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RESEARCH

Variation in sexual size dimorphism and fit to rensch's rule in Costa Rican hummingbirds

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Abstract

Rensch's rule predicts that sexual size dimorphism (SSD) increases with body mass in species where males are larger but decreases when females are larger. To analyze patterns of SSD in body mass and test Rensch's rule in 45 species of Costa Rican hummingbirds. We hypothesize that the physiological capacity to buffer environmental variation increases with body mass, creating a size-dependent tolerance for SSD that explains interspecific differences in SSD. Larger species were expected to exhibit greater SSD variation than smaller, more energetically constrained species. We evaluated SSD in body mass across 45 hummingbird species to test for conformity with Rensch's rule using Bayesian phylogenetic regression. Hummingbirds exhibited mixed allometry and conformed to Rensch's rule, with a phylogenetic regression slope of male vs. female body mass significantly less than 1.00 (0.84). Male-biased allometry was observed in 80% of species. On average, SSD variation in body mass was 12% and was significantly associated only with male size. In hummingbirds, the predominant polygynous mating systems generated the male-biased SSD pattern across species through sexual selection, while physiological constraints associated with extreme metabolic demands and hovering flight limit variation around this sexually selected baseline. Our findings are consistent with sexual selection representing the primary evolutionary force shaping SSD in this clade, with energetic limitations as critical modulating factors.

Keywords Display agility hypothesis · Hummingbird ecology · Mating competition hypothesis · Physiological limits to SSD · Sexual size dimorphism · Sexual selection

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Introduction

Differences in body mass between the sexes are widely distributed across a diversity of organisms, from vertebrates (Fairbairn 1997; Gayford and Sternes 2024; Slavenko et al. 2025; Caron and Pie 2025) to arthropods (Blanckenhorn et al. 2007). The difference in body size between males and females is referred to as *sexual size dimorphism* (SSD). In birds, SSD varies extensively and is linked to diverse ecological, physiological, and evolutionary processes, including competition for mates, specialization of reproductive roles, predation risk, and resource partitioning (Fairbairn 1997; Blanckenhorn et al. 2007). SSD has significant selective consequences, as it influences trophic niche segregation (i.e., Bravo et al. 2016) and reproductive success (Kingsolver and Huey 2008; Herczeg et al. 2010; Barber et al. 2024). A recurring macroevolutionary pattern related to SSD is Rensch's rule, which predicts that SSD increases with body size when males are larger (positive allometry or hyperallometry), but decreases when females are larger (negative allometry or hypoallometry, Rensch 1950; Blanckenhorn 2005). Both SSD and Rensch's rule are the primary result of sexual selection (Andersson 1994; Slatkin 1984; Shuker and Kvarnemo 2021). The underlying causes of SSD are multifaceted and, in addition to sexual selection by female choice (Janicke and Fromonteil 2021), SSD is affected by male-male competition for mates, sexual display agility (Andersson 1994; Shuker et al. 2021; Slavenko et al. 2025), and ecological pressures (e.g., niche segregation, size-dependent survival, e.g., Darwin 1871; Payne 1984; Székely et al. 2007; Temeles et al. 2010; Maglianesi et al. 2022; Barber et al. 2024), which present modulating factors influencing the variation in SSD.

The interplay between sexual selection and ecological processes is not mutually exclusive and can operate simultaneously (Andersson 1994; Slavenko et al. 2025). Conditions such as the mating system (e.g., polygyny in lekking species vs. monogamy) and the breeding aggregation of one sex can intensify intraspecific competition for mates, thereby increasing the magnitude of SSD through sexual selection. Sexual selection also acts on non-morphological traits, including vocalizations, plumage, and behavioral displays such as lekking. Additional selective pressures, not directly related to sexual selection, could also act on SSD, such as the increase in brain size relative to body mass in hummingbirds (see Ocampo et al. 2018), which impacts foraging behavior and habitat selection (Gonzalez-Gomez et al. 2014). Disentangling the evolution of allometry of SSD implies understanding many key questions in evolutionary biology, such as the evolution of groups of correlated traits and the influence of phenotypic plasticity associated with the expression of SSD (Lande 1980). Field studies are needed to estimate population parameters that affect the evolution of size and SSD, thereby distinguishing between overlapping hypotheses.

Birds serve as important models for studying sexual size dimorphism (SSD) and Rensch's rule (Caron and Pine 2025). Numerous comparative and phylogenetic studies across avian orders have shown that both patterns are widespread in birds, with strong links to mating systems, sexual selection intensity, and ecological strategies (Dale et al. 2007; Lislevand et al. 2007; Székely et al. 2007; Cox and Calsbeek 2010; Weeks et al. 2020). In many taxa, male-biased SSD is associated with lekking or polygynous systems, while female-biased SSD appears in raptors and other groups subject to selection for high fecundity (Andersson and Norberg 1981; Székely et al. 2007). Although sexual selection is the primary driver of SSD in birds, ecological pressures and energetic constraints contribute additional variation around this baseline (Beltrán et al. 2022); the extent to which these factors interact remains poorly understood (Blanckenhorn 2005; Caron and Pie ; Zhou et al. 2024). Sexual and natural selection (i.e., physical and physiological constraints) set sex-specific upper and lower limits on body mass and thus define the extent of variation in SSD (Zhou et al. 2024.

