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Pre-Copulatory Sexual Selection Predicts Sexual Size Dimorphism: A Meta-Analysis of Comparative Studies

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ABSTRACT

Size differences between males and females are common across the tree of life (termed sexual size dimorphism; SSD), and have fundamental implications for ecology, life history and behaviour of both sexes. Conventionally, SSD is thought to evolve in response to sex-specific sexual selection but more recent work suggests that ecological processes can also promote sex-differences in size. Here, we provide a global test for the role of sexual selection in the evolution of sexual size dimorphism using data from 77 comparative studies spanning the major classes of the animal kingdom. We show that intense sexual selection typically correlates with male-biased SSD across species. Importantly, pre-copulatory but not post-copulatory sexual selection predicts SSD, suggesting a pervasive role of premating male–male competition and female choice to drive sex differences in body size. Collectively, our findings suggest that pre-copulatory sexual selection plays a major role in the evolution of male-biased SSD.

1 | Introduction

Throughout the animal kingdom, males and females often differ in body size (Blanckenhorn 2005; Fairbairn et al. 2007). This phenomenon, known as sexual size dimorphism (SSD), is considered to have profound evolutionary and ecological implications (Blanckenhorn 2005; De Lisle 2019; Fairbairn et al. 2007) including its effect on sex-specific life histories and behaviours (Blanckenhorn 2005), demographics (Ancona et al. 2017; Eberhart-Phillips et al. 2018), predator–prey relationships (Schoener 1967) and dietary niche-separation of females and males (Slatkin 1984).

Theory predicts that SSD can emerge both from sexual selection and (non-sexual) natural sexual selection (De Lisle 2019; Isaac 2005; Lande and Kirkpatrick 1988) with the former being defined as a type of natural selection that arises from competition for resources provided by mating partners (Janicke 2024; see also Jones and Ratterman 2009). Historically, however, sexual selection has been considered as the main driver for the evolution of SSD (Andersson and Iwasa 1996; Fairbairn et al. 2007). In particular, contest competition has been argued to trigger the evolution of SSD if larger individuals of one sex gain an advantage in intra-sexual competition over mating opportunities (Parker 1992). In addition, SSD can evolve

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in response to mate choice (Blanckenhorn 2005) if one sex evolves a preference for larger individuals of the opposite sex. Moreover, scramble competition for mates might play a role for the evolution of SSD because larger body size may facilitate locomotion and therefore promotes the acquisition of mating partners (Able 1999). Finally, sexually selected traits, such as ornaments and armaments (Eberhard et al. 2018; McCullough and O'Brien 2022) typically show an allometric relationship, which could indirectly drive the evolution of SSD (Fromonteil et al. 2023). As a result of the these mechanisms of pre-copulatory sexual selection, males and females may exhibit different optima for body size and the evolution of SSD offers a resolution of such intra-locus sexual conflict (Lande 1980; Reeve and Fairbairn 2001).

Independent of pre-copulatory drivers of SSD, post-copulatory sexual selection (in terms of sperm competition (Parker 1997) and cryptic female choice (Firman et al. 2017)) can drive the evolution of SSD. Specifically, post-copulatory sexual selection may not necessarily promote SSD but can also relax selection for increased body size. This is because a resource allocation trade-off between pre- and post-copulatory investment may favour smaller body size in species in which larger size confers a selective advantage in pre- but not post-copulatory sexual selection (Fitzpatrick et al. 2012; Parker 1992). Therefore, traits evolving in response to post-copulatory sexual selection, like testis size, may exhibit a negative cross-species correlation with SSD (Fitzpatrick et al. 2012). However, such a negative correlation may not always arise because inter-specific differences in the total amount of resources allocated towards sexually selected traits may alternatively promote a positive correlation between investment into pre- and post-copulatory competitiveness across species.

Sexual selection can operate in both sexes (Fromonteil et al. 2023; Janicke et al. 2016) and could in principle lead to the evolution of either female-biased or male-biased SSD. Nevertheless, theory predicts that sexual selection is typically stronger in males than females (Bateman 1948) giving rise to so-called Darwinian sex roles, which have been found to predominate the animal tree of life (Janicke et al. 2016). Hence, in most species stronger sexual selection in males might drive the evolution of male-biased SSD. However, sexual selection might not always favour larger males but may sometimes select for smaller body size whenever small individuals have a competitive advantage. For example, sexual selection for smaller body size has been reported for species in which courtship displays depend on high levels of agility (Mikula, Toszogyova, and Albrecht 2022; Serrano-Meneses and Székely 2006; Székely, Freckleton, and Reynolds 2004). Moreover, there are notable exceptions from Darwinian sex roles when competition for mating opportunities is more intense among females than males, such as in shorebirds, pipefish and seahorses (Rosenqvist and Berglund 2011; Székely et al. 2024; Vincent et al. 1992). In addition, even in species with Darwinian sex roles, sexual selection can lead to a female-biased SSD if males show a preference for larger females because they are typically more fecund (López-Cortegano et al. 2020; Ng et al. 2019). In fact, recent meta-analytic evidence suggests that females usually benefit from—and hence might compete for—additional matings (Fromonteil et al. 2023).

