

Sexual size dimorphism and the strength of sexual selection in mammals and birds

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ABSTRACT

Background: Sexual selection has been used as a proximate explanation for sexual size dimorphism (SSD) in many taxa, but the relationship between SSD and a quantitative measure of the strength of sexual selection has yet to be tested.

Hypothesis: The strength of sexual selection is positively correlated with SSD in birds and mammals.

Methods: We used two measures of SSD: the SSD ratio and the size dimorphism index (*SDI*). The SSD ratio is $\log(\text{male body mass}/\text{female body mass})$. *SDI* is the ratio of the larger sex to the smaller sex and minus 1; the resulting value is then made negative for male-biased dimorphism and positive for female-biased dimorphism. Our measure of the strength of sexual selection is the standardized variance in male fitness (*I*) calculated as the square of the coefficient of variation in male mating or reproductive success, which reflects the maximum potential strength of sexual selection. We carried out a phylogenetic generalized least squares regression (PGLM) of SSD ratio or *SDI* on *I*.

Results: There was no consistent relationship between SSD and *I*, as they were strongly positively related in mammals, but not in birds. This may relate to the form of competition (contests vs. display) that is found most often in mammals and birds.

Keywords: lekking, mating system, monogamy, opportunity for sexual selection, polyandry, polygyny, sexual dimorphism.

INTRODUCTION

Differences in body size between the sexes have been recognized in a range of taxa for a long time (Darwin, 1874). Sexual selection theory predicts that in polygynous species, differences in life-history strategies between the sexes lead to more intense competition for mates among males, promoting an increase in male body size relative to females and the evolution of complex fighting structures (Andersson, 1994). In both birds and mammals, there is considerable empirical evidence to support the role of sexual selection in sexual size dimorphism (SSD),

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with a positive relationship between SSD and both mating system and mating competition (Owens and Hartley, 1998; Dunn *et al.*, 2001; Lindenfors *et al.*, 2007; Székely *et al.*, 2007). However, the use of mating system or mating competition as a categorical variable is crude, as social and genetic mating systems may in fact correlate poorly (Griffith *et al.*, 2002; Soulsbury, 2010) meaning that mating system categorizations may be a poor measure of the strength of sexual selection. Hence, a better understanding of the link between SSD and sexual selection requires other, more accurate measures of the strength of sexual selection.

There are a number of ways to quantify the strength of sexual selection (Jones, 2009; Klug *et al.*, 2010a). These include the opportunity for (sexual) selection, the Bateman gradient, sexual selection gradients and differentials, the Morisita index, the index for resource monopolization, the operational sex ratio, and the potential reproductive rate (see Table 1 in Klug *et al.*, 2010a). The opportunity for sexual selection [I_{ss} , the square of the coefficient of variation in mating success for a given sex (Arnold and Wade, 1984)] is a dimensionless measure of variation in mating success that reflects the maximum potential directional strength of sexual selection (Jones, 2009; Klug *et al.*, 2010a). It is, however, extremely challenging to measure male mating success accurately in natural populations, which would require large-scale simultaneous field observations to record copulations of an unbiased sample of males in each studied population (Shuster, 2009). Moreover, dominant males often have more conspicuous displays, while subordinates might adopt alternative mating strategies (e.g. Worthington Wilmer *et al.*, 1999; Jones *et al.*, 2001); and copulations may simply go unnoticed (e.g. Lanctot *et al.*, 1997), meaning that obtaining unbiased measures of male mating success based on field observations is often impossible for many species.

Molecular markers may be used to deduce male mating success. However, estimates of individual male mating success require the sampling of a large number of broods, and might still be substantially underestimated if some copulations result in no offspring production or if post-copulatory sexual selection occurs (Eberhard, 1996; Birkhead and Møller, 1998; Brommer *et al.*, 2007). Nevertheless, sexual selection is widely expected to lead to substantial differences in male reproductive success (Shuster and Wade, 2003; Shuster, 2009), because individuals' reproductive success is the product of male mating success and female fecundity (see, for example, Webster *et al.*, 1995). Hence any difference in males' ability to attract mates might lead to major differences in their reproductive success, and a limited variance in female fecundity should lead to a strong direct relationship between the variances in mating and reproductive success. Therefore, differences between the sexes in the opportunity for selection [I ; the square of the coefficient of variation in reproductive success (Crow, 1958)] are often used as evidence for sexual selection (Shuster and Wade, 2003; Shuster, 2009). Thus, measures of the opportunity for selection (I) might be used as proxies of the opportunity for sexual selection (I_{ss}).