Hummingbirds (Trochilidae) provide an exceptional model for studying SSD and Rensch's rule, as they exhibit a broad range of SSD, including mixed allometries, with species in which females are the larger sex, as well as species in which males are larger. Some hummingbirds show sex segregation in habitat and resource use (Howell and Gardali 2003; Leimberger et al. 2022). Males and females have distinctive reproductive roles, characterized by a predominantly polygynous reproductive system, where leks are prevalent. Some hummingbirds may have reached the upper energetic limits of miniaturization for any group of flying vertebrates, adapting their physiology to conserve heat on cold nights in some of the higher-elevation habitats colonized by small vertebrates (Shankar et al. 2022). Their high metabolic rates necessitate almost constant access to high-energy food sources and place severe constraints on their ability to cope with environmental variation. However, their size has not been an obstacle to the colonization of high-altitude habitats (Altshuler and Dudley 2002). The quality of food resources, as well as morphological limitations in accessing floral resources, impacted the evolution of hummingbird morphology and physiology due to considerable energy constraints associated with miniaturization and their high dependency on nectar consumption (see Kessler et al. 2020).

Organismic responses to environmental change are strongly influenced by body size, which varies along a continuous gradient of intra- and interspecific variation (Peters 1986). Smaller species typically exhibit faster physiological responses and greater plasticity to short-term environmental fluctuations due to their higher surface-area-to-volume ratios. However, their limited energy reserves make them more susceptible to extreme or prolonged stresses, such as resource shortages or temperature extremes. In contrast, larger species generally have greater energy reserves and lower relative metabolic rates (Groom et al. 2018), enabling them to buffer or tolerate environmental changes over more extended periods, although they may not respond as rapidly to acute fluctuations (Blanckenhorn 2005; Cox and Calsbeek 2010). These contrasting strategies, mediated by the scale and intensity of environmental changes, can shape both intra- and interspecific variation in body size and influence patterns of SSD, as individuals of different sizes and sexes exploit distinct ecological niches and microhabitats. Empirical studies in birds reflect these dynamics, as climate warming has been associated with increased variation in body size traits, demonstrating the interplay between selective pressures and plastic responses (Zimova et al. 2023). For instance, Weeks et al. (2020) found that reductions in body size among migratory birds may enhance thermal adaptability, a trend often offset by increased wing length to maintain flight efficiency. Nonetheless, the evidence remains mixed, as body size is shaped by a complex interplay of sexual selection with genetic, environmental, and ecological factors (Nord et al. 2024). Overall, these findings highlight the central role of body size in determining species resilience and guiding evolutionary responses to changing climatic conditions.

This study seeks to quantify SSD and evaluate the fit to Rensch's rule across 45 species of hummingbirds. By integrating comparative analyses with current phylogenetic methods and leveraging the substantial avian literature on the drivers of SSD, we aim to clarify how ecological, physiological, and evolutionary processes interact to shape SSD in this clade. We include species spanning a wide body size range, from the largest hummingbird in Costa Rica, the Violet Sabrewing (*Campylopterus hemileucurus*), to the smallest species, the Scintillant Hummingbird (*Selasphorus scintilla*). We hypothesize that the physiological capacity to buffer environmental variation scales positively with body mass, resulting in size-dependent constraints on SSD. Specifically, large-bodied species, with greater energy reserves and enhanced ability to tolerate periods of environmental stress, may allow for greater ecological and morphological divergence between males and females, resulting in a wider range of SSD. In contrast, small-bodied species, being more energetically constrained and less able to buffer resource shortages, should present a smaller range of morphological variation between males and females. Our findings will stress the importance of analyzing male- and female-biased allometries and will help define future research questions for understanding the ecological and evolutionary implications of SSD across diverse animal taxa.

Materials and methods

Sources of morphological data

We compiled body mass data for 45 species of Costa Rican hummingbirds from three sources: (a) our own field database of 19 hummingbird species representing 731 mist net captures registered between 2012 and 2016 at multiple sites in Costa Rica, (b) museum specimens ($n = 154$) representing 35 species from the ornithological collection of the Museum of Zoology at the University of Costa Rica; and (c) species accounts on the Birds of the World online platform (https://birdsoftheworld.org/bow/home?*)* Billerman et al. (2026). These sources provided body mass values (in grams), a morphological trait commonly reported in the literature and museum databases, and one that is ecologically meaningful due to its correlation with resource acquisition and energetic demands (Dalsgaard et al. 2009). This composite dataset, referred to as the "large dataset" (Table 1), served as the basis for our analyses of sexual size dimorphism (SSD). We classified species into eight of the nine major hummingbird clades following McGuire et al. (2014): Bees, Coquettes, Hermits, Brilliants, Emeralds, Mangoes, Mountain Gems, and Topazes.

Lovich-Gibbons sexual dimorphism index

We quantified sexual size dimorphism (SSD) in body mass using the Lovich-Gibbons index (Lovich and Gibbons 1992), calculated as the ratio of the average body mass of the larger sex to that of the smaller sex, minus one:

$$\text{SSD index} = (\text{larger sex}/\text{smaller sex}) - 1$$

By convention, the index is positive when females are the larger sex and assigned a negative value when males are the larger sex. As a ratio, the index can also be interpreted as a percentage. For example, in *Selasphorus flammula*, the index value is 0.096 (Table 1), indicating that females are 9.6% larger than males. The Lovich–Gibbons index values across species followed a normal distribution (Shapiro–Wilk test: $W = 0.96$, $P = 0.28$).

