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The macroevolution of sexual size dimorphism in birds

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ABSTRACT

There is considerable variation of sexual size dimorphism (SSD) in body mass among animal groups, yet the drivers of interspecific variation in SSD are still poorly understood. Possible mechanisms have been suggested, including sexual selection, selection for fecundity in females, niche divergence between sexes, and allometry, yet their relative importance is still poorly understood. Here, we tested predictions of these four hypotheses in different avian groups using a large-scale dataset on SSD of body mass for 4761 species. Specifically, we estimated the probability of transition between male- and female-biased SSD, tested for differences in evolutionary rates of body mass evolution for males and females, and assessed the potential ecological and spatial correlates of SSD. Our results were consistent with the sexual selection, fecundity, and niche divergence hypotheses, but their support varied considerably among avian orders. In addition, we found little evidence that the direction of SSD affected the evolution of male or female body mass, and no relationship was detected between SSD and environmental predictors (i.e. temperature and precipitation seasonality, productivity, species richness, and absolute latitude). These results suggest that avian evolution of SSD is likely to be multifactorial, with sexual selection, fecundity, and niche divergence playing important roles in different avian orders.

Keywords: body size; evolutionary rates; phylogenetic comparative methods; sexual selection

INTRODUCTION

Sexual size dimorphism (SSD) in body mass varies greatly across animal species, even among closely related taxa (e.g. Nuñez-Rosas *et al.* 2017, Agha *et al.* 2018, Portik *et al.* 2020). For instance, female-biased SSD is common in invertebrates and ectothermic vertebrates, such as the blanket octopus, *Tremoctopus violaceus*, in which females can reach ≤40 000 times the weight of the male (Norman *et al.* 2002). In contrast, male-biased SSD is prevalent in birds and mammals, such as elephant seals, in which males can weigh ≤10 times more than females (Ralls and Mesnick 2009). Although extreme SSD is relatively rare, moderate SSD (e.g. when the sexes differ by <10%) is widespread across various animal taxa (Fairbairn *et al.* 2007). Despite this pervasiveness, the mechanisms that generate and maintain SSD are still poorly understood.

Although many mechanisms have been proposed as potential drivers of the evolution of SSD, they can be summarized tentatively into four main hypotheses. According to the sexual selection hypothesis, SSD could result from male–male competition, given that larger males could be favoured in the context of female choice or direct combat (Székely *et al.* 2000, 2007, Owen *et al.* 2017). Alternatively, the fecundity hypothesis posits that SSD might be attributable to selection towards larger females for greater reproductive capacity (Darwin 1874, Reeve and Fairbairn 1999, Székely *et al.* 2007), which might be enhanced in regions with shorter breeding seasons (Tarr *et al.* 2019). In the niche divergence hypothesis, SSD would be associated with ecological factors, such that differences among sexes would result in resource partitioning, allowing for the exploitation of distinct niches by males and females and leading to decreased intraspecific competition (Darwin 1874, Selander 1966, Shine 1994). Finally, the allometry hypothesis suggests a more structuralist explanation for SSD based on Rensch's rule (i.e. male-biased SSD increases and female-biased SSD decreases with body size; Rensch 1959). In particular, if SSD is strongly allometric, selection for increased or decreased body size could lead indirectly to variation in SSD as a byproduct. It is important to note, however, that Rensch himself posited that his rule is valid only for birds and that even in this group there are exceptions (e.g. harpy eagle).

These different hypotheses posed to explain the evolution of SSD did not receive the same level of investigation over the years. The study of the evolution of secondary sexual characteristics in vertebrates has influenced hypotheses related to these

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traits. As a result, the sexual selection and the fecundity hypotheses have been invoked increasingly in recent publications (e.g. Székely *et al.* 2000, 2007, Lislevand *et al.* 2009, García-Navas *et al.* 2017, Owen *et al.* 2017, Tarr *et al.* 2019, Horne *et al.* 2020). Alternatively, the allometry hypothesis was invoked mostly at the beginning of the study of sexual dimorphism mechanisms (e.g. Abouheif and Fairbairn 1997, Webb and Freckleton 2007, Lislevand *et al.* 2009), whereas niche divergence is still mentioned in a handful of studies (e.g. Székely *et al.* 2000, Serrano-Meneses and Székely 2006, Lislevand *et al.* 2009), but it is not as common as the first two hypotheses. Traditionally, previous studies tended to focus on only one of these hypotheses at a time (but see Shine 1994, Cox *et al.* 2003, Serrano-Meneses and Székely 2006, Lislevand *et al.* 2009, Stephens and Wiens 2009, García-Navas *et al.* 2016). These studies typically used proxies related to sexual selection, such as contrasting mating systems and parental care (e.g. Horne *et al.* 2020, Gonzalez-Voyer *et al.* 2022), or related to the fecundity hypothesis by measuring egg and clutch sizes (e.g. Serrano-Meneses and Székely 2006, Liang *et al.* 2022).

Our approach in this study differs from previous work in two main ways. First, we test all four of these hypotheses within a similar, comparable framework and with a comprehensive dataset involving information on thousands of species. Second, we explore predictions from each hypothesis using an explicitly macroevolutionary approach (Table 1). For instance, if the sexual selection hypothesis is the best descriptor of SSD evolution, then the differences in SSD would be driven largely by changes in male body mass, predicting that: (i) transitions from female-biased SSD to male-biased SSD should be more likely than in the other direction; and (ii) the rate of male body mass evolution would be higher than the rate of female body mass evolution. Likewise, the same argument could be made for the fecundity hypothesis, but with opposite predictions, because SSD would be driven largely by changes in female body mass. In contrast, given that the niche divergence hypothesis predicts only character displacement, it would not predict changes preferentially in one of the sexes, thus both transition rates and rates of evolution should be similar between males and females. Finally, given that either one or the other sex would depart more markedly from the line of isometry according to the allometry hypothesis, the rate of body mass evolution should be faster in whichever sex has the largest body mass, whereas it makes no clear prediction regarding differences in transition rates.

We also explored ecological predictions of different hypotheses, given that the fecundity hypothesis predicts a positive relationship between female-biased SSD and seasonality (see Tarr *et al.* 2019), whereas the niche divergence hypothesis predicts a positive relationship between absolute SSD and species richness and productivity, given that they would reflect local opportunity for interspecific competition (Dayan and Simberloff 1994, Butler *et al.* 2007). Finally, if one envisions a scenario in which the evolution of body mass is strongly affected by latitude (i.e. Bergmann's rule; Bergmann 1847), changes in SSD could be a byproduct of latitudinal variation in overall body mass, such that absolute SSD values should be correlated positively with latitude (Table 1). We focused on birds as our model system for this study, given the extensive availability of data on their species diversity, distribution, and body mass.

MATERIALS AND METHODS

Data sources

Body mass data for males and females of a total of 4761 bird species were obtained from Lislevand *et al.* (2007), Myhrvold *et al.* (2015), and Ocampo *et al.* (2021). We focused our analyses on the nine most species-rich orders, namely Accipitriformes, Anseriformes, Apodiformes, Charadriiformes, Columbiformes, Galliformes, Passeriformes, Piciformes, and Psittaciformes. We chose to use this criterion rather than others (such as orders with high SSD variability) in order to comprehend the universality of SSD mechanisms across birds, avoiding the potential bias of focusing solely on orders that are more inclined to yield significant results. When a species was present in more than one source, the average of the corresponding estimates was used in subsequent analyses (for the complete compiled dataset, see Supporting Information, Table S2). Phylogenetic relationships were retrieved from Jetz *et al.* (2012) (Ericson backbone trees). Species distribution data were obtained from the BirdLife International database (BirdLife International and Handbook of the Birds of the World 2021). Finally, bioclimatic data were retrieved from WorldClim (Fick and Hijmans 2017), and net primary productivity (NPP) data were extracted from Sun *et al.* (2020). To analyse the NPP data, owing to computational limitations, we averaged only the estimates of the last 10 years of the 38 years from Sun *et al.* (2020).