Recently, there has been confusion in terminology between I_{ss} and I , probably because of the significant interdependence of the two (Klug *et al.*, 2010a). We use estimates of male mating and reproductive success from observations and genetic data. Despite the problems and the limitations in their estimation, they still provide useful measures of the strength of sexual selection in a population, as they both capture key differences in individuals' reproduction.

Although large I and I_{ss} values reflect stronger sexual selection (Shuster and Wade, 2003; Klug *et al.*, 2010b), there is considerable discussion about their utility (Klug *et al.*, 2010a, 2010b; Krakauer *et al.*, 2011; Jennions *et al.*, 2012), partly because I and I_{ss} values integrate random and deterministic events (i.e. natural and sexual selection), leading to inconsistent or weak correlations to the magnitude of sexual selection gradients (i.e. the relationship between male traits and their mating success). While other, better measures have been suggested (e.g. Kokko *et al.*, 2012), these

are often impossible to calculate from previously published data, limiting their use. Comparative studies are important to understand general patterns of sexual dimorphism and ornamentation, and I and I_{ss} remain useful for quantifying the strength of sexual selection (Vanpé *et al.*, 2008). In this study, we aimed to determine whether SSD in body mass is related to the strength of sexual selection as measured by I and I_{ss} . To date, tests of the strength of sexual selection and SSD have been limited to specific taxonomic groups, such as ungulates (Vanpé *et al.*, 2008). Thus in this paper we test this idea more generally.

MATERIALS AND METHODS

Data collection

Data on I and I_{ss} were taken or recalculated from published studies (evolutionary-ecology.com/data/2858Appendix.pdf, Tables S1 and S2). For birds, we were able to use two measures of the strength of sexual selection, the first based on genetic paternity data ($I_{(genetic)}$) and the second based on behavioural observations ($I_{(apparent)}$); the two measures are highly correlated but not identical (Spearman's rank order correlation: $r_s = 0.76$, $P < 0.001$) because both can lead to errors in estimates of the opportunity for selection (Lebigre *et al.*, 2012). For mammals, we were only able to locate enough data for genetic paternity data ($I_{(genetic)}$).

Body mass data were taken from adult or breeding individuals as near to the breeding season as possible ([2858Appendix](http://evolutionary-ecology.com/data/2858Appendix.pdf), Tables S1 and S2). To avoid geographical variation in body size impacting our results, we tried to match our data geographically, although this was not always possible.

Data analysis

We calculated two measures of SSD: the SSD ratio ($\log(\text{male body mass/female body mass})$) and the size dimorphism index, SDI (Lovich and Gibbons, 1992). We first compared $I_{(genetic)}$, the SSD ratio, and SDI between birds and mammals using Wilcoxon tests.

Comparative studies need to account for non-independence of residuals in models that include evolutionarily related species (Felsenstein, 1985). A commonly used method is generalized least squares, GLS (Martins and Hansen, 1997; Pagel, 1997, 1999). We carried out a phylogenetic generalized least squares approach (PGLM) between the SSD ratio or SDI and $I_{(genetic)}$ or $I_{(apparent)}$ (Pagel, 1999; Freckleton *et al.*, 2002). For both mammals and birds, $I_{(genetic)}$ and $I_{(apparent)}$ were overdispersed. To account for this, we ranked the variables before using them in the analysis. The `pglmEstLambda` function of the 'CAIC' package was used to identify the maximum likelihood value of lambda, λ (Pagel, 1999; Orme *et al.*, 2009; Revell, 2010), which measures the degree to which the matrix follows a Brownian model; λ can vary between 0 (no phylogenetic autocorrelation) and 1 (complete phylogenetic autocorrelation). We present results from the PGLM along with the OLS (ordinary least squares) for comparison (Freckleton, 2009): where $\lambda = 0$, the resulting model is equivalent to a standard linear model. Model residuals were examined for heteroscedasticity and outliers; potential outliers were tested using a Grubbs test (Grubbs, 1969). Analysis was carried out using R code kindly provided by R.P. Freckleton (University of Sheffield, UK). We used avian (Jetz *et al.*, 2012) and mammalian phylogenies with branch lengths (Bininda-Emonds *et al.*, 2007) and calculated effect sizes and 95% confidence intervals for factors (Nakagawa and Cuthill, 2007). All analyses were run in R version 2.15.2 (R Development Core Team, 2012).