Table 1 Body mass (g) and Lovich-Gibbons sexual dimorphism index of the 45 hummingbird species considered in this study according to phylogenetic clade and sex. Phylogenetic clades follow the classification of McGuire et al. (2014). Data source and sample size[1]

Common name	Scientific name	Phylogenetic clade	Body mass of male	Body mass of female	Lovich-Gibbons ratio	Source (*N* Males and *N* Females)[1]
Magenta-throated Woodstar	*Philodice bryantae*	Bees	3.3	3.5	0.061	1
Ruby-throated Hummingbird	*Archilochus colubris*		2.7	3	0.111	2 (Males = 4), 1 (Females)
Scintillant Hummingbird	*Selasphorus scintilla*		2.05	2.3	-0.122	2 (Males = 2, Females = 1)
Volcano Hummingbird	*Selasphorus flammula*		2.5	2.74	0.096	3 (Males = 4, Females = 34)
Green-crowned Brilliant	*Heliodoxa jacula*	Brilliants	9.06	8.54	-0.061	3 (Males = 48, Females = 112)
Black-crested Coquette	*Lophornis helenae*	Coquettes	2.15	2.52	0.172	2 (Males = 1, Females = 2)
Green Thorntail	*Discosura conversii*		3.1	2.9	-0.069	3 (Males = 1, Females = 1)
Black-bellied Hummingbird	*Eupherusa nigriventris*	Emeralds	3.425	3.25	-0.054	2 (Males = 4, Females = 1)
Blue-chested Hummingbird	*Polyerata amabilis*		4	3.8	-0.053	1
Blue-throated Goldentail	*Chlorestes eliciae*		3.8	3.3	-0.152	1
Blue-vented Hummingbird	*Saucerottia hoffmanni*		4.4	4.3	-0.023	3 (Males = 4, Females = 1)
Bronze-tailed Plumeleteer	*Chalybura urochrysia*		7.1	6.1	-0.164	3 (Males = 6), 2 (Females = 4)
Cinnamon Hummingbird	*Amazilia rutila*		4.9	4.2	-0.167	2 (Males = 1, Females = 4)
Coppery-headed Emerald	*Microchera cupreiceps*		4.7	3.64	-0.291	3 (Males = 4, Females = 6)
Crowned Woodnymph	*Thalurania colombica*		4.5	4	-0.125	2 (Males = 2, Females = 1)
Mangrove Hummingbird	*Chrysuronia boucardi*		4.95	4.2	-0.179	2 (Males = 21, Females = 12)
Rufous-tailed Hummingbird	*Amazilia tzacatl*		4.82	4.54	-0.062	2 (Males = 13, Females = 10)
Scaly-breasted hummingbird	*Phaeochroa cuvierii*		9.38	8.6	-0.091	2 (Males = 4, Females = 2)
Snowcap	*Microchera albocoronata*		2.48	2.56	0.032	2 (Males = 4, Females = 3)
Snowy-bellied Hummingbird	*Saucerottia edward*		5	4.3	-0.163	1, 3 (Females = 4)
Stripe-tailed Hummingbird	*Eupherusa eximia*		4.68	4.06	-0.153	3 (Males = 24, Females = 10)
Violet Sabrewing	*Campylopterus hemileucurus*		12.42	9.18	-0.353	3 (Males = 11, Females = 3)
Violet-headed Hummingbird	*Klais guimeti*		2.9	2.7	-0.074	2 (Males = 4, Females = 3)
White-bellied Emerald	*Chlorestes candida*		3.7	3.8	0.026	1

Table 1 (continued)

Common name	Scientific name	Phylogenetic clade	Body mass of male	Body mass of female	Lovich-Gibbons ratio	Source (*N* Males and *N* Females)[1]
White-tailed Emerald	*Microchera chionura*		3.3	3.1	-0.065	1
Band-tailed Barbthroat	*Threnetes ruckeri*	Hermits	6.09	5.82	-0.046	2 (Males = 6, Females = 13)
Bronzy Hermit	*Glaucis aeneus*		5.08	4.9	-0.037	3 (Males = 3, Females = 3)
Green Hermit	*Phaethornis guy*		5.9	5.6	-0.054	3 (Males = 3, Females = 2)
Long-billed Hermit	*Phaethornis longirostris*		6.04	5.65	-0.069	3 (Males = 12, Females = 8)
Stripe-throated Hermit	*Phaethornis striigularis*		2.43	2.69	0.107	3 (Males = 7, Females = 5)
White-tipped Sicklebill	*Eutoxeres aquila*		10.8	10.11	-0.068	3 (Males = 10, Females = 7)
Brown Violet-ear	*Colibri delphinae*	Mangoes	8	6.1	-0.311	1
Green-breasted Mango	*Anthracothorax prevostii*		6.9	6.15	-0.122	3 (Males = 5, Females = 2)
Green-fronted Lancebill	*Doryfera ludovicae*		5.9	5.5	-0.073	3 (Males = 1, Females = 1)
Lesser Violetear	*Colibri cyanotus*		5.3	4.8	-0.104	3 (Males = 3, Females = 7)
Purple-crowned Fairy	*Heliothryx barroti*		5.5	5.63	0.024	3 (Males = 3 Females = 2)
Canivet's Emerald	*Cynanthus canivetii*	Mountain Gems	2.5	2.3	-0.087	3 (Males = 5 Females = 3)
Fiery-throated Hummingbird	*Panterpe insignis*		5.9	4.9	-0.204	3 (Males = 26, Females = 13)
Gray-tailed Mountain-gem	*Lampornis castaneoventris*		5.86	4.35	-0.347	3 (Males = 3, Females = 1)
Long-billed Starthroat	*Heliomaster longirostris*		6.04	5.65	-0.069	1
Plain-capped Starthroat	*Heliomaster constantii*		8.2	7.15	-0.147	3 (Males = 4, Females = 2)
Purple-throated Mountain-gem	*Lampornis calolaemus*		5.9	5.2	-0.135	2 (Males = 47, Females = 41)
Talamanca Hummingbird	*Eugenes spectabilis*		10.54	9.31	-0.132	2 (Males = 125, Females = 28)
White-bellied Mountain-gem	*Lampornis hemileucus*		6.2	5	-0.240	3 (Males = 5, Females = 1)
White-necked Jacobin	*Florisuga mellivora*	Topazes	7.4	6	-0.233	3 (Males = 9, Females = 11)