Table 1. Academic predictions of the four hypotheses tested in the present study as potential drivers of sexual size dimorphism (SSD). See main text for details.

Hypothesis	Transitions between types of SSD	Rates of body mass evolution	Spatial/ecological correlates
Sexual selection	♂ SSD → ♀ SSD < ♀ SSD → ♂ SSD	Rate of ♂ > Rate of ♀	No clear prediction
Fecundity	♂ SSD → ♀ SSD > ♀ SSD → ♂ SSD	Rate of ♂ < Rate of ♀	Positive relationship between ♀ SSD and seasonality
Niche divergence	♂ SSD → ♀ SSD ≈ ♀ SSD → ♂ SSD	Rate of ♂ ≈ Rate of ♀	Positive relationship between absolute SSD and species richness + productivity
Allometry	No clear prediction	Rate of body size evolution should be faster in the larger sex	Positive relationship between absolute SSD and latitude

Analyses

Sexual size dimorphism was measured according to the size dimorphism index (SDI) of Lovich and Gibbons (1992), which is calculated as the ratio of the size of the larger sex in relationship to the smaller sex, and subtracting one, arbitrarily made negative if the male is larger and positive if the female is larger. This measure of SSD is symmetric around zero, does not asymptote, and contains information on direction, giving it desirable properties as a measure of SSD (Lovich and Gibbons 1992). We mapped SDI and the $\log_{10}$-transformed average body mass of each species onto the phylogeny to explore how these traits are distributed across taxa, using the PHYTOOLS v.1.0-3 package (Revell 2012). In this analysis, SDI was characterized as minus one if the species have male-biased SSD or one if the species have female-biased SSD, disregarding the degree of SSD for the purposes of visualization. We also explored geographical variation in male- and female-biased SSD by mapping the median SDI across all species present in a given cell at a resolution of 10 arc-min. Maps were generated either using all species or separately, only for species with male- and female-biased SSD.

To test for asymmetry in the transition rates between female-biased SSD and male-biased SSD, we fitted Mk models of discrete character evolution to our data. The SDI was treated as a binary variable, where minus one corresponded to male-biased SSD and one to female-biased SSD. To simplify parameter estimation and model selection, monomorphic species (i.e. males and females having exactly the same size) were excluded from this analysis (N = 177, which accounted for ~3.72% of the entire dataset). Including a third discrete state for monomorphic species would considerably increase the complexity of the analysis, including the comparison of non-nested models, making model comparisons challenging. A symmetrical model, in which forward and backward rates are the equivalent, and an all-rates-different model were fitted to the data using the function fitMk from PHYTOOLS v.1.0-3 (Revell 2012) and evaluated according to their Akaike weights (AICw). We used the package AICCMODAVG v.2.3-1 (Mazerolle 2020) to calculate AICw values and transition rates by averaging the estimates calculated for each model. A common concern is that an association between character states with diversification rates might bias transition rate estimates (Goldberg and Igić 2008). To mitigate this potential bias, we tested for an association between SSD and diversification rates, using a semi-parametric test for trait-dependent diversification analyses (Harvey and Rabosky 2018), named 'ES-sim' (available at https://github.com/mgharvey/ES-sim), which uses a tip-specific metric, λ_{DR}, as a measure of diversification rate. Parametric state-dependent diversification methods were not chosen owing to their high rates of false-positive results (Beaulieu and O'Meara 2016) and because simulations using ES-sim showed power similar to or higher than QuaSSE (Harvey and Rabosky 2018).

To determine whether divergent rates of evolution between male and female sizes are causing the SSD, evolutionary rates were estimated using the function mvBM from the MVMORPH v.1.1-4 package (Clavel *et al.* 2015). Two alternative models were tested according to constraints on evolutionary rates, in which the values of σ^2 from a Brownian motion model were either the same between states (male or female body mass) or allowed to differ. A loglikelihood-ratio test was then applied to determine the best-fitting model. Another method for testing evolutionary rate variation and shifts in SSD evolution was applied, named RRPHYLO, which is based on phylogenetic ridge regression (Castiglione *et al.* 2018). As a first step, we used the auto-recognize feature of the search.shift function from the RRPHYLO v.2.6-0 package (Castiglione *et al.* 2018) to identify any shifts in the degree of SSD across the phylogenies of each order. As a second step, we applied the status type 'sparse' of the function search.shift to the evolution of male and female body mass, separately, and evaluated whether their rates of evolution differed when SDI was positive (female-biased SSD) or negative (male-biased SSD). This allowed us to test whether the evolution of body mass in each sex was affected by the direction of dimorphism.

We tested for geographical correlates of SDI by extracting bioclimatic data (temperature seasonality, precipitation seasonality, and net primary productivity) and the latitude centroid for each species based on their corresponding shapefiles and calculating species means at a resolution of 10 arc-min. We performed a multiple phylogenetic least-squares regression (PGLS), with the SDI of each species as the dependent variable and with temperature seasonality, precipitation seasonality, species richness (of the same order), NPP, and absolute latitude as independent variables. We chose not to include any interaction terms in our model owing to the lack of prior expectations regarding their effects on SSD. This decision was made to prevent a significant increase in model complexity owing to the large number of predictors, which would have made the interpretation of results more challenging.

All analyses in this study were performed in R v.4.2.0 (R Core Team 2022) and repeated for 100 alternative topologies (1000 in the case of PGLS) to account for phylogenetic uncertainty. Transition rates, evolutionary rates, and PGLS were estimated separately for each studied order.

RESULTS

Different avian orders varied considerably in their distribution of body sizes, in both their mean and degree of skewness, yet the shape of the distributions of male and female body sizes remained relatively similar within each order (Fig. 1). Overall, Apodiformes and Passeriformes showed the lowest body mass of all orders (median of 5.2 and 21.456 g, respectively), whereas Anseriformes and Accipitriformes had the highest masses (median of 896.562 and 670 g, respectively).

The degree of SSD varied substantially among species, ranging from −5.28 (the male body mass representing 528% of the body mass of the female) to 1.5 (the female mass representing 150% the body mass of the male). Altogether, 31.15% of the species across the nine studied orders showed female-biased SSD, whereas 65.13% of the species showed male-biased SSD, and only 3.72% were monomorphic. The majority of the orders (seven of nine) had predominantly negative (male-biased SSD) SDI, whereas the remaining two (Accipitriformes and Charadriiformes) tended to have positive SDIs (Fig. 2). The orders showing the most disproportionate frequency of species with only one type of SDI were Accipitriformes, with 95% of