RESULTS

Differences in SSD and $I_{(\text{genetic})}$ in birds and mammals

Mammals had significantly stronger $I_{(\text{genetic})}$ than birds (Wilcoxon test: $W = 166$, $P < 0.001$; Fig. 1a). Also, mammals were more sexually dimorphic than birds (Wilcoxon test: SSD ratio, $W = 417$, $P = 0.004$; SDI , $W = 943$, $P = 0.004$; Fig. 1b, c).

The relationship between SSD and $I_{(\text{genetic})}$ in mammals

There was a significant positive relationship between $I_{(\text{genetic})}$ and the SSD ratio (PGLM: $R^2 = 0.38$, $F = 19.27$, $P < 0.001$; Table 1, Fig. 2a), and a significant negative relationship between $I_{(\text{genetic})}$ and SDI (PGLM: $R^2 = 0.29$, $F = 13.51$, $P = 0.001$; Table 1, Fig. 2b) in

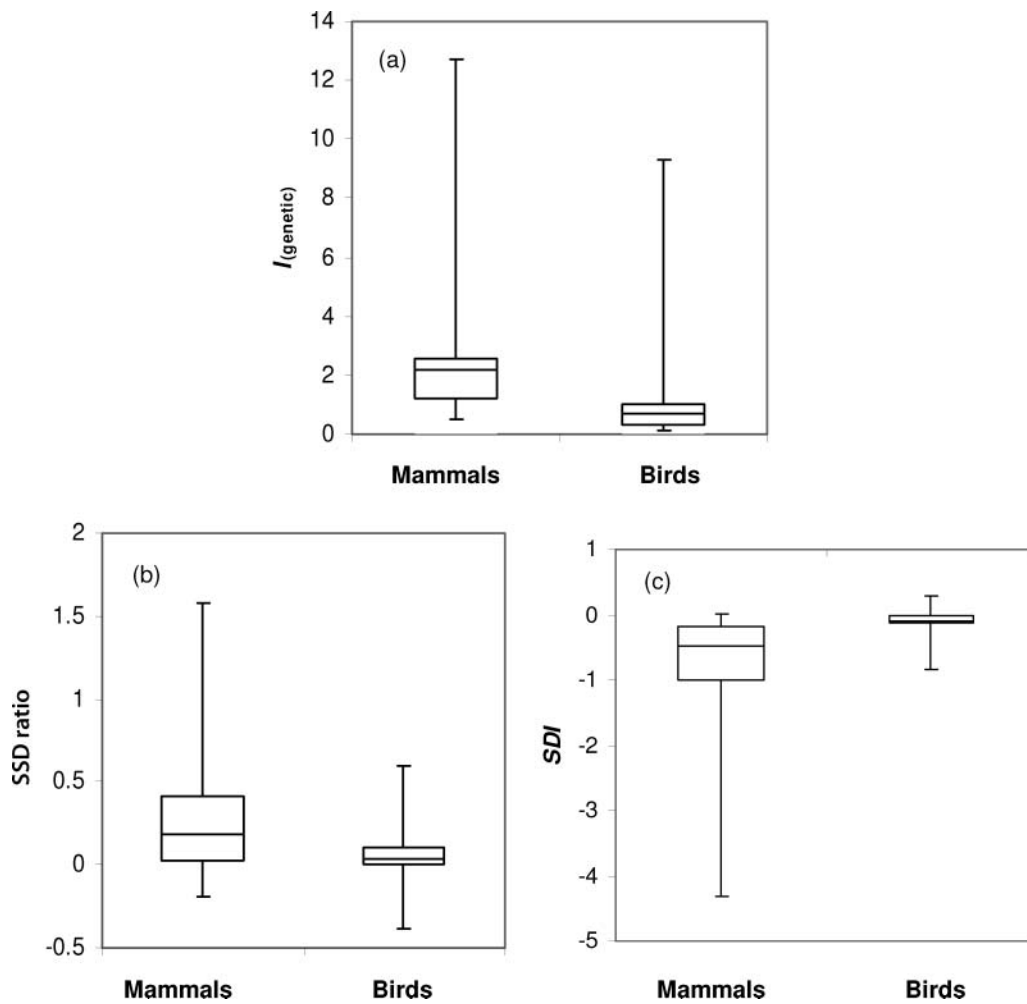


Fig. 1. Box plots showing the differences between birds and mammals in (a) $I_{(\text{genetic})}$, (b) the SSD ratio, and (c) SDI .