[1] Source: 1 = Birds of the World (if more than one value was reported we selected the lowest). 2 = Zoology Museum UCR. 3 = Our own database of captured specimens

Statistical analyses

We designated male body mass as the predictor and female body mass as the response variable, following standard convention in studies of SSD (e.g., Colwell 2000). We used Bayesian linear regression models implemented in the brms package in R (Bürkner 2017) to test Rensch's rule by estimating the allometric relationship between male and female body size and assessing whether the scaling exponent differed from unity. This approach was chosen over common alternatives (e.g., PGLS, PRMA) because Bayesian models can explicitly incorporate phylogenetic uncertainty while providing a single, unified model fit for statistical inference. Specifically, we used regression models to examine the relationship between the absolute value of SSD (as calculated by the Lovich–Gibbons index) and body mass in both males and females. To account for phylogenetic non-independence, we used a set of 100 phylogenetic trees from the posterior distribution published by McGuire et al. (2014). A phylogenetic covariance matrix derived from these trees was incorporated as a random effect in the models. Models were fitted using weakly informative priors. Fixed effects were assigned Normal(0, 10) priors, and the intercept was given a Normal(0, 50) prior. Group-level and residual standard deviations were specified with Student-t(3, 0, 20) priors to allow heavy-tailed uncertainty while providing weak regularization. We ran the models for each of the 100 phylogenetic trees of the posterior distribution. The resulting posterior distributions of model parameters were combined into a single model fit, allowing us to account for uncertainty in evolutionary relationships among species. Models were run for 10,000 iterations per chain (1 chain for each phylogenetic tree), discarding the first 5000 iterations as warm-up. For all parameters, both the bulk and tail effective sample size from the posterior distribution were kept above 100 per chain. We plotted the trace and distribution of posterior estimates for all chains for visual evaluation of model performance. We also estimated the potential scale reduction factors for checking model convergence (kept below 1.01 for all parameter estimates). All analyses were conducted in R version 3.6.0 (R Core Team, 2019).

Results

We observed substantial variation in body mass across species, ranging from the largest male, the Violet Sabrewing (*Campylopterus hemileucurus*, 12.42 g, $n=11$), and the largest female, the White-tipped Sicklebill (*Eutoxeres aquila*, 10.11 g), to the smallest species, the Scintillant Hummingbird (*Selasphorus scintilla*), with males averaging 2.05 g and females 2.30 g (Table 1).

Fit to rensch's rule

We found a significant relationship between the $\log_{10}$-transformed body mass of males and females across species (Fig. 1; Table 2; intercept = 0.09, slope = 0.84, 95% CI: 0.78–0.90). The slope was significantly less than 1.00, consistent with Rensch's rule, and indicates mixed allometry (i.e., larger, male-biased species occurred at the upper end of the distribution, while smaller, female-biased species clustered at the lower end of the scatterplot). The magnitude of SSD increased significantly with male body mass (Table 2; intercept = 0.01, slope = 0.15, 95% CI: 0.02–0.29), but not with female body mass (intercept = 0.05, slope = 0.10; Figs. 2

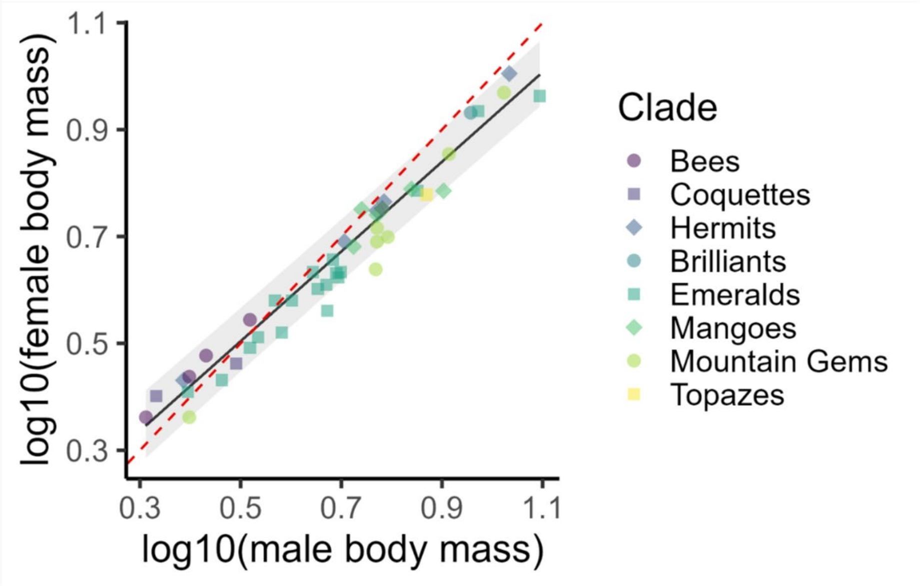

Fig. 1 Rensch's rule in hummingbirds across Costa Rica. We built the regression using 45 species from Costa Rica and subjected the data to a phylogenetic correction. The red dashed line indicates isometry (slope = 1.0) between male and female body size

