. *Proc. Biol. Sci.* **271**, 1009–1014 (2004).
175. R. E. Thibault, R. J. Schultz, Reproductive adaptations among viviparous fishes (Cyprinodontiformes: Poeciliidae). *Evolution* **32**, 320–333 (1978).
176. A. E. Magurran, *Evolutionary Ecology: The Trinidadian Guppy* (Oxford Univ. Press, New York, 2005).
177. D. Serbezov, L. Bernatchez, E. M. Olsen, L. A. Vøllestad, Mating patterns and determinants of individual reproductive success in brown trout (*Salmo trutta*) revealed by parentage analysis of an entire stream living population. *Mol. Ecol.* **19**, 3193–3205 (2010).
178. C. Tentelier, M. Larrieu, J.-C. Aymes, J. Labonne, Male antagonistic behaviour after spawning suggests paternal care in brown trout, *Salmo trutta*. *Ecol. Freshw. Fish* **20**, 580–587 (2011).
179. E. Petersson, T. Järvi, Reproductive behaviour of sea trout (*Salmo trutta*)—The consequences of sea-ranching. *Behaviour* **134**, 1–22 (1997).
180. E. Petersson, T. Järvi, Both contest and scramble competition affect the growth performance of brown trout, *Salmo trutta*, parr of wild and of sea-ranched origins. *Environ. Biol. Fishes* **59**, 211–218 (2000).
181. D. Garant, J. J. Dodson, L. Bernatchez, A genetic evaluation of mating system and determinants of individual reproductive success in Atlantic salmon (*Salmo salar* L.). *J. Hered.* **92**, 137–145 (2001).
182. T. F. Næsje, L. P. Hansen, T. Järvi, Sexual dimorphism in the adipose fin of Atlantic salmon, *Salmo salar* L. *J. Fish Biol.* **33**, 955–956 (1988).
183. M. Kottelat, J. Freyhof, *Handbook of European Freshwater Fishes* (Publications Kottelat, Cornol, 2007).
184. L. Marie-Orleach, J.-M. Roussel, J. Bugeon, J. Tremblay, D. Ombredane, G. Evanno, Melanin-based coloration of sneaker male Atlantic salmon is linked to viability and emergence timing of their offspring. *Biol. J. Linn. Soc.* **111**, 126–135 (2014).
185. D. R. Levitan, Gamete traits influence the variance in reproductive success, the intensity of sexual selection, and the outcome of sexual conflict among congeneric sea urchins. *Evolution* **62**, 1305–1316 (2008).
186. J. J. Gonor, Sex ratio and hermaphroditism in Oregon intertidal populations of the echinoid *Strongylocentrotus purpuratus*. *Mar. Biol.* **19**, 278–280 (1973).
187. K. Fritzsche, G. Arnqvist, Homage to Bateman: Sex roles predict sex differences in sexual selection. *Evolution* **67**, 1926–1936 (2013).
188. J. L. Dickinson, Determinants of paternity in the milkweed leaf beetle. *Behav. Ecol. Sociobiol.* **23**, 9–19 (1988).
189. D. M. Windsor, J. C. Choe, in *Novel Aspects of the Biology of Chrysomelidae*, P. H. Jolivet, M. L. Cox, E. Petitpierre, Eds. (Springer Science+Business Media, Berlin, 1994), pp. 111–117.
190. D. K. McLain, R. D. Boromisa, Male choice, fighting ability, assortative mating and the intensity of sexual selection in the milkweed longhorn beetle, *Tetraopes tetraophthalmus* (Coleoptera, Cerambycidae). *Behav. Ecol. Sociobiol.* **20**, 239–246 (1987).
191. W. S. Lawrence, Male choice and competition in *Tetraopes tetraophthalmus*: Effects of local sex ratio variation. *Behav. Ecol. Sociobiol.* **18**, 289–296 (1986).
192. D. E. McCauley, An estimate of the relative opportunities for natural and sexual selection in a population of milkweed beetles. *Evolution* **37**, 701–707 (1983).
193. A. Bjork, S. Pitnick, Intensity of sexual selection along the anisogamy–isogamy continuum. *Nature* **441**, 742–745 (2006).
194. A. Hoikkala, J. Lumme, Genetic control of the difference in male courtship sound between *Drosophila virilis* and *D. lummei*. *Behav. Genet.* **14**, 257–268 (1984).
195. R. R. Snook, N. A. Gidaszewski, T. Chapman, L. W. Simmons, Sexual selection and the evolution of secondary sexual traits: Sex comb evolution in *Drosophila*. *J. Evol. Biol.* **26**, 912–918 (2013).
196. H. T. Spieth, Courtship behavior in *Drosophila*. *Annu. Rev. Entomol.* **19**, 385–405 (1974).
197. N. Luck, D. Joly, Sexual selection and mating advantages in the giant sperm species, *Drosophila bifurca*. *J. Insect Sci.* **5**, 10 (2005).
198. A. Kopp, I. Duncan, S. B. Carroll, Genetic control and evolution of sexually dimorphic characters in *Drosophila*. *Nature* **408**, 553–559 (2000).
199. T. A. Markov, Perspective: Female remating, operational sex ratio, and the arena of sexual selection in *Drosophila* species. *Evolution* **56**, 1725–1734 (2002).
200. D. C. Droney, Sexual selection in a lekking Hawaiian *Drosophila*: The roles of male competition and female choice in male mating success. *Anim. Behav.* **44**, 1007–1020 (1992).
201. A. T. Markov, P. M. O'Grady, *Drosophila: A Guide to Species Identification and Use* (Elsevier, London, 2006).
202. R. J. Hodosh, J. M. Ringo, F. T. McAndrew, Density and lek displays in *Drosophila grimshawi* (Diptera: Drosophilidae). *Z. Tierpsychol.* **49**, 164–172 (1979).
203. M.-C. Gagnon, P. Duchesne, J. Turgeon, Sexual conflict in *Gerris gillettei* (Insecta: Hemiptera): Influence of effective mating rate and morphology on reproductive success. *Can. J. Zool.* **90**, 1297–1306 (2012).
204. G. Arnqvist, in *The Evolution of Mating Systems in Insects and Arachnids*, C. Choe, B. J. Crespi, Eds. (Cambridge Univ. Press, Cambridge, 1997), pp. 146–163.
205. T. Nishida, Measurement of the opportunity for natural and sexual selection in a breeding population of the coreid bug (*Colpula lativentris*). *Res. Popul. Ecol.* **29**, 271–289 (1987).
206. T. Nishida, Spatial relationships between mate acquisition probability and aggregation size in a gregarious coreid bug, (*Colpula lativentris*): A case of the ideal free distribution under perceptual constraints. *Res. Popul. Ecol.* **35**, 45–56 (1993).
207. R. Rodríguez-Muñoz, A. Bretman, J. Slate, C. A. Walling, T. Tregenza, Natural and sexual selection in a wild insect population. *Science* **328**, 1269–1272 (2010).