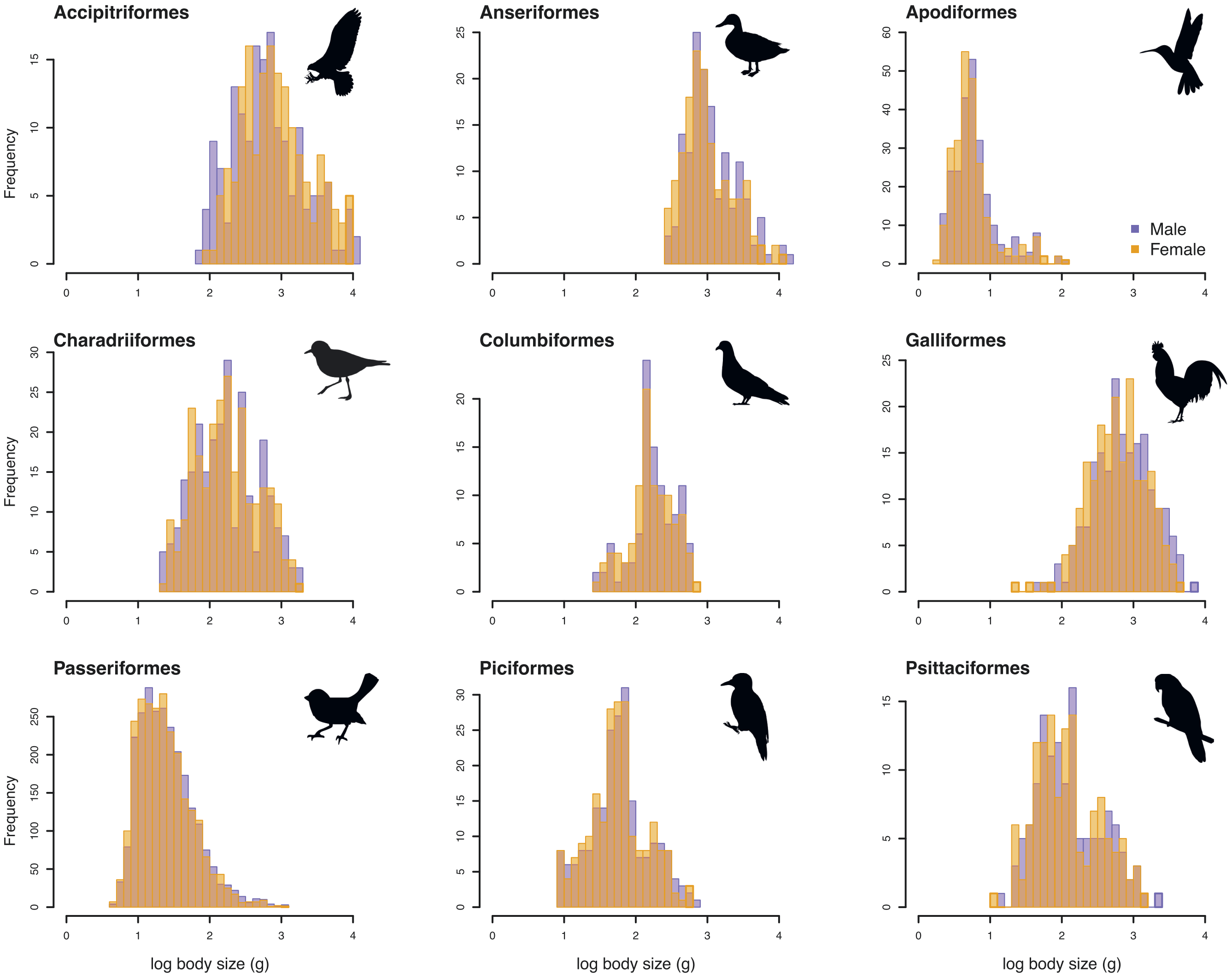

Figure 1. Frequency distributions of body mass (in grams) across the nine studied orders. Within each order, different colours represent the distribution of each sex. Values were $\log_{10}$-transformed before visualization.

their species having positive SDI, and Anseriformes, with 91% of their species having negative SDIs.

There were a number of differences in the geographical distributions of male- and female-biased SSD (Fig. 3). The first map indicated the spatial distribution of SSD, as measured by the median absolute SDI of all species in each cell (Fig. 3A). Given that it used the absolute SDI values, this map described spatial variation in the degree of SSD, regardless of whether it was male or female biased. There was a relatively loose association between SSD and overall environmental conditions. In the New World, SSD was less pronounced in the humid tropics of South and Central America (yet considerably stronger in the humid forests of Africa), but also in the dry conditions of northern Africa and the Middle East and in the temperate climates of Eurasia (Fig. 3A). In contrast, high SSD was found both at high latitudes and in more mesic conditions in Southeast Asia and Eastern Australia (Fig. 3A). Additionally, male-biased SSD tended to follow closely the same geographical patterns as the absolute SDIs, except for a relatively higher intensity in Sub-Saharan Africa (Fig. 3B). However, this observation could be attributed to the fact that more than half of the species in our dataset (65%) displayed male-biased SSD. Female-biased SSD, however, showed important differences from the overall geographical distribution of SSDs, with disproportionately higher values, especially throughout northern Eurasia and northern Australia (Fig. 3C).

The analysis of transition rates showed that transitions from female-biased SSD to male-biased SSD were more likely than the reverse (Fig. 4). This pattern was apparent in Apodiformes, Columbiformes, Galliformes, Passeriformes, Piciformes, and Psittaciformes, all of which showed a predominance of male-biased SSD. Conversely, Accipitriformes and Charadriiformes showed higher transition rates from male-biased SSD to female-biased SSD than the reverse, and were the only two orders analysed here to have more species with female-biased SSD. Finally, Anseriformes were the only order in which the symmetrical model was preferred according to the Akaike information criterion (Table 2). It is important to note that these results are unlikely to have been attributable to an association between the character states and diversification rates, given that our analyses

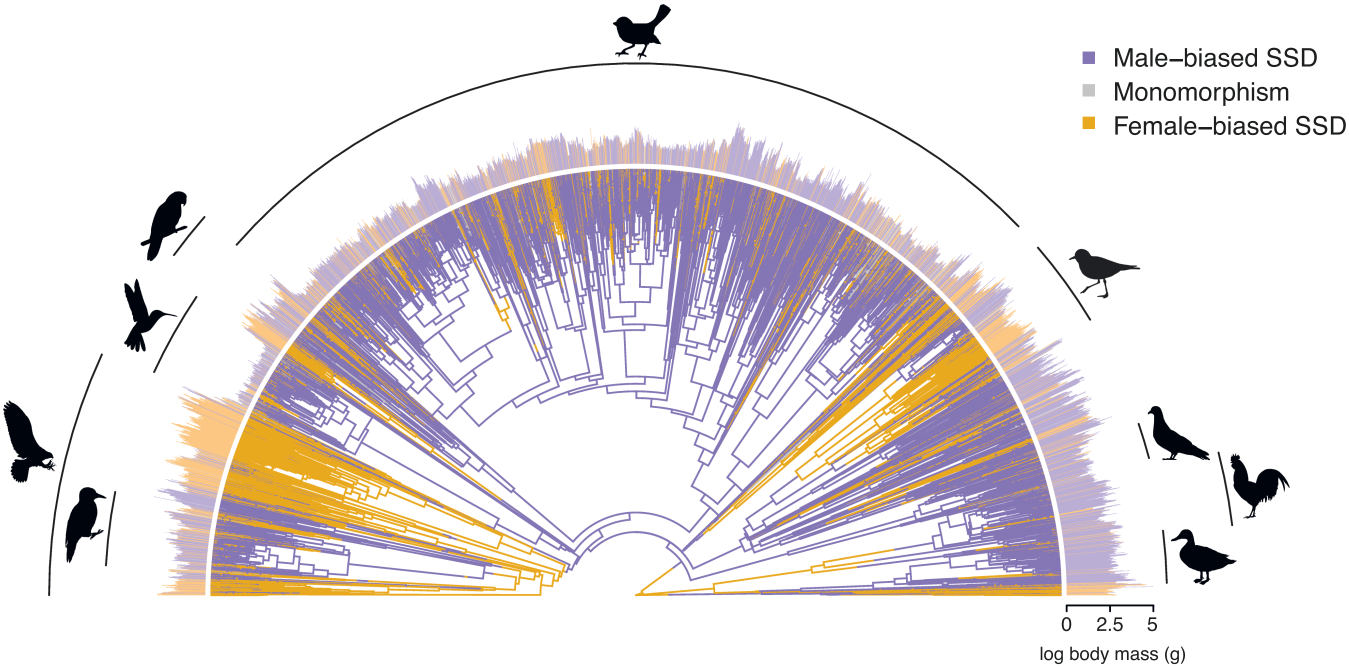

Figure 2. Stochastic character mapping of sexual size dimorphism coded as male-biased, female-biased, or monomorphic. Bars at the top of the phylogeny tips correspond to $\log_{10}$ body mass (in grams) of each species, calculated as the average of the male and female body mass. As shown in Figure 1, the nine orders selected for the present study are represented by arcs with their respective silhouettes.

using λ_{DR} did not show any association between them (Fig. 5; $P > .05$ for 100 simulations for each alternative topology).