Table 2 Summary of the results from the bayesian phylogenetic models used to assess rensch's rule and variation in SSD expressed as the Lovich-Gibbons index

Model	Formula	Parameters	Estimate	l-95% CI	u-95% CI	Rhat
log10(Female weight) ~ log10(Male weight)	log10(female weight) ~ log10(male weight) + (1 | gr(Species, cov = phy.tree))	Intercept	0.09	0.04	0.14	1.00
		Slope	0.84	0.78	0.90	1.00
SSD (Lovich-Gibbons Ratio) ~ log10(Male weight)	Lovich-Gibbons Ratio ~ log10(male weight) + (1 | gr(Species, cov = phy.tree))	Intercept	0.01	-0.10	0.11	1.00
		Slope	0.15	0.02	0.29	1.00
SSD (Lovich-Gibbons Ratio) ~ log10(Female weight)	Lovich-Gibbons Ratio ~ log10(female weight) + (1 | gr(Species, cov = phy.tree))	Intercept	0.05	-0.07	0.17	1.00
		Slope	0.10	-0.06	0.26	1.00

and 95% CI: -0.06–0.26), further supporting a male-biased allometric pattern. Patterns of SSD varied among phylogenetic clades. Based on the Lovich–Gibbons index, Bees and Coquettes generally exhibited female-biased SSD (positive values), whereas larger-bodied clades, such as Brilliants, Topazes, and Mountain Gems, tended to exhibit male-biased SSD (negative values; Fig. 3). Some species within the Mangoes, Emeralds, and Hermits clades showed female-biased SSD, although the overall trend within these groups remained male-biased. Of the 45 species examined, 36 (80%) exhibited male-biased SSD.

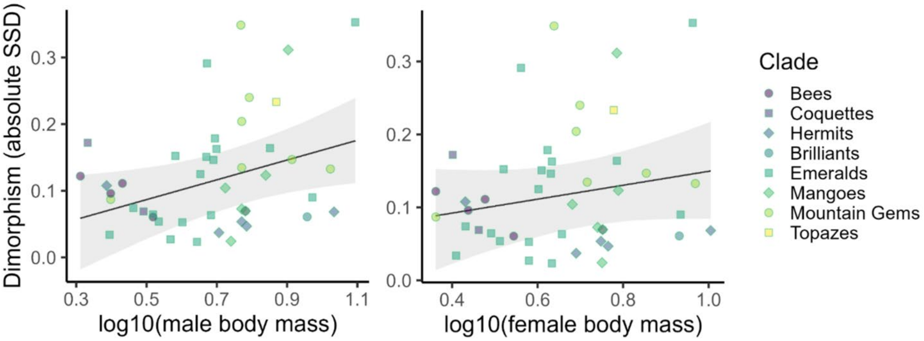

Fig. 2 Regression between the absolute sexual size dimorphism (Lovich-Gibbons Ratio) and the log10 body mass of each sex. We perform the analyses for 45 Costa Rican hummingbird species that underwent a phylogenetic correction

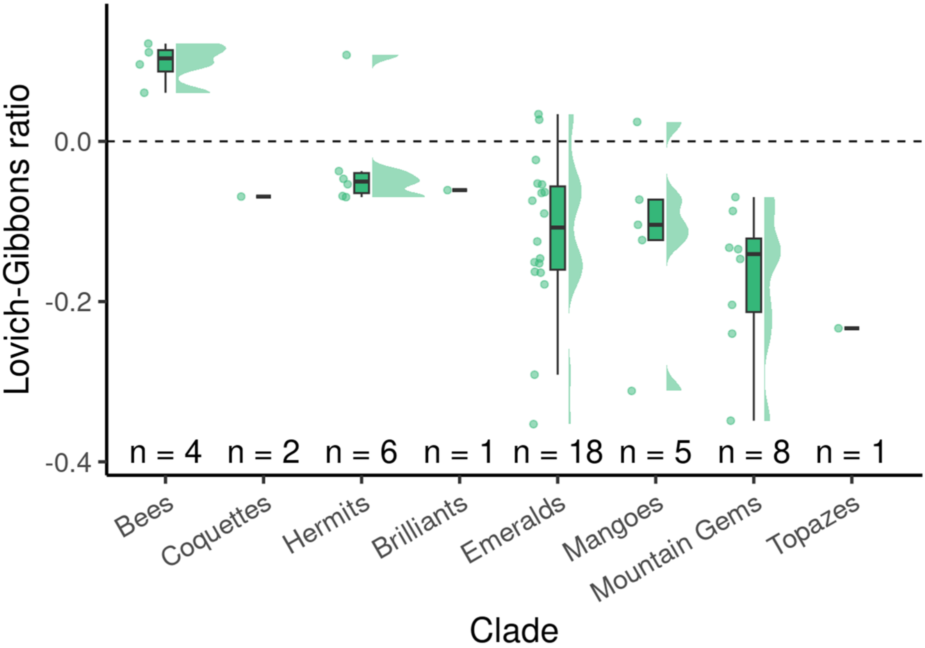

Fig. 3 Variation in the Lovich-Gibbons ratio for SSD in body mass among eight hummingbird clades following McGuire et al. (2014). Below zero, there is a male-biased allometry, and above zero, there is a female-biased allometry