Forms of natural selection, other than sexual selection, have also increasingly been discussed as a potential driver of SSD (Rivas and Burghardt 2001) including fecundity selection (Fox, Cooper, and Hayes 2015; Cassini 2017; Jiménez-Arcos, Sanabria-Urbán, and Cueva del Castillo 2017) and selection arising from temperature regulation (Stillwell et al. 2010), predation risk (Schoenjahn, Pavey, and Walter 2020) and resource acquisition (Cassini 2022). Furthermore, ecological factors like latitude (García-Navas 2017), food abundance (Brown, Madsen, and Shine 2017), niche segregation (Cassini 2022; González-Suárez and Cassini 2014; Krüger et al. 2014) and population density (Isaac 2005; Shine 1989) might play an important role in SSD evolution. In particular, ecological character displacement has been suggested to explain the evolution of sexual dimorphism independently of sexual selection (De Lisle 2019). Specifically, competition for a shared resource and imperfect genetic correlations between the sexes might enable disruptive selection on ecologically sexually dimorphic traits (De Lisle 2019). For instance, SSD could evolve if males and females have different nutritional optima (Slatkin 1984). This can lead to SSD if the optimal body size to acquire food in the 'dimorphic niches' of the sexes differ (Cassini 2022). Importantly, any SSD can only evolve if selection acts on body size in both sexes with different optima, with the exception of SSD arising due to genetic drift under relaxed selection on body size. While the evolution of SSD is likely not driven by a single force, but a multitude of different processes (Allen, Zwaan, and Brakefield 2011; Cassini 2017; Gordon 2006; Isaac 2005; Li and Kokko 2021), the relative importance of natural and sexual selection remains unclear and empirical evidence equivocal.

Comparative studies testing for an evolutionary link between various proxies of sexual selection and SSD have provided mixed results. For example, male-biased SSD has been documented to positively correlate with the presence of male combat over mating opportunities in turtles suggesting that sexual selection is a driver for SSD in this clade (Berry and Shine 1980). Similarly, lekking and intra-sexual competition have been argued to lead to the evolution of SSD in birds (Payne 1984; Székely, Lislevand, and Figuerola 2007). In a comparative study of 3700 bird species the best predictor for SSD was social mating system followed by display agility (Székely, Lislevand, and Figuerola 2007). In contrast, recent studies have questioned whether sexual selection is the main driver of SSD. For example, Cassini speculated that SSD in primates is mainly due to natural selection, because SSD seems to have evolved prior to polygyny (Cassini 2020). Moreover, contrary to the prediction that SSD often results from sexual selection acting on male body size, a phylogenetic study in birds has shown that in about 50% of the tested species, selection for decreased female size led to the observed male-biased SSD (Karubian and Swaddle 2001). Finally, a recent meta-analysis compiled estimates of standardised sexual selection metrics (i.e., the Bateman gradient and the opportunity for sexual selection) of 59 animal species, showing that there is only a weak relationship between pre-copulatory sexual selection and SSD across a broad range of animal taxa (Janicke and Fromonteil 2021). While the authors found evidence for a significant correlation of the opportunity for selection (i.e., a measure of the upper boundary of pre-copulatory sexual selection) with SSD, there was no such correlation for the sex-difference in Bateman gradients (Janicke and Fromonteil 2021).

Here we synthesise the existing literature of comparative studies to provide a general test for the role of sexual selection in the evolution of SSD in animals. Specifically, we included a wide array of different proxies for the strength of sexual selection. This allowed us to synthesise our current knowledge and to analyse the relationship between SSD and sexual selection on a broader taxonomic range using a more comprehensive and diverse dataset compared to previous studies focusing on Bateman metrics for the strength of sexual selection (e.g., Janicke and Fromonteil 2021). We addressed the hypothesis that stronger sexual selection drives the evolution of a more male-biased SSD and explored whether pre- and post-copulatory episodes of sexual selection shape SSD differently. Finally, we studied how methodological differences among studies contribute to potential heterogeneity among studies.

2 | Materials and Methods

The study was conducted in three steps. First, we performed a systematic literature search for comparative studies and meta-analyses testing for a relationship between proxies of sexual selection (see Table S1) and adult SSD. Next, we extracted Pearson correlation coefficients and the associated sampling variance from each primary study quantifying the relationship between sexual selection and SSD across the included species. Finally, we performed a phylogenetically controlled meta-analysis testing globally for a non-zero correlation coefficient and the effect of diverse moderators.