Comparisons between evolutionary rates of male and female body size are provided in Table 3. The rate of evolution of female body mass was higher than in males only for Passeriformes; rates were either similar (Columbiformes, Galliformes, Piciformes, and Psittaciformes) or higher in males (Accipitriformes, Anseriformes, Apodiformes, and Charadriiformes). Analyses using RRphylo to auto-detect shifts in the evolutionary rate also showed distinct patterns among orders (Figs 6, 7). Most shifts in the degree of SDI involved a decrease in its rate of evolution in five orders, namely Accipitriformes, Anseriformes, Columbiformes, Piciformes, and Psittaciformes. For another three orders (Apodiformes, Charadriiformes, and Passeriformes), most shifts accounted for an increase in the evolutionary rate of SDI, whereas the same amount of positive and negative shifts was found in Galliformes. The second analysis of RRphylo did not detect evidence that the rates of evolution of male or female body mass were influenced by the direction of SDI (Supporting Information, Table S1; Figs S1, S2). Only Accipitriformes had the rate of female body mass higher when species had female-biased SSD than when they had male-biased SSD. Finally, PGLS analyses of species richness, absolute latitude, temperature and precipitation seasonality, and NPP against SDI did not reveal any detectable trends in any of the tested bird orders (Table 4; Supporting Information, Figs S3–S7).

DISCUSSION

In this study, we explore a large-scale dataset on body size across different avian lineages to test four alternative hypotheses on the evolution of SSD, namely the sexual selection, fecundity, niche divergence, and allometry hypotheses (Table 1). There was no clear support for a single mechanism, and the level of support for different hypotheses varied across avian orders. Taxa in which female-biased SSD is more prevalent (i.e. Accipitriformes and Charadriiformes) tended to favour both the fecundity (higher transition rates to female-biased SSD) and sexual selection (higher evolutionary rate for male size) hypotheses. In contrast, taxa in which male-biased SSD were most common were more varied in their favoured hypotheses. In Passeriformes, fecundity selection and sexual selection hypotheses were also supported, but with the reverse order of the corresponding tests in relationship to Accipitriformes and Charadriiformes (i.e. higher evolutionary rate for female size and higher transition rate to male-biased SSD, respectively). Likewise, niche divergence (equal transition rates between different types of SSD) and sexual selection (a higher rate of evolution for male size) were supported for Anseriformes, but reverse order of the corresponding tests for Columbiformes, Galliformes, Piciformes, and Psittaciformes (higher transition rates to male-biased SSD and similar evolutionary rates for males and females). The allometry hypothesis was supported in Anseriformes and Apodiformes, as evidenced by higher evolutionary rates in male body size and a predominantly male-biased SSD. Finally, we found no evidence that the direction of SSD (i.e. whether male or female biased) affected the rate of evolution of male or female body size, except for female size in Accipitriformes (Supporting Information, Table S1; Fig. S2). These results suggest that, although the allometry hypothesis received limited support, all three remaining hypotheses seem to be supported, to different degrees, in each avian order. In conclusion, the primary hypothesis used to explain SSD evolution (i.e. allometry) is less preferred when compared with more recent ones, which focus primarily on secondary sexual characteristics but also niche partitioning.

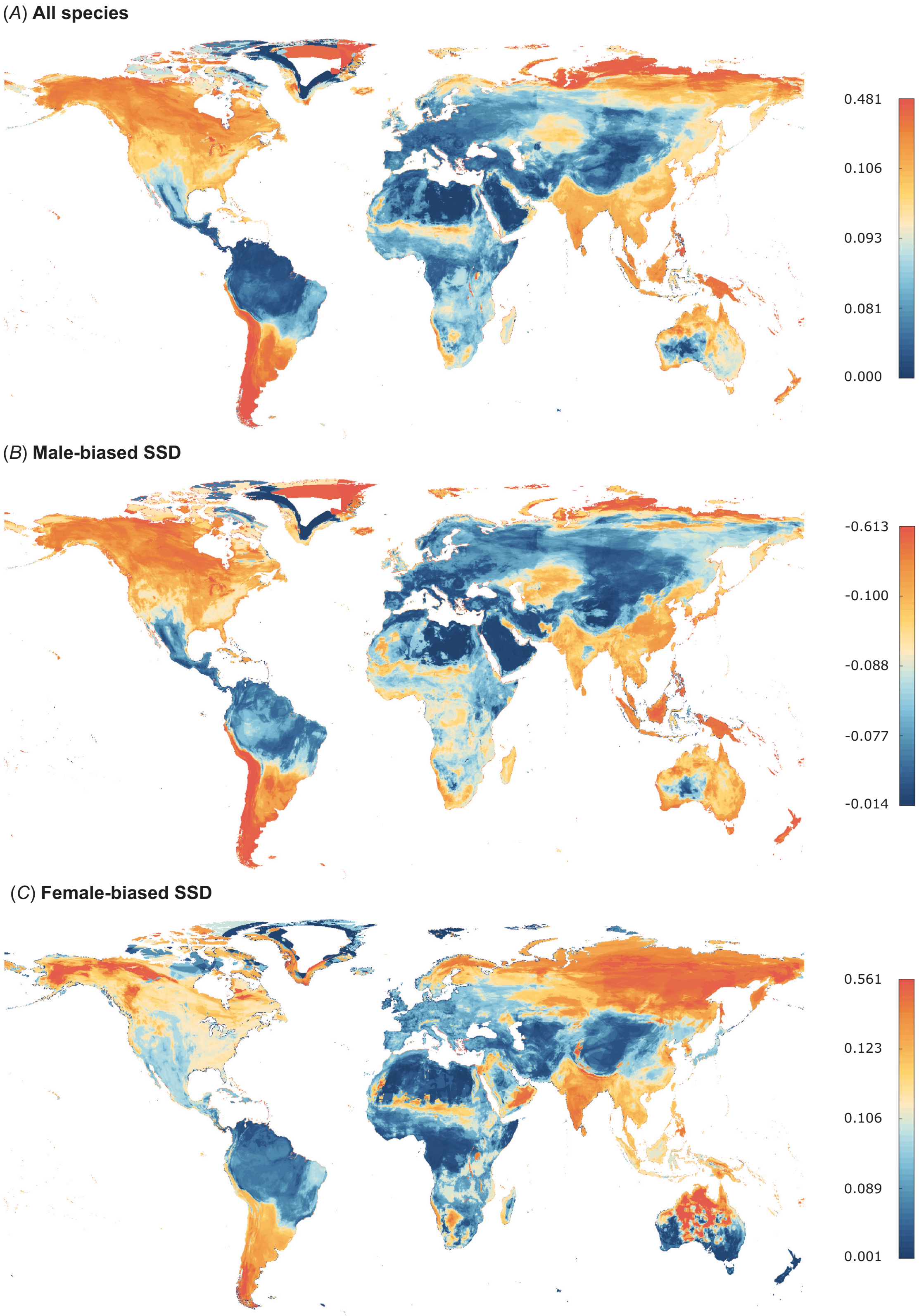

Figure 3. Geographical distribution of avian sexual size dimorphism (SSD), measured by the index of Lovich and Gibbons (1992). A, median value across all species found in each cell. B, median values considering only species with male-biased SSD. C, median values considering only species with female-biased SSD.