Variation in SSD among hummingbird groups

Box plots of the Lovich–Gibbons index (Fig. 3) illustrate the distribution and dispersion of SSD values across the eight taxonomic groups. Nearly half of the species (48%, $n=22$) exhibited modest SSD variation (<10%), whereas 18 species showed SSD values exceeding 10%, including *C. hemileucurus*, *Lampornis castaneoventris*, *Colibri delphinae*, and

Microchera cupreiceps, which displayed index values greater than 0.3 (30%). The largest species, *C. hemileucurus*, exhibited the highest male-biased dimorphism (−0.36), consistent with observations that males of this species dominate competitive interactions at artificial feeders.

Conversely, six mid-sized species (*Threnetes ruckeri*, *Glaucis aeneus*, *Microchera albocoronata*, *Chlorestes candida*, *Heliothryx barroti*, and *Saucerottia hoffmanni*) showed less than 5% SSD variation. Only five species, including small Bees, Coquettes, and the Stripe-throated Hermit (*Phaethornis striigularis*, mean body mass 2.6 g), exhibited reversed sexual dimorphism, with SSD ranging from 10% to 17%. Thus, while our prediction that larger species will show greater SSD variation was supported by large and some mid-sized species, the expectation that smaller species would display lower SSD variation was not supported by the data.

The relationship between body mass and the absolute value of the Lovich–Gibbons ratio (Fig. 2) was significant for males but not for females, indicating that sexual selection increasingly promotes greater sexual dimorphism with male body size. Across the 45 species, the average absolute Lovich–Gibbons ratio was 0.12 ± 0.08, reflecting a moderate, overall male-biased SSD of approximately 12%.

Discussion

Our findings on SSD are consistent with Rensch's rule: larger hummingbird species exhibit male-biased SSD, whereas smaller species tend to show female-biased or less pronounced male-biased SSD. This scaling pattern, common across animal taxa (Abouheif and Fairbairn 1997; Székely et al. 2007; Slavenko et al. 2025), suggests that the magnitude of selection acts differently across the body size spectrum of males and females, consistent with the evolutionary allometries predicted by Rensch's rule (Caron and Pie 2025). Aerodynamic constraints favoring more agile males in small species (Núñez-Rosas et al. 2017), sexual selection for increased fecundity in females due to reproductive costs (Caron and Pie 2025), and competitive advantages favoring larger males in larger species (Temeles and Kress 2010) likely drive these macroevolutionary trends. Thus, our data not only highlight species- and sex-specific selective pressures shaping SSD but also provide support for its allometric evolution. This interpretation is reinforced by Colwell's (2000) comparative analysis of 154 hummingbird species, which also found mixed allometry and reported the same slope value (0.84) observed in our study, although he did not correct for phylogenetic bias. The predominant polygynous mating systems of hummingbirds, which drive intense male-male competition for mates through intrasexual selection, directly explain the high proportion (80%) of male-biased SSD documented in this study, satisfying Abouheif and Fairbairn's (1997) criterion that a taxon exhibits male-biased dimorphism when ≥80% of species show larger males.

Larger males may gain advantages in competing for food and access to mates through physical combat (Rico-Guevara and Araya-Salas 2015). However, in species that exhibit reversed sexual size dimorphism, where females are larger, selection may favor smaller males for enhanced maneuverability and larger females for greater reproductive capacity (Caron and Pie 2025). In the case of the aerial agility hypothesis mediated through female choice (Raihani et al. 2006), such differences in morphology may promote intersexual niche divergence (Bravo et al. 2024). In smaller species, for example, males often perform complex, acrobatic courtship displays, where aerodynamic traits such as wing area and wing loading can increase reproductive success (e.g., the elaborate aerial displays of *Selasphorus flammula* and *S. scintilla*; Clark et al. 2011). In these small species, the energetic cost of reproduction (e.g., egg production) is proportionally greater for females, potentially favoring a larger female body size (Wheeler and Greenwood 1983).

Other hypotheses may also contribute to the observed SSD patterns. The intersexual niche divergence hypothesis posits that size differences between sexes reduce competition for food, while the small-male hypothesis suggests that smaller males forage more efficiently (Krüger 2005). These mechanisms are likely to interact to add to the variation in SSD observed among large and small hummingbird species (Bravo et al. 2024). Sexual selection plays a primary role, as evidenced by the predominant male-biased SSD, the pronounced sexual dimorphism in plumage and the presence of exaggerated male traits such as elongated tails and iridescent crown and throat feathers, which are linked to reproductive success and thus may interact with body mass and flight agility (Caron and Pie 2025).