Table 1. PGLM model results for the relationship between the SSD ratio and *SDI* and the strength of sexual selection in birds ($N = I_{(\text{genetic})} = 35$; $N = I_{(\text{apparent})} = 33$) and mammals ($N = 32$)

Model	λ	Dependent variable	Predictor	Estimate	S.E.	t	P	r	95% CI
Birds	0.75*	SSD ratio	Intercept	0.02	0.09				
			$I_{(\text{genetic})}$	0.00	0.00	1.39	0.173	0.22	-0.10/0.49
Birds	0.70*	<i>SDI</i>	Intercept	-0.00	0.11				
			$I_{(\text{genetic})}$	-0.00	0.00	-1.49	0.147	-0.24	-0.51/0.09
Birds	0.84*	SSD ratio	Intercept	0.00	0.11				
			$I_{(\text{apparent})}$	0.00	0.00	1.40	0.172	0.24	-0.10/0.51
Birds	0.70*	<i>SDI</i>	Intercept	-0.02	0.12				
			$I_{(\text{apparent})}$	-0.00	0.00	-1.52	0.139	-0.26	-0.52/0.08
Mammals	0.00**	SSD ratio	Intercept	-0.14	0.11				
			$I_{(\text{genetic})}$	0.03	0.01	4.39	< 0.001	0.61	0.35/0.76
Mammals	0.00**	<i>SDI</i>	Intercept	0.35	0.23				
			$I_{(\text{genetic})}$	-0.05	0.01	-3.68	0.001	-0.51	-0.69/-0.21

Note: For each model, the table provides the estimate $\pm$ S.E., t - and P -values. In addition, the estimate of Pagel's λ (Pagel, 1999) was calculated, along with effect sizes (Pearson's r) with 95% confidence intervals for predictor variables.

* λ is significantly different from 0 and from 1.

