**Variation in sexual size dimorphism and fit to Rensch's rule in 45 species of Costa Rican hummingbirds**

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**Abstract**

According to Rensch’s rule, in species where males are the larger sex, increasing body size is coupled with increased sexual size dimorphism (SSD), whereas in species where females are larger, SSD decreases with body size. We describe the variation in SSD for body mass and its fit to Rensch´s rule in 45 species of Costa Rican hummingbirds. We examine SSD in body mass, bill length, and wing size and their fit to Rensch´s rule in nine species of hummingbirds for which we have detailed data. We expected that physiological constraints will limit the variation in SSD since hummingbirds have high metabolic rates, high dependence on energy-dense food, and high costs imposed by small size and hovering flight; these factors scale with body size and elevation. Large species should be physiologically capable of withstanding greater variation in SSD compared to small species, which are more energetically limited. Hummingbirds showed mixed allometry and fit Rensch's rule (slope of the RMA regression male vs female body mass = 0.8630). Eighty percent of the species showed male-biased allometry for SSD in body mass. Average variation in SSD was 12% and varied regardless of size. Physiological limitations act on hummingbirds as a group affecting SSD, independently of body size. SSD differences in body size, bill length, and wing area could influence ecological performance, sexual displays, food resource access, and foraging behavior. The SSD mixed allometry, and the positive relationship between the standard deviation of body mass, wing chord, and wing area with hummingbird size found only in males (9 species), suggests that selective pressures act differentially on the sexes and influence sexual niche segregation. Future research should examine intersexual variation in morphology, and quantify intersexual habitat use, niche segregation, and interspecific and intraspecific competitive interactions, targeting species located at the extremes of the Rensch's rule scatterplot.

**Introduction**

Differences in body size between the sexes are widely distributed across a diverse variety of organisms, from vertebrates (Fairbairn 1997) to arthropods (Blanckenhorn et al. 2007). This sexual size dimorphism (abbreviated SSD) has important selective consequences, since it influences trophic niche segregation (i.e., Bravo et al. 2016), specialization in reproductive roles, and reproductive success (Kingsolver and Huey 2008; Herczeg et al. 2010). The variation in SSD has been attributed to diverse ecological and evolutionary factors (Webster 1992; Székely 2007). These include classic sexual selection theory (Darwin 1871; Payne 1984; Dale et al. 2007) such as the mating competition (i.e., large males are better competitors) and display agility hypotheses (small males are more agile in sexual displays, Székely et al. 2007), the sexual niche segregation and specialization for food resources hypothesis (Temeles et al. 2010; Maglianesi et al. 2022), size- and sex-dependent predation risk (Blanckenhorn 2005), correlational selection (i.e., the effects that morphological changes in one sex that affect the morphology of the opposite sex, Fairbairn 1997), as well as phenotypic plasticity related to environmental changes influencing the expression of sex-related differences in ontogenetic trajectories, reproductive allocation, and body size (West-Eberhard 2003).

Rensch (1950) was among the first to observe that in species where males are larger than females, SSD increases with increasing body size (hyperallometry) whereas in species where females are larger, the pattern is reversed, and thus relative differences in SSD decrease with increasing body size (hypollometry, Rensch 1950). This pattern is known as Rensch's rule, and is predominant across a variety of taxa, including birds, mites, primates, lizards, snakes, and turtles (Blackenhorn 2005). However, the causes responsible for SSD leading to Rensch´s rule remain unclear, although comparative analyses of diverse bird groups converge on sexual selection leading to mate competition and higher sexual display agility(Székely et al. 2007). Natural selection, as well as physical and physiological constraints, set the limits of the variation in SSD defining the upper and lower bounds of body size.

In addition to sexual selection explanations, the hypothesis of specialization in reproductive roles and sexual niche segregation (Slatkin 1984) suggests that SSD is caused by differential selective pressures acting upon males and females leading to intersexual niche divergence. These explanations are not mutually exclusive and could be operating simultaneously. In addition, the mating system (e.g., polygyny in lekking species vs. monogamy), and the breeding aggregation of one sex, could intensify intraspecific competition for mates and thus increase the magnitude of SSD. Sexual selection goes beyond morphological traits and includes characters such as differences in vocalizations and plumage in birds, and behavioral displays (i.e., lekking behavior). Additional selective pressures, not directly related to sexual selection, could also act on SSD, such as the increase in brain size in relation to body size in hummingbirds (see Ocampo et al. 2018 ), which impacts foraging behavior and habitat selection (Gonzalez-Gomez et al. 2014). Disentangling the evolution of the allometry of SSD implies understanding many of the key questions in evolutionary biology, such as the evolution of groups of correlated characters, or the influence of phenotype plasticity associated to the expression of SSD. Field studies estimating population parameters affecting SSD, and more rigorously designed experiments, are needed to distinguish between overlapping hypotheses.