2.1 | Search Protocol

We searched the 'Web of Knowledge (Web of Science Core Collection)' and 'Scopus' on 20.03.2024 for studies including the keywords 'size dimorphism' and 'sexual selection', 'mating system', 'sexual conflict', 'sex ratio', 'competition', 'sperm competition', 'testis', 'testes', 'ornament' or 'armament' (see supporting information for Boolean search terms). Overall, the search yielded 3444 hits after removing duplicates of which we examined 225 full-texts after scanning the title and abstract. In addition, we performed a backward-forward search on 26.7.2024 in 'Web of Knowledge (Web of Science Core Collection)' and 'Scopus' for four landmark papers (Blanckenhorn 2005; Isaac 2005; Lande 1980; Reeve and Fairbairn 2001). After removing duplicates with our original search, we scanned the title and abstract of 1845 articles and 33 full texts. This search yielded five additional effect sizes from four studies. Finally, we removed duplicate data, that is data that was published in multiple papers ($N = 7$). A total of 77 studies comprising 127 effect sizes were included in the analyses (PRISMA diagram: Figure S4; after Page et al. 2021). Overall, primary studies covered on average 149 different species ranging from 6 to 1861 species.

2.2 | Moderators

We extracted several moderators from each primary study to explore biological and methodological causes underlying among-study heterogeneity in effect sizes. First, we tested if the type of sexual selection proxy used in primary studies correlated with the observed effect sizes. We classified proxies into their types as pre-copulatory, post-copulatory or pre- and post-copulatory (see Table S1 for details). This was followed by a finer classification into population density, mating system, sex ratio, post-mating competition, pre-mating competition, trait-based and 'other' (see Table S1 for details). Second, we tested if the studied taxon influenced effect sizes (see Figure 1). Third, we explored several methodological differences between primary studies that might affect outcomes. Specifically, we tested whether effect sizes depended on (1) whether SSD was measured using body size or body mass, (2) whether tests for a relationship between sexual selection and SSD accounted for inter-specific variation in body size or body mass and (3) whether the analysis performed in the primary study accounted for phylogenetic non-independence. Finally, we inspected if the publication year of primary studies affected the reported effect sizes, to test for the so-called bandwagon effect (i.e., after initial publications of influential studies with large effect sizes, the study topic becomes 'mainstream' and effect sizes dwindle) (Bindra et al. 2022).

2.3 | Statistical Analysis

We performed all analyses in R (version 4.4.0) (R Core Team 2022). First, we extracted correlation coefficients (Pearson's r) from each primary study, which served as an effect size in our meta-analysis. If primary studies did not provide correlation coefficients, we transformed other test-statistic values (i.e., t values, χ^2 & F values) to r using formulas reported elsewhere (Borenstein et al. 2009) or

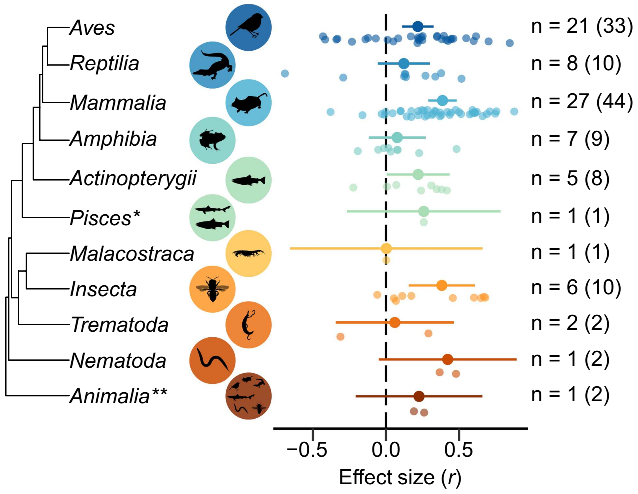

FIGURE 1 | Phylogeny covering the taxonomic classes included in the meta-analysis. For each taxonomic clade estimates of effect sizes (r) are shown with 95% CIs obtained from non-phylogenetic model (Table S2). Sample sizes (n) are reported as the number of studies and number of effect sizes (in brackets). *Pisces are a paraphyletic group. Pisces were placed equidistantly between the next neighbouring classes. **Animalia were included as an outgroup at an arbitrary distance.

the 'esc' package (Lüdecke 2019). Correlation coefficients were set as positive when indicating a positive relationship between sexual selection and estimates of more male-biased SSD. We also obtained the sample size (i.e., the number of tested species) from each primary study, which allowed us to compute the sampling variance for each correlation coefficient. We then fitted meta-analytic multilevel mixed-effects models using a restricted maximum likelihood approach implemented in the 'rma.mv' function of the 'metafor' package (Viechtbauer 2010). We addressed the question if sexual selection is correlated positively with a more male-biased SSD as typically assumed in the sexual selection literature (Fairbairn et al. 2007). For this, we ran a global model on correlation coefficients that were either positive (indicating a positive relationship between sexual selection and a more male-biased SSD) or negative (indicating a negative relationship between sexual selection and a more male-biased SSD). Next, we separately added different moderators to the latter model to explore possible sources for the heterogeneity between effect sizes. All models included an observation-level index and the study identifier as random terms. Furthermore, each analysis was performed with and without accounting for phylogenetic non-independence of effect sizes (see section Phylogeny for details). Both phylogenetic and non-phylogenetic analyses led to qualitatively similar conclusions and all non-phylogenetic analyses are presented in Tables S3, S4 and S5B. When testing for effects of categorical moderators, we quantified the partial effect size for each factor level and corrected *p* values for multiple testing by applying the 'false discovery rate' method (FDR) (Benjamini and Hochberg 1995).