** λ is significantly different from 1, but not significantly different from 0.

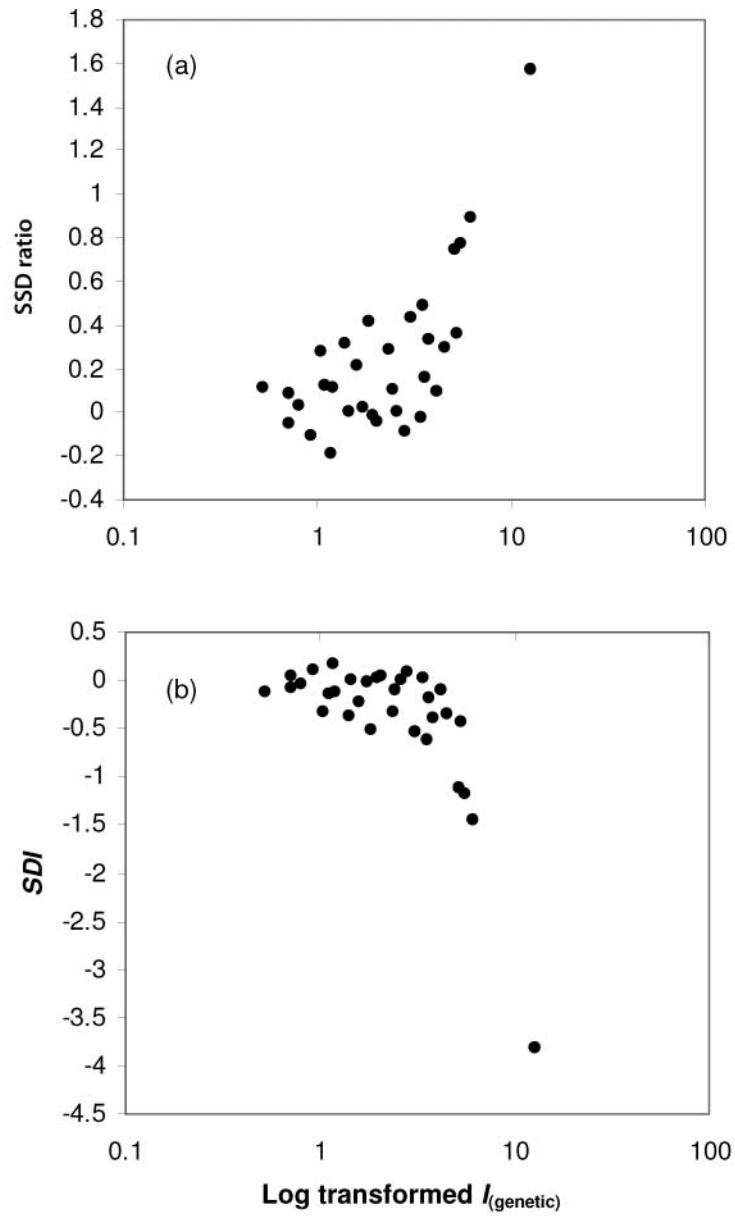


Fig. 2. The relationship between log transformed I_{genetic} and (a) the SSD ratio and (b) SDI in mammals. Significant regression lines are not shown, as the data were rank transformed before analysis (see Methods).

mammals. For mammals, there was no phylogenetic effect in both models (Table 1). As expected, if phylogeny was having no effect, the OLS regression results were equivalent to the PGLM results (SSD ratio: $R^2 = 0.42$, $F = 24.99$, $P < 0.001$; SDI : $R^2 = 0.32$, $F = 16.81$, $P < 0.001$).

Grubbs' test ($G = 3.42$, $P = 0.002$) indicated one significant outlier (Antarctic fur seal, *Arctocephalus gazella*). However, exclusion of this data point did not alter the overall conclusions of the model (PGLM: SSD ratio, $\lambda = 0$, $R^2 = 0.35$, $F = 16.38$, $P < 0.001$; SDI , $\lambda = 0$, $R^2 = 0.35$, $F = 16.93$, $P < 0.001$).

The relationship between SSD and $I_{(\text{genetic})}$ or $I_{(\text{apparent})}$ in birds

In contrast to mammals, there was no significant relationship between $I_{(\text{genetic})}$ and SSD ratio or SDI in birds (PGLM: SSD ratio, $R^2 = 0.01$, $F = 1.27$, $P = 0.267$; SDI , $R^2 = 0.01$, $F = 1.51$, $P = 0.227$; Table 1 and Fig. 3a, b). There was also no significant relationship between $I_{(\text{apparent})}$ and the SSD ratio (PGLM: $R^2 = 0.00$, $F_{1,39} = 1.12$, $P = 0.297$; Table 1) or SDI (PGLM: $R^2 = 0.01$, $F = 1.19$, $P = 0.283$; Table 1 and Fig. 4a, b). For all models, there was a significant effect of phylogeny on the results (Table 1).

Without the controlling effect of phylogeny, the OLS regressions were close to significance for the SSD ratio ($I_{(\text{apparent})}$: $R^2 = 0.06$, $F_{1,39} = 3.39$, $P = 0.073$; $I_{SS(\text{genetic})}$: $R^2 = 0.04$, $F = 2.44$, $P = 0.0126$) and SDI ($I_{(\text{apparent})}$: $R^2 = 0.06$, $F_{1,39} = 3.76$, $P = 0.060$; $I_{(\text{genetic})}$: $R^2 = 0.05$, $F = 3.27$, $P = 0.078$).

Grubbs' tests identified two outliers in the $I_{(\text{apparent})}$ dataset (wild turkey, *Meleagris gallopavo*; red-winged blackbird, *Agelaius phoeniceus*) and three outliers in the $I_{SS(\text{genetic})}$ dataset (wild turkey; ring-necked pheasant, *Phasianus colchicus*; red-winged blackbird). Exclusion of these data points did not impact the overall PGLM results for either $I_{(\text{apparent})}$ (SSD ratio: $\lambda = 0.96$, $R^2 = 0.02$, $F = 1.61$, $P = 0.214$; SDI : $\lambda = 0.95$, $R^2 = 0.03$, $F = 2.09$, $P = 0.158$) or $I_{(\text{genetic})}$ (SSD ratio: $\lambda = 0.76$, $R^2 = 0.05$, $F = 1.91$, $P = 0.176$; SDI : $\lambda = 1$, $R^2 = 0.02$, $F = 1.57$, $P = 0.221$).