Hummingbirds (family Trochilidae) represent an ideal group to examine the selective pressures influencing SSD allometry (Colwell 2000). 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 present sex segregation in habitat and resource use (Howell and Gardali 2003; Leimberger et al. 2022). Males and females have distinctive reproductive roles and polygynous reproductive systems, where leks are prevalent. Hummingbirds may have reached the upper energetic limits of miniaturization of any group of flying vertebrates, adapting their physiology to conserve heat in cold nights (Shankar et al. 2022). Their high metabolic rates force them to secure almost constant access to high-energy food sources, in addition to placing severe constraints on their ability to deal with environmental variation, although this has not been an obstacle for 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 due to considerable energy constraints and high dependency on nectar consumption (see Kessler et al. 2020).

The objective of this study is to measure the degree of SSD variation in body mass and the fit to Rensch´s rule in 45 of Costa Rica's 52 species of hummingbirds and investigate possible explanations for such variation. We also examine the prevalence of Rensch´s rule in 9 species of hummingbirds for which data on bill length and wing size have been gathered, including the largest hummingbird in Costa Rica, the Violet Sabrewing (*Campylopterus hemileucurus*), and one of the smallest, the Volcano Hummingbird (*Selasphorus flammula*). We propose the hypothesis that the physiological capacity to buffer morphological changes, which varies with body size, can explain the degree of variation in SSD. A large size provides a better physiological buffering against environmental challenges, such as food shortages or extremes in environmental variables. Since large species would have more physiological plasticity to adapt to environmental challenges, we would expect greater variation in SSD in these species than in small species, which are more energetically limited. Greater variation in SSD should reinforce sexual niche segregation. Due to greater physiological limitations, small species should present a smaller range of morphological variation between males and females than larger species. The family Trochilidae stands as an appropriate system to analyze this hypothesis within the context of Rensch's rule, since it has species exposed to diverse ecological and life history pressures, as well as diverse sexual strategies. Our results will emphasize the importance of examining male- and female-biased allometries and help establish future directions in the analysis of the ecological importance of SSD in hummingbirds.

**Materials and Methods**

**Sources of morphological data**

For our analysis we used three sources of morphological data: a) our own database of 19 hummingbird species representing 731 mist net captures registered between 2012 and 2016 in different sites in Costa Rica. Of these, nine species with sexual dimorphism had detailed measurements of morphological characters that included bill length, wing chord, wing area, and body mass. We refer to this data as the small dataset (Table 1), b) we compiled data from 35 species from the bird collection of the Museum of Zoology at the University of Costa Rica (154 specimens in total), and c) we used the e-bird platform (https://birdsoftheworld.org/bow/home?) from Cornell University Ornithology Laboratory to gather body mass data. Using these three sources, we assembled information on body mass for 45 hummingbird species (i.e., the large dataset, Table 2). We analyzed SSD for the large dataset using body mass (g) because this morphological variable is the most frequently reported in the literature, as well as in databases and museum specimens, and is correlated with resource access (Dalsgaard et al. 2009). We used the classification of McGuire et al. (2014) to distribute the 45 species into eight of the nine hummingbird phylogenetic clades (Table 2).

**Lovich-Gibbons sexual dimorphism index**

We calculated the Lovich-Gibbons ratio (Lovich and Gibbons 1992) to quantify SSD for body mass in the large dataset as well as for the morphological variables of the small dataset. This index of sexual dimorphism is the ratio of the average size of the larger sex over the average size of the smaller sex minus 1. The index is positive when females are the larger sex, and arbitrarily declared negative when males are the larger sex. Since this index is a ratio, it can also be expressed as a percentage of SSD. For instance, in *S. flammula* the index is 0.096 (Table 2), and it shows that females are 9.6% larger than the males. The Lovich-Gibbons ratio followed a normal distribution (Shapiro-Wilk test = 0.96, P = 0.28).