2.4 | Phylogeny

We reconstructed the phylogeny of all sampled classes based on published data of median divergence times (http://www.timetree.org/) (Kumar et al. 2022) to account for phylogenetic non-independence between estimates from different animal classes (Figure 1). Two included studies did not contain a taxonomic class to be used in the phylogeny. First, Pisces were placed equidistantly between the next neighbouring clades (Actinopterygii and Nematoda/Insecta) as they are a paraphyletic group. Second, Animalia were included as an outgroup at a distance of 768 million years apart (same distance as between the two most basal classes in the phylogeny) to mimic the independence of the underlying effect sizes relative to the effect sizes that focus on taxonomic groups within Animalia.

2.5 | Publication Bias

To test for publication bias, we transformed r into Fisher's z (Borenstein et al. 2009) and ran multilevel mixed-effects models with z as the predictor and its standard error as the response with study ID and an observation level random effect (Nakagawa et al. 2022). As throughout, we ran this model with and without controlling for phylogenetic non-independence. While the sampling variance in r depends on the effect size itself and the sample size, the sampling variance in z is only a function of the underlying sample size. Hence, if large z values are associated with a large standard error in z, this indicates that underpowered studies were only published if the effect was large, suggesting publication bias (Nakagawa et al. 2022).

3 | Results

We explored the hypothesis that stronger sexual selection correlates with a more male-biased SSD by defining effect sizes positive when indicating support for a positive relationship between sexual selection and a more male-biased SSD. Overall, 106 of the 127 correlation coefficients between SSD and proxies for sexual selection were positive (83%; Figure 2). This translated into a significantly positive global effect size (phylogenetic model: r [95% CI] = 0.26 [0.12, 0.40]; $n = 127$; $z = 3.57$; $p < 0.001$; Figure 2) suggesting that sexual selection promotes the evolution of male-biased SSD. The phylogenetic relatedness among taxa accounted for 15% of the heterogeneity, 27% were explained by study identity whereas 58% of heterogeneity remained unexplained. Effect sizes did not differ among the 11 taxonomic groups included in the dataset (Table S2 and Figure 1).

Then we tested whether the form of sexual selection proxy used in primary studies explained between-study variance in effect sizes. First, we partitioned sexual selection proxies into its three major episodes: pre- and post-copulatory proxies and proxies that engulfed both forms (here called 'sexual selection episode'; see Table S1 for classification). The episode of sexual selection had a significant effect on the estimated correlation coefficient (Table 1 and Figure 3). Overall, pre-copulatory sexual selection proxies and proxies that encompassed pre- and post-copulatory episodes of sexual selection were positively correlated with the male-bias in SSD (Table 1 and Figure 3). Nevertheless, traits involving both pre- and post-copulatory episodes of sexual selection showed significantly larger correlation coefficients compared to solely pre-copulatory traits (phylogenetic model: estimate [95% CI] = 0.14 [0.04, 0.24]; $n = 108$; $z = 2.72$; $p = 0.006$). By contrast, post-copulatory sexual selection proxies showed a statistically non-significant negative correlation with a male-bias in SSD (Table 1), and had significantly lower correlation coefficients compared to pre-copulatory proxies (phylogenetic model: estimate [95% CI] = −0.36 [−0.52, −0.20]; $n = 71$; $z = -4.46$; $p < 0.001$).

Second, we made a finer classification of sexual selection proxies into population density, mating system, sex ratio, post-mating competition, pre-mating competition, trait-based and other (containing all traits not attributable to the former categories). When sexual selection proxies were compared at this finer scale, premating competition, mating system and sex ratio were significantly positively correlated with the male-bias in SSD (Table S4 and Figure S1). By contrast, trait-based proxies (e.g., male aerial displays and plumage dimorphism in birds) and post-mating competition (e.g., sperm competition, as indicated by relative testes size) were non-significantly associated with male-biased SSD (Table S4 and Figure S1).