DISCUSSION

SSD and the strength of sexual selection

In this study, we tested whether a measure of the strength of sexual selection ($I_{(\text{genetic})}$ or $I_{(\text{apparent})}$) was related to the degree of sexual size dimorphism in mammals and birds. We found that in mammals, species with high $I_{(\text{genetic})}$ were more sexually dimorphic, whereas in birds this relationship was non-significant. Overall, mammals were more sexually dimorphic than birds and had higher $I_{(\text{genetic})}$. The effect of phylogeny differed in birds and mammals. In mammals there was no phylogenetic effect probably due to the broader range of taxonomic groups and their spread across the regression line. In contrast, birds had a strong phylogenetic effect ($\lambda > 0.70$), reflecting the uneven spread of taxonomic groupings across the regression line; specifically, the Galliformes showed high SSD and high $I_{(\text{genetic})}$ or $I_{(\text{apparent})}$ in the dataset compared with other taxonomic groups.

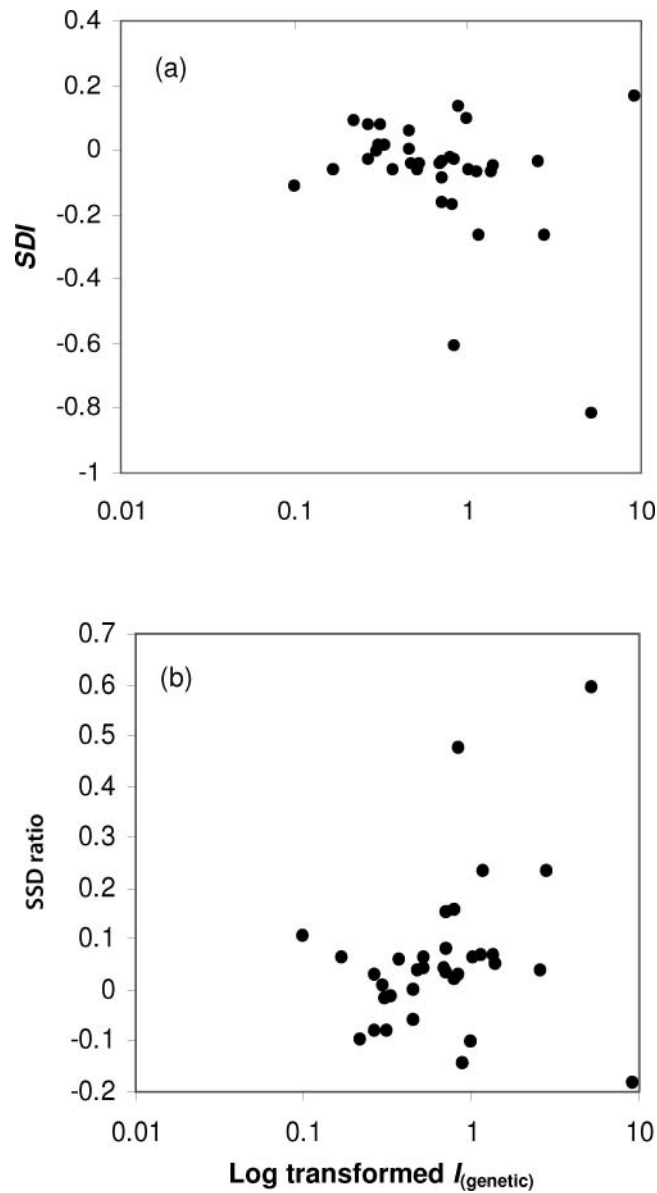


Fig. 3. The relationship between log transformed $I_{(genetic)}$ and (a) the SSD ratio and (b) SDI in birds.