While direct experimental evidence is lacking to test these hypotheses, our findings provide a valuable foundation for future research. For instance, in *S. flammula* (SSD = 9.6%), we documented intersexual habitat segregation. In this species, males are more frequently observed in páramo vegetation above the tree line, whereas females predominantly occupy forest edges, canopy gaps, and the interior of oak forests. Comparable patterns of habitat segregation have also been reported for *S. sasin* and *S. rufus* in California, where males and females forage in distinct habitats (Howell and Gardali 2003). There is also an urgent need to further research into the diverse and complex mating behaviors of hummingbirds (Núñez-Rosas et al. 2017), especially regarding reproductive success, which will help disentangle the intricate interplay between sexual and natural selection affecting the magnitude of SSD.

Causes of variation in SSD

The average absolute variation in sexual size dimorphism (SSD) in body mass across species was 12%, a value we consider moderate (Fairbairn 2007). Rather than scaling strictly with body mass, our findings suggest that physiological constraints may limit SSD across hummingbirds as a group. Hummingbirds exhibit extremely high metabolic rates, a strong dependence on near-constant access to energy-rich food sources, and substantial energetic costs due to small body size and hovering flight. These physiological demands may modulate overall body mass variation, as well as SSD, despite the presence of sex-specific selective pressures.

Contrary to our expectations, we did not observe a consistent trend of increasing SSD variation from smaller to larger species. We hypothesized that larger hummingbirds would exhibit greater SSD, while smaller species, more constrained by energetic limitations, would show reduced variation. This prediction also assumed that higher SSD would promote greater intersexual niche differentiation. However, our results showed relatively modest SSD variation across species (see also Székely et al. 2007).

While we might expect variation in SSD to correspond with functional differences, such as competitive ability or resource partitioning (Maglianesi et al. 2022), hummingbirds exhibit high behavioral plasticity that may buffer the ecological consequences of morphological divergence (Rojas-Rodríguez et al. 2023). Differences in size, though relevant to determining competitive hierarchies and access to resources, can be offset by opportunistic foraging strategies and behaviors such as nectar robbing (Ornelas 1994; Boehm 2018). This behavioral flexibility likely facilitates access to floral resources across the full spectrum of body sizes, reducing the selective pressure for more pronounced morphological divergence between sexes.

The relationship between body mass and the absolute value of SSD increased with species size only in males. This pattern shows a predominant role of sexual selection acting more strongly on male body size (i.e., intrasexual selection driving male-male competition for mates), potentially contributing to intersexual niche segregation. However, the underlying mechanisms remain unclear and warrant further investigation through field studies that would quantify both intersexual and intraspecific morphological variation.

Finally, it is important to recognize a limitation of most SSD analyses: the use of average values for morphological traits, often derived from museum specimens and small sample sizes, tends to obscure the true range of variation within and between sexes. This issue has been previously noted (Smith 1999). As shown in our study, relying solely on male-to-female ratios of trait means masks meaningful patterns of variation, particularly when one sex shows high variability in a given trait. Future studies should incorporate measures of dispersion to better understand the functional and evolutionary significance of SSD.

Other morphological traits influencing SSD beyond body mass

While body mass is the most frequently analyzed trait in studies of SSD (Fairbairn 1997; Colwell 2000), it is not the only morphological characteristic affecting competitive performance, foraging strategies, or resource access. One reason for its prominence is that body mass is routinely recorded in both field studies and museum specimens. However, a broader exploration of additional traits is necessary to fully understand the ecological and evolutionary implications of SSD. For instance, the size of the hallux (rear toe) can influence foraging efficiency. In some mountain gem species, such as *Panterpe insignis*, relatively large legs and a well-developed hallux allow individuals to perch while feeding, thereby reducing the energetic costs associated with hovering flight (R. Colwell pers. comm.) Similarly, bill morphology plays a key role in determining access to floral resources. Long-billed hummingbirds can exploit a wider range of corolla lengths than short-billed species, enabling both legitimate and illegitimate (nectar-robbing) visits (Rojas-Rodríguez et al. 2023). Opportunistic and generalized foraging strategies are widespread in pollination networks, further highlighting the importance of flexible bill traits (Simmons et al. 2019). In addition to bill length, bill shape and specialized structures, such as serrations along the edges, can influence foraging for both nectar and arthropods (Feinsinger and Colwell 1978; Rico-Guevara et al. 2019). These serrations, which enable piercing of corollas during nectar robbing, also facilitate insect capture and may function as secondary sexual traits that enhance male–male competition (Ornelas 1994; Rico-Guevara and Araya-Salas 2015). While evidence for consistent sex differences in these traits remains limited, integrating additional morphological traits represents a valid avenue for future research to improve our understanding of the ecological and evolutionary implications of SSD.

Comparative trends across major vertebrate groups

The SSD patterns observed here reflect vertebrate-wide evolutionary trends, especially regarding the importance of the mating system determining the magnitude and direction of SSD. Székely et al. (2007) analyzed SSD across 3,767 species within 125 bird families. They tested four hypotheses explaining SSD (mating-competition, display-agility, resource-segregation, and fecundity hypotheses) using a rank system to categorize species according to their fit to these hypotheses. However, their data was unbalanced and limited by sample size within each bird family. They found that male-biased SSD was dominant across families, with Rensch's rule being more common than expected by chance and driven primarily by polygynous mating competition favoring larger males, and aerial display agility selecting for smaller males in small species. In contrast, raptors showed a female-biased SSD. Trochilidae showed a strong association with the mating-competition and display-agility hypotheses (Caron and Pie 2025). Their conclusions are consistent with our findings that predominantly polygynous mating systems driven by sexual selection in hummingbirds explain the high prevalence (80%) of male-biased SSD and the mixed allometry (slope = 0.84), while modest variation (12%) reflect physiological constraints modulating the variation in SSD.