We did not find any evidence for a direct association between environmental factors (seasonality, productivity, richness, or latitude) and the degree of SSD (Table 4; Supporting Information, Figs S3–S7). Two previous studies explored the relationship between SSD and latitude. Friedman and Remeš (2016) found substantial spatial heterogeneity in bird SSD,

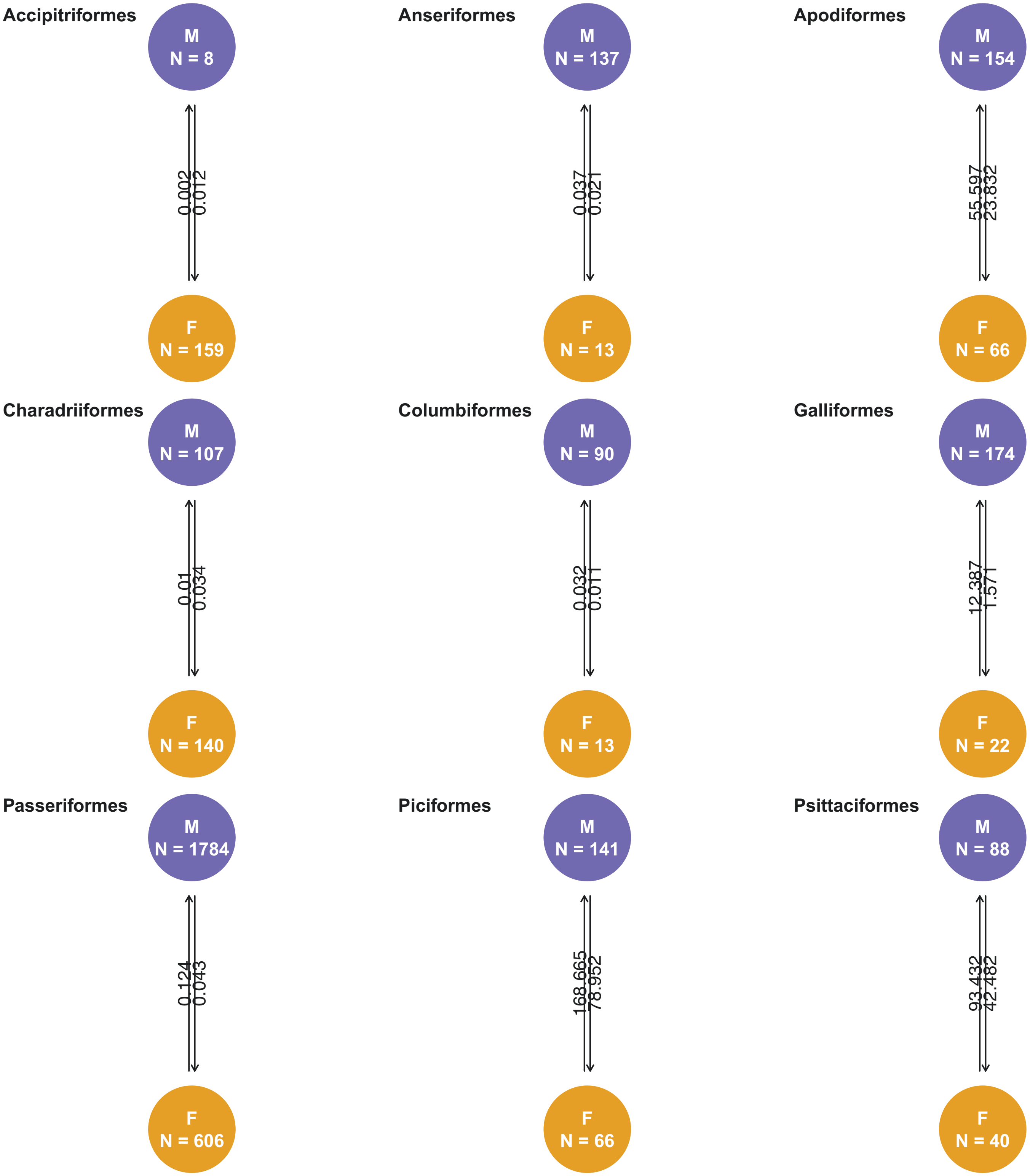

Figure 4. Transition rates between states of sexual size dimorphism (SSD) averaged across phylogenies. Purple indicates a male-biased SSD state and yellow a female-biased SSD state. Inside each circle is also given the number of species in each order with that respective state. Anseriformes were the only order in which forward and backward transition rates were not significantly different.

but no association between SSD and latitude. One possible explanation for these results could be that the effect of productivity might be apparent only at lower trophic levels, as in the case of herbivores (Henry *et al.* 2023), and therefore might not affect the higher trophic levels characteristic of most avian lineages in our analyses. However, Tarr *et al.* (2019) showed that lizards from Central and North America tend to have more male-biased SSD at low latitudes, but that female-biased SSD is more common at higher latitudes. This discrepancy might suggest that the effects of environmental factors on SSD might be

Table 2. Values of Akaike weights (AICw) for the two models tested to assess the rate of transition between the types of sexual size dimorphism. Abbreviations: ARD, model in which all rates are different; SYM, symmetric model, in which rates can vary for different transitions, but forward and backward rates are the same. Variation in AICw values corresponds to the mean (range) of values across 100 alternative topologies.

Order	***N***	**SYM**	**ARD**
Accipitriformes	167	0.174 (0.08–0.496)	0.826 (0.504–0.92)
Anseriformes	150	0.552 (0.355–0.691)	0.448 (0.309–0.645)
Apodiformes	247	0.218 (0–0.644)	0.782 (0.356–1)
Charadriiformes	255	0.006 (0–0.028)	0.994 (0.972–1)
Columbiformes	103	0.488 (0.304–0.604)	0.512 (0.396–0.696)
Galliformes	196	0.054 (0–0.498)	0.946 (0.502–1)
Passeriformes	2510	0 (0–0)	1 (1–1)
Piciformes	212	0.072 (0–0.57)	0.928 (0.43–1)
Psittaciformes	130	0.26 (0–0.871)	0.74 (0.129–1)