SSD and strength of sexual selection in mammals

Sexual selection has long been used as a proximate explanation of SSD in mammals (Trivers, 1972; Isaac, 2005). Our results are in line with previous analyses in mammals showing that SSD correlates to the strength of sexual selection both in specific groups [primates (Mitani *et al.*, 1996); pinnipids (Lindenfors *et al.*, 2002); ruminants (Weckerly, 1998)] and mammals more generally (Lindenfors *et al.*, 2007). Previous work, however, has shown inconsistencies in the pattern

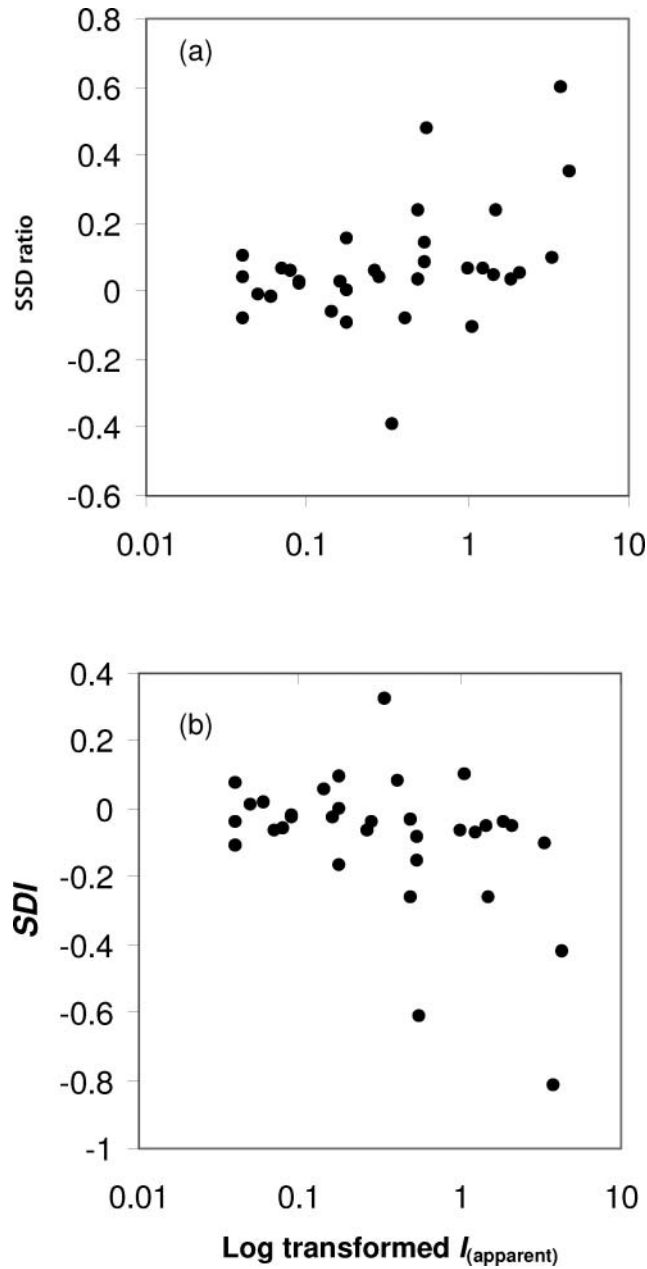


Fig. 4. The relationship between log transformed I_{apparent} and (a) the SSD ratio and (b) SDI in birds.

between specific groups (Isaac, 2005), with, for example, a degree of SSD in monogamous species [e.g. 15.6% in red foxes, *Vulpes vulpes* (Iossa *et al.*, 2008)] and high SSD in species believed to have weaker sexual selection (Isaac, 2005). First, sexual selection occurs even in monogamous species with patterns of mass-related reproductive success (e.g. Iossa *et al.*, 2008), similar to what might be expected in polygynous species (e.g. McElligott *et al.*, 2001). Second, rates of

multiple paternity and extra-pair paternity are quite high in mammals, even within socially monogamous species (Soulsbury, 2010), meaning that mating success is unequal and thus providing the opportunity for sexual selection. Although multiple mechanisms contribute to SSD in mammals (Isaac, 2005), sexual selection – and, importantly, the strength of sexual selection – is clearly one of them (Vanpé *et al.*, 2008).