The effect of sexual selection as the major driver of male-biased SSD with physiological constraints modulating SSD variation observed here, is consistent with the patterns described by Lindenfors et al. (2007) in their analysis of 1,370 mammal species. Lindenfors et al. (2007) found male-biased SSD in 45% of mammal species, primarily driven by sexual selection through male-male competition in strongly polygynous taxa like primates, pinnipeds, and ungulates. In these cases, intense mating competition results in larger males whereas fecundity selection limits a correlated increase in female size. Overall, mammals conformed to Rensch's rule when including the latter mentioned large-bodied orders; smaller-bodied orders showed different patterns: Marsupialia was largely monomorphic, while Chiroptera and Lagomorpha exhibit female-biased SSD due to physiological constraints, particularly flight energetics in bats (Wu et al. 2018) and strong fecundity selection in rabbits and hares, which overrode sexual selection effects. Once again, polygynous mating systems were strongly correlated with higher male-biased SSD, while small-bodied taxa demonstrated limited dimorphism (a modest 12% variation in hummingbirds; and monomorphism or reversal in bats and lagomorphs) due to taxon-specific metabolic demands that modulate SSD variation (see Jones and Sheard 2023).

In reptiles, Cox et al. (2007) analyzed SSD variation across 832 species. These authors divided reptiles into three groups, lizards, snakes and turtles. SSD was male-biased in lizards, whereas snakes and turtles leaned towards female-biased SSD. In all the groups there were families with both male-biased and female-biased SSD. Almost all snakes had female-biased SSD except for the family Viperidae. Adjustment to Rensch's rule took place in most taxa, with sexual selection for large male size via male combat and territoriality as the primary driver of male-biased SSD and ecological factors influencing SSD variation (i.e., Cox and Calsbeek 2010). However, support for fecundity selection favoring larger female size was weak, and evidence for ecological niche divergence was lacking.

In the case of amphibians, Kupfer (2007) reported a female-biased SSD as the predominant pattern in frogs and salamanders due to fecundity selection (i.e., larger females produce more eggs), with male-biased SSD rare and restricted to lineages exhibiting territoriality and male-male combat. Caecilians showed mostly monomorphism or weak female bias.

Unlike the predominantly polygynous hummingbirds with male-biased SSD, amphibians demonstrated the opposite pattern where fecundity selection typically dominated SSD. This contrast illustrates how the mating system determines SSD direction: polygynous systems with strong male-male competition result in male-biased SSD; when fecundity selection is strong SSD is female-biased.

Fishes display a wide diversity of mating systems (Taylor and Knight 2008) and patterns of SSD. Horne et al. (2020) demonstrated across 619 fish species that SSD variation (female-biased in 68% of cases) was primarily driven by sexual selection intensity for larger males (e.g., via territoriality, paternal care, external fertilization), not fecundity selection in females, with no clear link to reproductive output relative to female size.

In summary, these vertebrate-wide comparisons show that sexual selection via polygynous mating systems and male competition predominantly drives male-biased SSD and adherence to Rensch's rule, as seen in hummingbirds (80% male-biased), birds (Székely et al. 2007), mammals (Lindenfors et al. 2007; Jones and Sheard 2023), lizards (Cox et al. 2007), and many fish species (Horne et al. 2020), while physiological constraints (e.g., flight energetics, fecundity selection) and ecological factors modulate variation or female-biased SSD in snakes, amphibians, bats, and some fish species.

Conclusions

The mixed allometry in SSD observed in this study indicates that males and females experience distinct sexual and selective pressures on body mass. In larger species, sexual selection may favor increased male size, while in smaller species, it may instead prioritize greater male agility and buffer reproductive costs in females. We hypothesized that the physiological capacity to buffer environmental variation scales positively with body mass, resulting in size-dependent constraints on SSD. Contrary to this expectation, average variation in SSD was modest (12%) and significantly related to body mass only in males. The results suggest a scenario in which sexual selection establishes the predominant male-biased SSD pattern across hummingbirds, while physiological constraints modulate the magnitude of size variation.

Our study highlights the importance of analyzing SSD within an integrative framework that combines evolutionary allometries, such as Rensch's rule, with ecological, behavioral, and physiological mechanisms. To advance this understanding, future research should prioritize field-based studies measuring a broader range of morphological traits, documenting habitat and resource use, and quantifying behavioral and ecological segregation between sexes. This information will complement the understanding of sexual selection pressures. Focusing only on average trait ratios between males and females overlooks intraspecific and intersexual variation, which can obscure the selective pressures acting on each sex. Our findings indicate mixed allometry, implying that various traits may evolve under divergent selective regimes in males and females; thus, it is imperative to include variation around trait means. While sexual selection is likely to drive the prevalent male-biased SSD observed here, natural selection through physiological and ecological constraints might modulate the magnitude and direction of variation in SSD.

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Author contributions GA conceived the idea, collected the field data, and wrote the manuscript. FT and JK Contributed data. All authors analyzed the data and edited the manuscript.

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Declarations

Competing interests The authors declare no competing interests.

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Consent to participate All the authors agreed to contribute intellectually to this research.

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