Next, we tested whether the obtained effect sizes were related to different methodologies used in primary studies. Primary studies used different types of SSD measures, with 58 estimates calculated from body mass and 67 from size measures (e.g., body length or wing length; two effect sizes were calculated using a combination of body size and body mass and were excluded from the latter analysis). Still, effect sizes did not differ significantly with regard to usage of body of size or body mass for estimating SSD (Table S5A and Figure S2A). Few primary studies (17

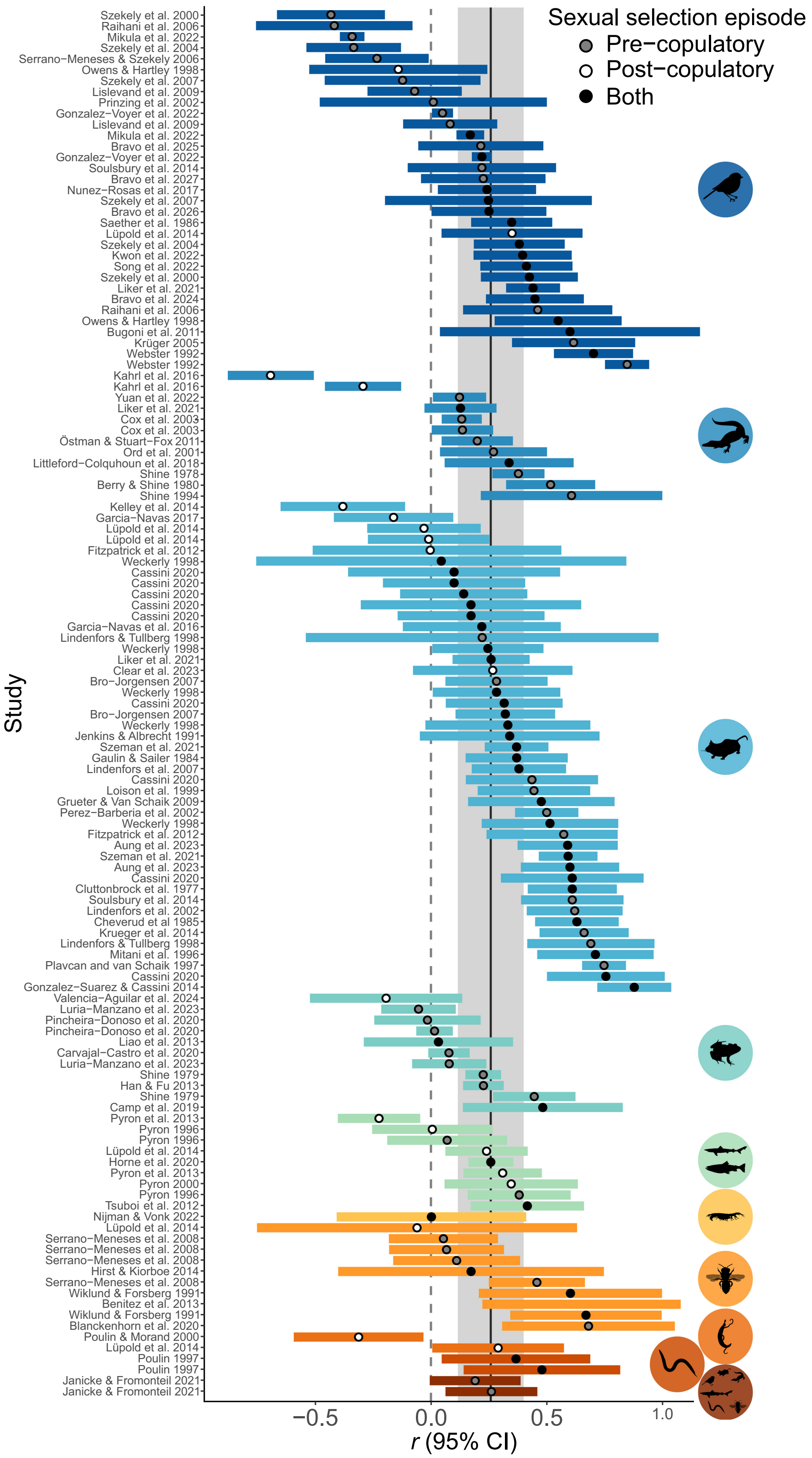

FIGURE 2 | Forest plot showing effect sizes from primary studies (Pearson correlation coefficients ±95% CIs; *n* = 77 studies and 127 effect sizes) and the global effect size (black line with grey area indicating 95% CIs). Taxonomic clades highlighted by coloured error bars (see Figure 1) and sexual selection episodes (i.e., pre-copulatory, post-copulatory and both pre- and post-copulatory) by the symbol of mean effect size. Positive effect sizes correspond to a positive relationship between sexual selection and male-biased sexual size dimorphism.

TABLE 1 | Effect of sexual selection episode (i.e., pre-copulatory, post-copulatory or pre- and post-copulatory) on effect sizes for the relationship between sexual selection and sexual size dimorphism (SSD).