SSD and the strength of sexual selection in birds

Our results for birds differ from previous work that used social mating system as a proxy for sexual selection (Björklund, 1990; Owens and Hartley, 1998; Dunn *et al.*, 2001; Székely *et al.*, 2007). A confounding factor might be differences between studies in the classification scheme for scoring mating systems (Dunn *et al.*, 2001). However, our measure is independent of such a difference in definition, though not without its own problems. At best, after controlling for phylogeny we showed a very weak trend for a positive relationship between the SSD ratio and *SDI* and the opportunity for sexual selection, and the effect size of birds was substantially weaker than in mammals. Our results are perhaps most directly comparable to previous work showing that behavioural mating systems were related to SSD (Owens and Hartley, 1998; Dunn *et al.*, 2001), whereas genetic mating systems were not related to SSD, but to plumage dimorphism (Owens and Hartley, 1998). Extra-pair paternity is taxonomically widespread in birds (Griffith *et al.*, 2002; Westneat and Stewart, 2003) and females control access to paternity (Birkhead and Møller, 1993), which explains the decoupling of genetic mating systems and behavioural mating systems and SSD. The effect of extra-pair paternity on strength of sexual selection may vary between mating systems; extra-pair paternity can lower sexual selection in polygynous mating systems (Sousa and Westneat, 2013) but can increase it in monogamous systems (Webster *et al.*, 2007). In our dataset, the most sexually dimorphic species were typically polygynous (e.g. red-winged blackbird: SSD ratio = 0.35, *SDI* = -0.42) or lekking (wild turkey: SSD ratio = 0.60, *SDI* = -0.81; black grouse, *Tetrao tetrix*: SSD ratio = 0.35, *SDI* = -0.42), which is consistent with behavioural mating systems (Dunn *et al.*, 2001). However, in the red-winged blackbird, none of the studies showed strong sexual selection (2858Appendix, Table S1), showing that behavioural mechanisms may not always reflect the true strength of sexual selection.

Fewer avian than mammal mating systems require direct physical contests. Polygynous mammals are often characterized by large armaments (Emlen, 2008), as well as the large body size needed in direct male–male physical interactions. In contrast, birds tend to have fewer and small armaments, such as spurs (Møller, 1992). Although many behavioural [e.g. song structure (Lampe and Espmark, 1994)] and phenotypic traits [e.g. plumage (Freeman-Gallant *et al.*, 2010)] can correlate with body size, such indirect selection does not act to increase SSD. Many birds rely heavily on sexually selected behavioural traits, such as display agility (e.g. Blomqvist *et al.*, 1997), that may in fact select for reduced male body mass (Székely *et al.*, 2004, 2007). Indeed, birds that display or fight for access to females show increased terrestriality and higher SSD (Székely *et al.*, 2000). Together, the lack of direct contests and the selection for agility likely weaken the direct relationship between SSD and the strength of sexual selection in birds.

The importance of the type of sexual display for the relationship between *I* and SSD in birds is perhaps best encapsulated in lekking bird species, which tend to have the largest $I_{(\text{genetic})}$ or $I_{(\text{apparent})}$ values. Species in which male acrobatic display is important, such as the lance-tailed manakin, *Chiroxiphia lanceolata* [$I_{(\text{genetic})} = 9.32$, SSD ratio = -0.18, *SDI* = 0.17

(DuVal and Kempenaers, 2008)] and white-bearded manakin, *Manacus manacus* [$I_{\text{(apparent)}} = 3.33$, SSD ratio = 0.10, $SDI = -0.10$ (Shorey, 2002)] have low or reverse sexual dimorphism in body mass, whereas in species in which physical contests are more important, such as the black grouse (Hämäläinen *et al.*, 2012), males are substantially larger than females. Hence lekking, a system with strong sexual selection, does not promote SSD *per se* (see also Höglund and Sillen-Tullberg, 1994; Lislevand *et al.*, 2009), whereas the type of male competition does [see also bustards (Raihani *et al.*, 2006)].

CONCLUSIONS

Our results show that there is a strong relationship between SSD and the strength of sexual selection in mammals but not in birds, meaning that the widespread assumption that size dimorphism reflects sexual selection is not consistent across taxa. Considering that there are multiple forms of sexual dimorphism and types of male–male competition (Owens and Hartley, 1998; Székely *et al.*, 2004, 2007), the lack of general relationship between SSD and the strength of sexual selection is not surprising and clearly calls for greater caution when suggesting overarching evidence of sexual selection. Our results reinforce the idea that, in birds, sexual selection can select against larger body size and that the form of competition (contests vs. display) in conjunction with sexual selection are crucial determinants of SSD.

ACKNOWLEDGEMENT

Funding was provided by the Emil Aaltonen Foundation to M.K.

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