208. J. W. Y. Wong, J. Meunier, M. Kölliker, The evolution of parental care in insects: The roles of ecology, life history and the social environment. *Ecol. Entomol.* **38**, 123–137 (2013).
209. K. Harz, *The Orthoptera of Europe* (Springer Science+Business Media, Dordrecht, 1969).
210. M. J. Banks, D. J. Thompson, Lifetime mating success in the damselfly *Coenagrion puella*. *Anim. Behav.* **33**, 1175–1183 (1985).
211. S. N. Gorb, Visual cues in mate recognition by males of the damselfly, *Coenagrion puella* (L.) (Odonata: Coenagrionidae). *J. Insect Behav.* **11**, 73–92 (1998).
212. J. E. Hafernik Jr., R. W. Garrison, Mating success and survival rate in a population of damselflies: Results at variance with theory? *Am. Nat.* **128**, 353–365 (1986).
213. A. Córdoba-Aguilar, A. Cordero-Rivera, in *Dragonflies and Damselflies: Model Organisms for Ecological and Evolutionary Research*, A. Córdoba-Aguilar, Ed. (Oxford Univ. Press, New York, 2008), pp. 189–202.
214. O. M. Fincke, Lifetime mating success in a natural population of the damselfly, *Enallagma hageni* (Walsh) (Odonata: Coenagrionidae). *Behav. Ecol. Sociobiol.* **10**, 293–302 (1982).
215. O. M. Fincke, Lifetime reproductive success and the opportunity for selection in a non-territorial damselfly (Odonata: Coenagrionidae). *Evolution* **40**, 791–803 (1986).
216. F. S. Barreto, J. C. Avise, Quantitative measures of sexual selection reveal no evidence for sex-role reversal in a sea spider with prolonged paternal care. *Proc. Biol. Sci.* **277**, 2951–2956 (2010).
217. B. A. Bain, F. R. Govedich, Courtship and mating behavior in the Pycnogonida (Chelicerata: Class Pycnogonida): A summary. *Invertebr. Reprod. Dev.* **46**, 63–79 (2004).
218. M. C. B. Andrade, M. M. Kasumovic, Terminal investment strategies and male mate choice: Extreme tests of Bateman. *Integr. Comp. Biol.* **45**, 838–847 (2005).
219. T. J. Hawkeswood, *Spiders of Australia: An Introduction to Their Classification, Biology and Distribution* (Pensoft Publishers, Sofia, Bulgaria, 2003).
220. L. M. Forster, The stereotyped behavior of sexual cannibalism in *Latrodectus hasselti* Thorell (Araneae, Theridiidae), the Australian Redback Spider. *Aust. J. Zool.* **40**, 1–11 (1992).
221. N. Pongratz, N. K. Michiels, High multiple paternity and low last-male sperm precedence in a hermaphroditic planarian flatworm: Consequences for reciprocity patterns. *Mol. Ecol.* **12**, 1425–1433 (2003).
222. N. Anthes, P. David, J. R. Auld, J. N. A. Hoffer, P. Jarne, J. M. Koene, H. Kokko, M. C. Lorenzi, B. Péliissié, D. Sprenger, A. Staikou, L. Schärer, Bateman gradients in hermaphrodites: An extended approach to quantify sexual selection. *Am. Nat.* **176**, 249–263 (2010).