					Test of moderator	
Sexual selection episode	***r* (95% CI)**	***n***	***z***	**Adj. *p***	**QM**	***p***
Pre-copulatory	0.26 (0.11, 0.40)	52	3.46	< 0.001	38.09	<0.001
Post-copulatory	−0.10 (−0.29, 0.08)	19	−1.07	0.285		
Pre- and post-copulatory	0.40 (0.25, 0.55)	56	5.31	<0.001		

Note: Results of restricted maximum likelihood (REML) controlling for phylogeny are shown including the test statistic of the omnibus test of the moderator (QM). *p* values are corrected for multiple testing by the 'false discovery rate' method (FDR; Benjamini and Hochberg 1995). See Table S4 for model not controlling for phylogeny.

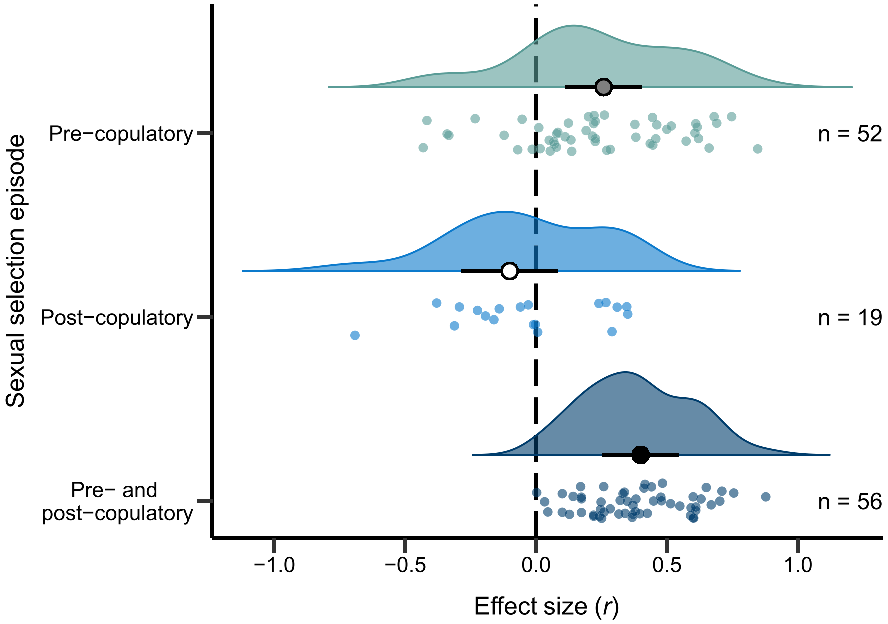

FIGURE 3 | Comparison of effect sizes between different episodes of sexual selection (i.e., pre-copulatory, post-copulatory or both pre- and post-copulatory) including sample sizes and estimates with 95% CIs obtained from a phylogenetic model (Table 1). Sample sizes (*n*) refer to the number of effect sizes.

effect sizes; 13%) controlled for total body mass or size of each species to exclude allometric effects on SSD (i.e., Rensch's rule Rensch (1959)) when testing for a relationship between sexual election and SSD. Our results suggest that effect sizes of studies that corrected for body size or body mass did not differ significantly from those that did not correct for it (Table S5A and Figure S2B).

A total of 23 effect sizes were obtained from studies which themselves did not control for phylogenetic non-independence (18%), and effect sizes of these studies were significantly larger compared to studies that accounted for phylogenetic non-independence in their analyses (Table S5A and Figure S2C). We therefore repeated all presented analyses excluding studies that did not account for phylogenetic non-independence (see supporting information). Nevertheless, there were no qualitative changes in main results and the conclusions drawn from the presented analyses are upheld in these alternative analyses. Primary studies varied regarding the overall sex difference in size across the studied taxonomic group (i.e., some studies focused on taxa with more male-biased SSD, while others on taxa with more female-biased SSD). Yet, we did not detect a significant relationship between the percentage of species with a female-biased SSD and effect sizes (Table S5A and Figure S3A).

To test for publication bias, we tested for a relationship between effect sizes (transformed to *z*) and their standard error. A significantly positive correlation would indicate that small studies were more likely to get published if the effect was large, which might be suggestive of publication bias (see Section 2 for details; Nakagawa et al. 2022). We found a non-significant trend for a positive correlation between effect sizes and their standard error indicating minimal evidence for bias (Table S5A and Figure S3B). Interestingly, we found a significantly negative relationship between effect sizes and their publication year (Table S5A and Figure S3C), suggesting the presence of the bandwagon effect (i.e., after initial publications of influential studies with large effect sizes, the study topic becomes 'mainstream' and effect sizes dwindle) (Bindra et al. 2022). However, the latter relationship was probably due to an overrepresentation of studies not accounting for phylogeny in the early years, which we found to show higher effect sizes compared to later studies which corrected for phylogenetic non-independence (see above).

When studies that did not control for phylogeny were excluded from the analysis, there was no significant relationship between publication year and effect size (Table S9).