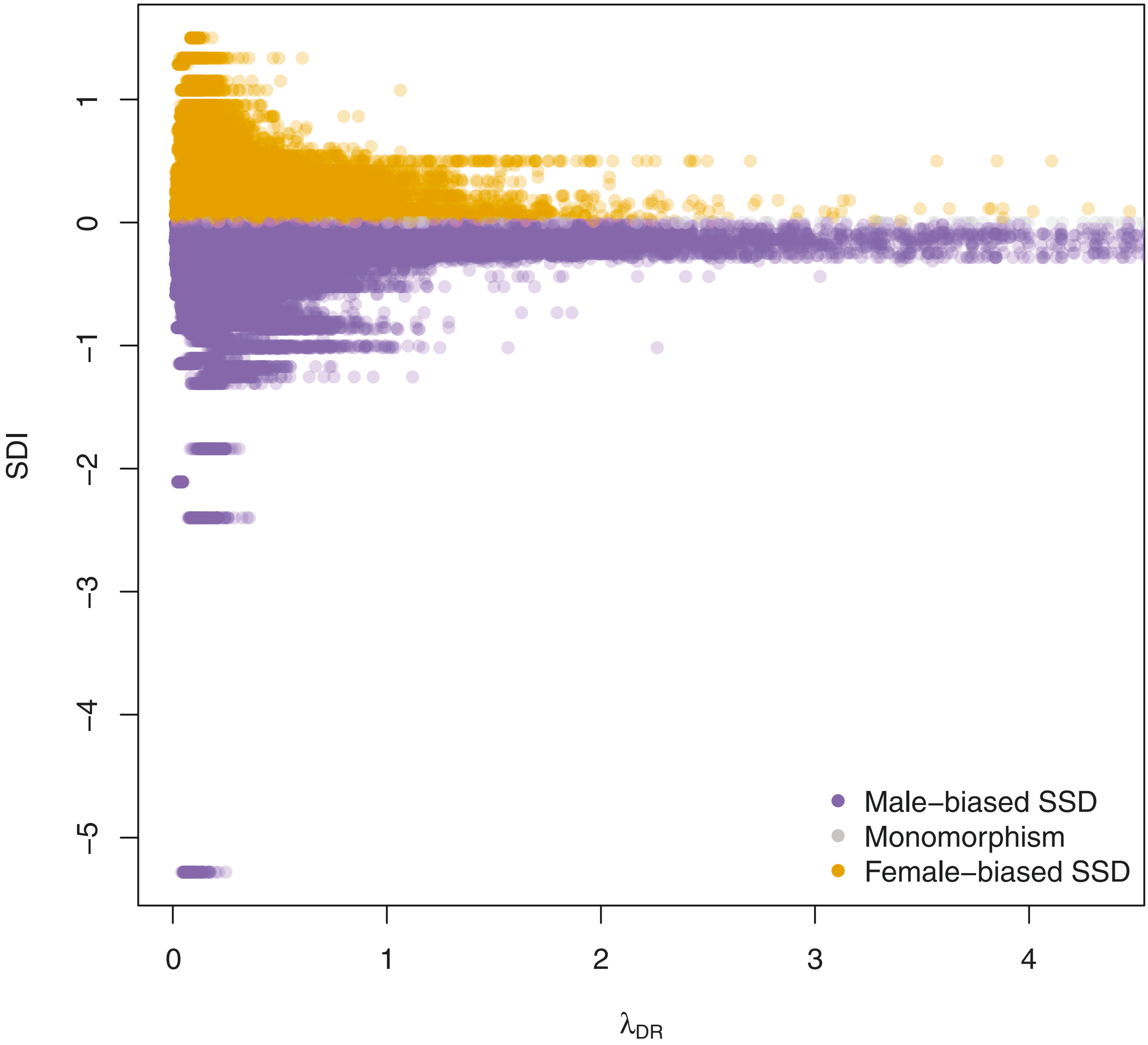

Figure 5. Relationship between the metric λ_{DR}, interpreted as the diversification rate, and the degree of sexual size dimorphism, i.e. the size dimorphism index (SDI). Different colours represent variations in the direction of SSD.

scale dependent and might not be as apparent at the large spatial scales involved in our study.

The lack of clear environmental correlates of SSD is intriguing, given the spatial patterns detected when mapping variation of SSD (Fig. 3). For instance, high latitudes are often characterized by extreme SSD of both sexes, with female-biased SSD being widespread in North America and parts of Europe, whereas male-biased SSD is more common in Africa. Previous studies showed inconsistent support for geographical patterns of SSD. Using display agility as a proxy for sexual selection, Serrano-Meneses and Székely (2006) found support for sexual selection predicting SSD in seabirds, but did not find support for fecundity selection or niche partitioning. Similar results were found by Lislevand *et al.* (2009) for Phasianidae and by Nuñez-Rosas *et al.* (2017) for hummingbirds, using lekking behaviour as a proxy for sexual selection. Pérez-Camacho *et al.* (2018), however, found ecological correlates to predict female-biased SSDs in diurnal raptors. Our study explored these hypotheses using a macroevolutionary approach and also found different levels of support for each hypothesis, suggesting not only that the mechanisms driving SSD are multifactorial but also that the most important mechanisms might change in different avian lineages.

Across other animal classes, the consensus about SSD drivers is no less controversial. In mammals, for instance, studies indicated that niche partitioning could be the main SSD driver (Huston and Wolverton 2011). However, other authors have suggested that fecundity selection is the main driver, owing to the consistent evidence for an association between female sizes and fecundity (Cassini 2017). Nevertheless, other studies also found evidence of sexual selection (Soulsbury *et al.* 2014, Cassini 2020). Regarding the effects of climate on SSD, Dunham *et al.* (2013) found no association between SSD and any climate parameter tested (i.e. seasonality, interannual variability, and annual temperature and precipitation). In reptiles, the scenario is not so distinct. Tarr *et al.* (2019) found no evidence for fecundity selection but found evidence for the niche partitioning hypothesis, as Agha *et al.* (2018) found in turtles. Alternatively, previous studies have also found evidence for sexual selection and fecundity selection (Cox *et al.* 2003, Scharf and Meiri 2013). Nonetheless, there are few studies with a broad macroevolutionary approach when analysing these possible drivers.

Although the main goal of our study was to evaluate the generality of drivers of SSD, some points should be noted regarding why different orders might be under distinct mechanisms. First, the majority of orders analysed here are largely monogamous, which would mitigate the efficacy of sexual selection as a driver of SSD. However, deviations of some species from this mating system, courtship behaviours (e.g. lek behaviour, aerial displays), territoriality, and unbalanced parental care are considered potential drivers of SSD (Fairbairn *et al.* 2007). According to our results, Accipitriformes, Charadriiformes, and Passeriformes are influenced by sexual selection and fecundity selection. Accipitriformes usually present efficient hunting and territoriality by males (Billerman *et al.* 2022), whereas other authors have suggested that female sizes are selected to increase owing to egg production (Negro and Galván 2018). Female–female competition, a possible SSD driver not considered in depth here, might also explain the higher transition rates for female-biased SSD (e.g. Lien *et al.* 2015). Charadriiformes tend to include territorial males (Billerman *et al.* 2022), but also present a higher degree of species with mating systems other than monogamy (Billerman *et al.* 2022), which might explain the higher transition rates for female-biased SSD. Passeriformes are very diverse in their reproductive and courtship behaviours, presenting display aerial and lek behaviour (Billerman *et al.* 2022), which are known to influence male sizes. Because of the diversity of this

Table 3. Rates of evolution of male and female body size calculated under a multiple-rate model. The *P*-value indicates the results from the likelihood ratio test between a multiple-rate model and a single-rate model. Size dimorphism index (SDI) values account for variation between species within each taxon, whereas variation in evolutionary rates and the *P*-value correspond to the median and range of values across 100 alternative topologies.

Order	*N*	SDI	σ^2 male body size	σ^2 female body size	*P*-value
Accipitriformes	167	Median = 0.278 (minimum = −0.587; maximum = 1.5)	0.057 (0.046–0.069)	0.056 (0.054–0.057)	.001 (0–.96)
Anseriformes	150	Median = −0.127 (minimum = −1.104; maximum = 0.333)	0.202 (0.09–0.315)	0.153 (0.075–0.232)	0 (0–.817)
Apodiformes	247	Median = −0.062 (minimum = −0.557; maximum = 0.5)	0.02 (0.018–0.022)	0.016 (0.014–0.019)	0 (0–.96)
Charadriiformes	255	Median = 0.017 (minimum = −0.657; maximum = 0.862)	0.076 (0.072–0.08)	0.07 (0.069–0.072)	.003 (0–.751)
Columbiformes	103	Median = −0.061 (minimum = −0.613; maximum = 0.183)	0.035 (0.013–0.057)	0.032 (0.013–0.05)	.254 (0–.977)
Galliformes	196	Median = −0.16 (minimum = −5.28; maximum = 0.444)	0.036 (0.035–0.037)	0.036 (0.034–0.037)	.251 (0–.995)
Passeriformes	2510	Median = −0.052 (minimum = −2.4; maximum = 1.286)	0.038 (0.031–0.045)	0.047 (0.025–0.07)	0 (0–.869)
Piciformes	212	Median = −0.043 (minimum = −0.905; maximum = 0.75)	0.03 (0.026–0.035)	0.028 (0.023–0.033)	.092 (0–.999)
Psittaciformes	130	Median = −0.065 (minimum = −0.468; maximum = 0.524)	0.028 (0.024–0.031)	0.028 (0.026–0.03)	.2 (0–.995)

order, female–female competition can also be common across families (e.g. Guo *et al.* 2020) and might explain the higher evolutionary rate in female body mass. Columbiformes, Galliformes, Piciformes, and Psittaciformes showed evidence for niche partitioning and sexual selection. These orders are characterized by monogamous systems (Billerman *et al.* 2022) and biparental care (Billerman *et al.* 2022), which do not say much about the drivers of SSD. One exception to this is Galliformes, which include a substantial number of species with polygyny, known to be a driver of male-biased SSD (Billerman *et al.* 2022). Finally, Anseriformes, which showed evidence for sexual selection, niche partitioning, and allometry, are usually monogamous and territorial, whereas the majority of Apodiformes, which showed evidence for sexual selection and allometry, are polygynous and showlekking behaviour (Billerman *et al.* 2022).