Acknowledgments: We are very grateful to the many people who provided additional information on primary studies, unpublished or inaccessible data sets, and/or advice regarding the analysis. These include M. C. B. Andrade, G. Arnqvist, P. Bergeron, A. Bjork, M. Borgerhoff Mulder, G. P. Brown, B. E. Byers, J. Collet, J. Conner, A. Courtiol, P. Dunn, P. S. Fitze, K. Fritzsche, N. Gerlach, M. Jokela, M. Kölliker, A. Krakauer, D. Levitan, J. T. Lifjeld, A. Magurran, A. McElligott, N. K. Michiels, S. Mills, K. Mobley, J. Moorad, S. Pitnick, T. Pizzari, K. Reinhold, D. Serbezov, P. J. Weatherhead, and L. A. Whittingham. We also thank P. Jarne, M. Jennions, H. Kokko, K. Mobley, J. H. Pantel, K. Reinhardt, and one anonymous reviewer for helpful comments on an earlier draft and K. Both for drawing the species illustrations included in Fig. 1. **Funding:** This study was funded by postdoctoral fellowships from the Swiss National Science Foundation (SNSF) to T.J. (SNSF grant nos. PBBSP3-135985 and PA00P3-145375/1), the NSF to M.J.L. (DBI-1262545), and the Deutsche Forschungsgemeinschaft (DFG) to N.A. (DFG grant no. AN549/3-1). **Author contributions:** T.J. conceived the study. T.J., I.K.H., and N.A. designed the meta-analysis, conducted the literature search, and extracted the effect sizes from primary studies. T.J. and M.J.L. performed the statistical analysis. T.J., I.K.H., M.J.L., and N.A. wrote the paper. **Competing interests:** The authors declare that they have no competing interests. **Data and materials availability:** All data needed to evaluate the conclusions in the paper are available from the Dryad Digital Repository (<http://dx.doi.org/10.5061/dryad.780d6>) and/or the Supplementary Materials. Additional data related to this paper may be requested from the authors.

Submitted 23 July 2015
Accepted 30 November 2015
Published 12 February 2016
10.1126/sciadv.1500983

Citation: T. Janicke, I. K. Häderer, M. J. Lajeunesse, N. Anthes, Darwinian sex roles confirmed across the animal kingdom. *Sci. Adv.* **2**, e1500983 (2016).

Darwinian sex roles confirmed across the animal kingdom

Tim Janickelnes K. HädererMarc J. LajeunesseNils Anthes

Sci. Adv., 2 (2), e1500983. • DOI: 10.1126/sciadv.1500983

View the article online

<https://www.science.org/doi/10.1126/sciadv.1500983>

Permissions

<https://www.science.org/help/reprints-and-permissions>

Use of this article is subject to the [Terms of service](#)