4 | Discussion

Our synthesis of comparative studies provides evidence for a relationship between SSD and sexual selection across animals. We found that sexual selection is typically correlated with a more male-biased SSD, strengthening the hypothesis that sexual selection plays a significant role in the evolution of SSD by favouring larger males. Importantly, primary studies focusing on pre-copulatory episodes of sexual selection provided particularly strong support for a relationship between sexual selection and the male-bias in SSD suggesting that pre-copulatory rather than post-copulatory sexual selection promotes the evolution of male-biased SSD.

Proxies encompassing both pre- and post-copulatory episodes of sexual selection (e.g., group size or sex ratio) showed the strongest positive correlation with SSD, whereas a statistically non-significant negative correlation was found proxies of post-copulatory sexual selection (e.g., relative testis size used as a proxy for sperm competition). Specifically, SSD tended to be less male-biased in species with proxies indicating more intense sperm competition. Such an effect might arise from a negative relationship between investment into sperm competition and somatic growth due to a negative genetic correlation and/or a resource allocation trade-off (Lüpold et al. 2014; Parker, Lessells, and Simmons 2013; Simmons, Lüpold, and Fitzpatrick 2017). For example, in heteromyid rodents the baculum size (i.e., penis bone size, as a proxy for post-copulatory sexual selection) negatively correlated with SSD, suggesting a trade-off between pre- and post-copulatory traits across species (García-Navas 2017). This is in line with theoretical work suggesting that investment into sperm competitiveness should decrease as pre-copulatory competition for mating partners increases (Parker, Lessells, and Simmons 2013). Importantly, a trade-off between pre- and post-copulatory sexual selection, that co-varies with the strength of male–male contest competition, has been shown in a broad comparative study (Lüpold et al. 2014). Nevertheless, the correlations between pre- and post-copulatory traits are often inconsistent, both within and across species, and the species specific biology can play an important role (Simmons, Lüpold, and Fitzpatrick 2017), which might explain the variation found between taxonomic classes and sexual selection proxies in this study.

Surprisingly, we found the largest effect size for measures that combined pre- and post-copulatory sexual selection. This seems counterintuitive as our data also seems to show that pre- and post-copulatory sexual selection are related to SSD in opposing ways. Hence, one might expect sexual selection proxies that encompass both pre- and post-copulatory sexual selection to show lower effect sizes compared to measures that purely capture pre-copulatory sexual selection. We can only speculate about the reasons for this result, but they highlight that the trade-off between pre- and post-copulatory sexual selection is not always straight forward (Simmons, Lüpold, and Fitzpatrick 2017). In fact, there are instances where pre- and post-copulatory sexual selection seems to work in concert (reviewed in Simmons, Lüpold, and Fitzpatrick 2017) and it might be that for some taxa included in our dataset, both promote the evolution of a male-biased SSD (Lüpold et al. 2014). For example, in taxa with intense sperm competition, males might also more likely engage in pre-copulatory male–male competition to avoid the former, leading to positive covariation between pre- and post-copulatory sexual selection (Lüpold et al. 2014).

Our meta-analysis revealed that trait-based proxies of sexual selection (e.g., male agility displays and plumage dimorphism) did not correlate with SSD uniformly across the taxa, with some effect sizes even indicating that stronger sexual selection is associated with a less male-biased SSD. For example in birds, the performance of male aerial displays can be negatively correlated with male body size as smaller males seem to be more agile (Mikula, Toszogyova, and Albrecht 2022; Serrano-Meneses and Székely 2006; Székely, Lislevand, and Figuerola 2007). This suggests that sexual selection can, at least indirectly, favour smaller males whenever a sexually selected trait is phenotypically and/or genetically negatively correlated with body size. Collectively, these findings indicate that the relationship between sexual selection and SSD depends on the episode of sexual selection, with pre- but not post-copulatory sexual selection favouring the evolution of male-biased SSD.

The primary studies we included in the analyses were correlational themselves meaning that our meta-analysis does not allow any inference of the underlying causal link between sexual selection and SSD. Furthermore, while we are focusing primarily on the hypothesis that sexual selection on males is driving a male-bias in SSD either as a result of male–male competition or by the choice of females, there is also the possibility that SSD results from sexual selection on females or both sexes. In fact, there is an increasing evidence that sexual selection directly influences females as well (Clutton-Brock 2009; Fromonteil et al. 2023; Hare and Simmons 2019), highlighting the potential of sexual selection in females to be involved in shaping the relationship between SSD and sexual selection. Interestingly, for Cardueline finches, it has been found that male-biased SSD is as likely to result from selection for increased size in males as from selection for decreased size in females, although it remains unclear if the latter scenario actually involves sexual selection on females (Karubian and Swaddle 2001). Nevertheless, natural selection and especially fecundity selection (Fox, Cooper, and Hayes 2015; Jiménez-Arcos, Sanabria-Urbán, and Cueva del Castillo 2017) in females likely play a paramount role in the evolution of SSD but direct evidence that natural selection contributes to the evolution of SSD across species is still lacking.