There are several caveats that should be noted in our study. First of all, like any global study, generalizations and omissions are unavoidable. Therefore, the results and interpretations presented here are based on selected data and do not reflect reality completely. We are constrained by the availability of data that overlap across sources and by the computational capacity of the methods used here. However, we believe that repeating

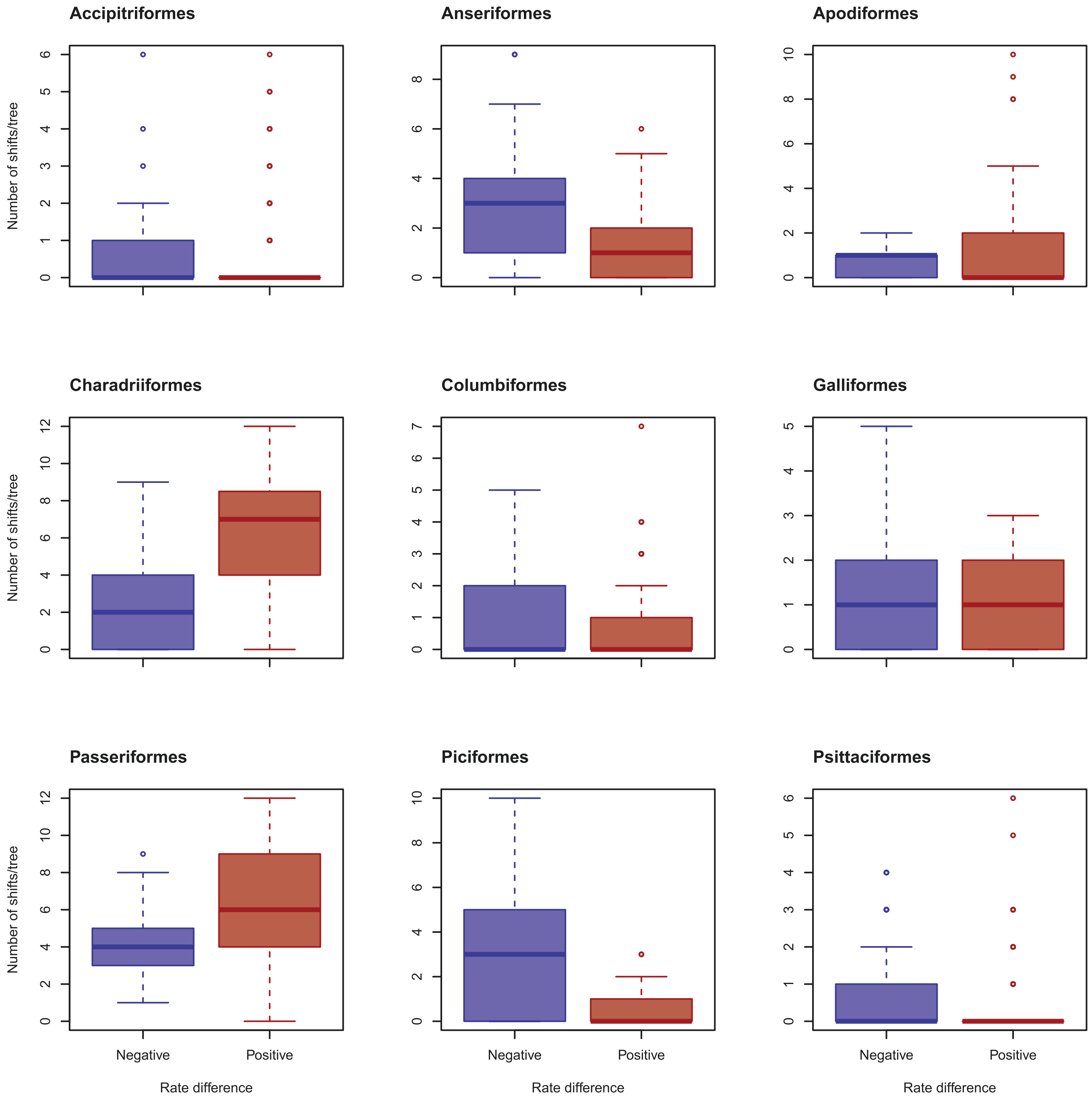

Figure 6. Boxplots representing the number of shifts in the evolutionary rate of sexual size dimorphism per tree across 100 alternative topologies. Negative shifts (i.e. decreases in evolutionary rate) are indicated in blue and positive shifts (i.e. increases in evolutionary rate) in red.

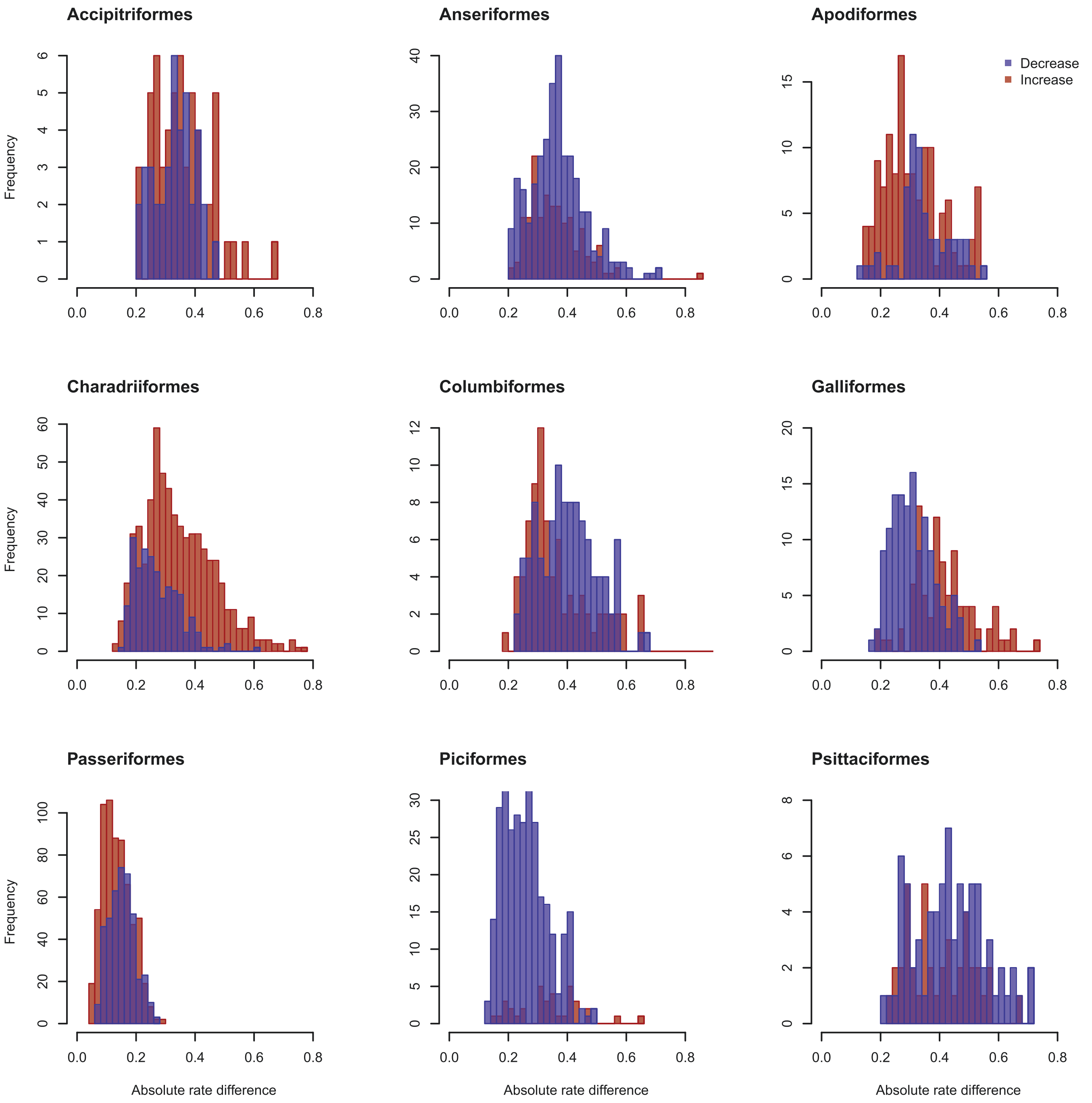

Figure 7. Frequency histograms representing the magnitude of the shifts estimated in the evolutionary rate of sexual size dimorphism. Negative shifts (i.e. decreases in evolutionary rate) are indicated in blue and positive shifts (i.e. increases in evolutionary rate) in red.