We detected substantial heterogeneity among effect sizes, which might result from methodological rather than biological differences among primary studies. For instance, SSD can be measured in different ways and the type of measurement could potentially affect the results of primary studies (Lovich and Gibbons 1992). Our analyses suggest that effect sizes did not depend on whether size (e.g., tarsus or wing length) or mass was used to estimate SSD. In addition, we did not detect an effect of controlling for an allometric relationship of SSD and body size (as expected to occur under Rensch's rule (Fairbairn 1997; Rensch 1959)) on the strength of the relationship between sexual selection and SSD. This suggests that, at least, major methodological differences between primary studies did not have a major impact on the presented results.

Based on the hypothesized causal effect of sexual selection, SSD has frequently been used as a proxy for the overall strength of and sex bias in sexual selection in comparative studies and meta-analyses over the last decades (for a non-exhaustive list of 45 of such studies see supporting information). Our finding of a general correlation between various measures of sexual selection and SSD suggests that SSD may indeed provide a useful proxy for the strength of sexual selection across species. A recent meta-analysis compiling data from similarly broad range of species across the animal kingdom found only mixed support for it (Janicke and Fromonteil 2021). However, this earlier study relied on a relatively limited number of species for which standardised metrics of pre-copulatory sexual selection (i.e., the opportunity for selection and Bateman gradients) are available. By contrast, our more comprehensive study in terms the number of sexual selection proxies and taxonomic range, provides clear evidence for a significant relationship between sexual section and SSD. Yet, our analysis relies primarily on estimates from birds and mammals, which might not necessarily be representative for the whole animal kingdom. Furthermore, primary research might have been biased towards taxa which show clear SSD. Indeed, 72 effect sizes (61%) were from studies with a clear overall male-bias in SSD and 30 effect sizes (25%) were from studies with more female-biased SSD. Only in 17 effect sizes (14%) data were collected in taxa that showed less than 10% deviation from parity in SSD across species. Still, a male-bias in SSD is not necessarily the norm across the animal kingdom and current evidence even challenges that males are typically larger than females in mammals (Tombak, Hex, and Rubenstein 2024).

Our global effect size suggests that sexual selection explains on average only about 6.25% of the total variance in the male-bias of SSD, which can be broadly classified as a moderate effect size (Cohen 1992). In this context, we stress that all proxies for the strength of sexual election used in the compiled primary studies are incomplete measures. This could have led to an underestimation of our global effect size quantifying the correlation between SSD and the actual strength of sexual selection. While all presented proxies for sexual selection are likely to be imperfect, we suspect that proxies of older studies might have been particularly incomplete because many older classifications of the mating system relied only on behavioural observations, which is known to lead to an overestimation of monogamy (Brouwer and Griffith 2019).

While overall SSD might be a useful and readily accessible proxy for sexual selection, our meta-analysis revealed clear limitations. First, proxies for post-copulatory sexual selection such as relative testis size and pre-copulatory traits like flight-agility displays in birds (Mikula, Toszogyova, and Albrecht 2022; Serrano-Meneses and Székely 2006) might correlate negatively with SSD. Second, opposing effects of pre- and post-copulatory sexual selection on the evolution of SSD could compromise SSD as a proxy for the total strength of sexual selection. We call for additional data to strengthen our currently limited understanding of the relationship of post-copulatory sexual selection and SSD. In particular, it remains unclear how resource allocation trade-offs between pre- and post-copulatory sexual selection contribute to the evolutionary patterns observed in this study. Most importantly, direct tests of the effect of sexual selection and SSD are virtually lacking and experimental evolution experiments provide a promising approach to establish a causal relationship (Kaufmann et al. 2021).

In conclusion, we found evidence that the strength of sexual selection is associated with the extent of SSD across the animal kingdom. Importantly, proxies encompassing pre- but not post-copulatory episodes of sexual selection correlated positively with the male-bias in SSD supporting arguments that pre-copulatory sexual selection is a primary driver for the evolution of SSD in animals. Yet, our synthesis suggests an only moderate global effect of sexual selection on SSD highlighting the need for more studies on the relative importance of (non-sexual) natural selection for generating SSD across the animal tree of life.

Author Contributions

T.J. conceived the study. T.J. and L.W. designed the meta-analysis, with help from R.P.F. and T.S., L.W. compiled the data, with help from T.J., L.W. and T.J. performed the statistical analyses, with help from R.P.F., L.W. and T.J. wrote the paper with help from R.P.F. and T.S. All authors read and approved the submitted version of this manuscript.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

All data and code used in the analyses have been published at Zenodo (https://doi.org/10.5281/zenodo.10406052). In addition, all code used in the analysis is available at GitHub via https://lennartwinkler.github.io/SSD_and_sexual_selection_2024/.

Peer Review

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.