the analyses consecutively across orders and considering phylogenetic uncertainty might help to address some of these issues. Moreover, the interpretation of transition rates as being common or uncommon within the orders must be taken with caution, considering that in some instances (or maybe in the majority of them) SSD might be maintained in the speciation process of these orders, rather than acquired through character state transitions. Transitions do occur, because we have found evidence here, but the majority of the descendent lineages only inherited the SSD from the ancestor in the speciation process. Furthermore, we focused on SSD in body mass, which is only one of the dimensions of sexual dimorphism. It is important to acknowledge that alternative dimensions of the dimorphism do not necessarily evolve in parallel with SSD (Figuerola and Green 2000, Gonzalez-Voyer *et al.* 2022). Body size is a major component of the life history of an organism, influencing several other physiological and ecological aspects, and is certainly one of the main components of sexual dimorphism (Fairbairn 2016). However, one might expect that, for instance, plumage dimorphism might already alleviate the need for SSD in the context of sexual selection, yet the exploration of potential trade-offs between different dimensions of sexual dimorphism is still

Table 4. Phylogenetic generalized least squared analyses of the relationship between order richness, absolute latitude, temperature and precipitation seasonality, and net primary productivity of different bird orders. Estimates are given as mean values and the range of values across 1000 alternative topologies.

Order	*N*	Order richness		Absolute latitude		Temperature seasonality		Precipitation seasonality		Net primary productivity		R^2
		Slope	*P*-value	Slope	*P*-value	Slope	*P*-value	Slope	*P*-value	Slope	*P*-value	
Accipitriformes	157	0.003 (−0.025 to 0.047)	.24 (0–.999)	0.002 (−0.035 to 0.019)	.362 (0–1)	0 (0–0)	.276 (0–.998)	−0.001 (−0.026 to 0.009)	.305 (0–.996)	0 (−0.006 to 0.003)	.216 (0–.999)	0.174 (0.006–0.985)
Anseriformes	127	0.004 (−0.024 to 0.028)	.242 (0–.998)	0.001 (−0.023 to 0.038)	.369 (0–.999)	0 (0–0)	.435 (0–1)	0 (−0.005 to 0.021)	.341 (0–1)	0 (−0.001 to 0.004)	.344 (0–.997)	0.305 (0.012–0.992)
Apodiformes	228	−0.002 (−0.018 to 0.009)	.297 (0–.994)	−0.003 (−0.027 to 0.01)	.333 (0–.999)	0 (0–0)	.393 (0–.997)	0 (−0.007 to 0.006)	.385 (0–.996)	0 (−0.001 to 0.003)	.188 (0–.999)	0.115 (0.002–0.959)
Charadriiformes	234	0.002 (−0.01 to 0.015)	.238 (0–.998)	0 (−0.005 to 0.001)	.662 (0–.999)	0 (0–0)	.348 (0–.998)	−0.001 (−0.013 to 0.003)	.165 (0–.987)	0 (−0.003 to 0.001)	.282 (0–1)	0.157 (0.008–0.971)
Columbiformes	93	−0.003 (−0.021 to 0.076)	.256 (0–.999)	0.002 (−0.029 to 0.012)	.263 (0–1)	0 (0–0)	.505 (0–.999)	0 (−0.007 to 0.005)	.343 (0–.999)	0 (−0.001 to 0.003)	.473 (0–.999)	0.259 (0.027–0.998)
Galliformes	164	−0.009 (−0.202 to 0.078)	.354 (0–.994)	0.006 (−0.023 to 0.155)	.42 (0–.998)	0 (0–0)	.632 (0–.999)	0.002 (−0.004 to 0.048)	.262 (0–1)	0 (−0.003 to 0.017)	.477 (0–1)	0.097 (0.003–0.764)
Passeriformes	1999	0 (−0.004 to 0.003)	.165 (0–.979)	0 (−0.022 to 0.013)	.156 (0–.998)	0 (0–0)	.18 (0–.998)	0 (−0.003 to 0.004)	.133 (0–.999)	0 (−0.002 to 0.002)	.147 (0–.984)	0.11 (0.001–0.988)
Piciformes	177	0.001 (−0.036 to 0.063)	.296 (0–.998)	0 (−0.089 to 0.047)	.457 (0–.999)	0 (0–0)	.428 (0–.995)	0 (−0.019 to 0.007)	.326 (0–1)	0 (−0.004 to 0.003)	.227 (0–.999)	0.134 (0.003–0.976)
Psittaciformes	115	0.005 (−0.01 to 0.037)	.092 (0–.971)	−0.001 (−0.01 to 0.01)	.429 (0–.999)	0 (0–0)	.458 (0–.998)	0 (−0.005 to 0.009)	.464 (0–.999)	0 (−0.002 to 0.003)	.272 (0–.996)	0.177 (0.051–0.96)

in its infancy, particularly in macroevolutionary studies (but see Gonzalez-Voyer *et al.* 2022). Finally, other variables are thought to influence the degree of sexual dimorphism, such as parental care (Horne *et al.* 2020) and mating systems (Nuñez-Rosas *et al.* 2017). However, it is worth noting that some of these traits are encompassed indirectly within the hypotheses we tested, such as parental care and mating systems stemming from the sexual selection hypothesis for larger males (Webster 1992, Dale *et al.* 2007, Gonzalez-Voyer *et al.* 2022). Additionally, it is important to consider the potential influence of the agility display hypothesis when interpreting the results of the sexual selection hypothesis. According to this scenario, smaller sizes would be advantageous for species that rely on aerial displays to attract females (Jehl and Murray 1986). Our findings suggest that Accipitriformes and Charadriiformes might provide support for this hypothesis, because they exhibit higher transition rates towards female-biased SSD (i.e. smaller males) and greater evolutionary rates for male body mass.

In this study, we demonstrate that evolution of SSD is likely to be multifactorial, with sexual selection, fecundity, and niche divergence playing important roles in different avian orders. In contrast, purely environmental factors, such as temperature seasonality and productivity, seem to be poor predictors of SSD. Further studies, particularly at smaller spatial and temporal scales, can be particularly useful to understand those differences across taxa. Finally, our study highlights the importance of an explicitly macroevolutionary approach to identify and rate drivers of SSD.

SUPPLEMENTARY DATA

Supplementary data is available at *Biological Journal of the Linnean Society* online.

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AUTHOR CONTRIBUTIONS

Fernanda S. Caron (conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, project administration, resources, software, validation, visualization, writing—original draft, writing—review & editing) and Marcio R. Pie (conceptualization, project administration, resources, supervision, writing—review & editing)

CONFLICT OF INTEREST

None declared.

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DATA AVAILABILITY

All data used in our analyses are available in the Supporting Information (Table S2). Codes used in our study are available at https://github.com/fernandacaron/dimorphism_evol.

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