**Statistical Analyses**

We used model II, reduced major axis (RMA) regression, to measure the relationship between the base 10 logarithms of the female and male morphological variables and its fit to Rensch´s rule. RMA regression is appropriate when both X and Y variables are measured with error, both are random variables, are measured in the same scale, and the aim is to estimate the slope value (Quinn and Keough 2002). We arbitrarily consider the logarithm in base 10 of body mass of males as the X variable and the logarithm in base 10 of the body mass of the females as the Y variable to conform to what has been traditionally used in the literature (i.e., Colwell 2000). We applied RMA regression to the log-10 transformed values of wing widths, wing chords, and bill lengths for the 9 species of hummingbirds for which we had data plotting the same morphological character in males against females. The slope and standard error of the regression were assessed for significant departure from the slope value of 1 (isometry). The package lmodel2 from the software R (Legendre and Oksanen 2018) was used to calculate the regression equation and its significance.

To test the prediction that SSD will be higher in large species and lower in small species, we examined the relationship between species size (i.e., body mass) and SSD using the Pearson correlation coefficient. To do this, we correlated the absolute value of SSD (i.e., the absolute value of the Lovich–Gibbons ratio) versus the body mass of male and females in the large dataset, and versus the average values of bill length, wing chord, wing area, wing width, and body mass in the small dataset.

Finally, we used the small data set to examine the extent of intraspecific and intersexual variation in morphological traits. We calculated the Pearson correlation coefficient between the average and the standard deviation (SD) of morphological traits separately for males and females. We expected SD to increase with trait magnitude from small to large species.

**Results**

We examined 45 hummingbird species from Costa Rica distributed into eight of the nine phylogenetic clades identified by McGuire et al. (2014). Our sample shows a wide range of sizes, and included the largest hummingbird in Costa Rica, the male Violet Sabrewing, *C. hemileucurus* (12.42g, n = 11), the White-tipped Sicklebill, *Eutoxeres aquila*, the largest female (10.11 g), and the Scintillant Hummingbird, *Selasphorus scintilla*, the smallest species for both males (2.05g) and females (2.3 g, Table 1).

**Fit to Rensch´s Rule**

For the large dataset (45 species) we found a significant relationship between the Log10 of male and female body mass (Log10 female body mass = 0.1358 + 0.8630\* Log10 male body mass, r2 = 0.96, P = 0.0001). The slope of the regression was <1 indicating conformity with Rensch’s rule. A similar pattern was found for the phylogenetic classification, using the average male and female weight for the study species belonging to each clade (Log10 female body mass = 0.1892 + 0.8429\* Log10 male body mass, r2 = 0.97, P = 0.0002). The magnitude of the regression slopes in both cases was very similar (Figure 1), showing divergence from isometry, and indicating mixed allometry. In this case, large, male-biased species were at the upper end, and small, female-biased species were at the lower end of the scatter plot.

The Lovich-Gibbons ratio of sexual dimorphism in the large dataset showed that Bees and Coquettes were on the positive side of the chart (indicating female-biased SSD), whereas large-sized clades were on the negative side (indicating male-biased SSD, Figure 2). However, Mangoes, Emeralds, and Hermits had species in which females were larger than males, although as a group, the dimorphism was male-biased. Of the 45 hummingbird species examined, 36 (80%) showed male-biased SSD.

In the small dataset, we found isometric SSD for bill length since the slope was not different from 1 (slope = 1.0264, Figure 3). However, these species had different leverage on the slope, with the allometry biased towards females in large species (such as *C. hemileucurus,* *Eugenes spectabilis*, *Eupherusa eximia*, *M. cupreiceps*, and *Phaetornis guy*), and biased towards males only in *Heiliodoxa jacula* and *Selasphorus flammula* (Figure 4A). Most hummingbirds had a 10% difference in bill length between males and females, except for the largest species, *C. hemileucurs* and *P. guy*, which reached 14%. The allometry of bill length shows that the slope could change according to the identity of the species included in the analysis. Although we examined species with large size differences, such as *S. flammula* and *C. hemileucurus*, and the overall slope indicated symmetry, we observed instead clear sex differences in bill length SSD in several species. The other three morphological traits examined here (wing chord, wing area, and body mass) had slopes < 1, which confirmed Rensch´s rule, and showed a similar sorting of species along the regression line (Figure 3). For these variables, there was a clear male-biased SSD except for *S*. *flammula* in which the pattern was reversed (Figure 4).

**Test of the hypothesis of physiological limits to SSD associated to body size**

Although hummingbirds fit Rensch's rule, 48% of the species (n = 22) showed less than 10% of SSD variation in body mass (Table 2, Figure 2). There were 18 species with SSD higher than 10%. This group included *C. hemileucurus*, *Lampornis castaneoventris*, *Colibri delphinae*, and *Microchera cupreiceps*, which showed an SSD over 30%. Except for *C. hemileucurus*, these were mid-size species. Thus, our prediction that the largest species will show higher variation in SSD, as a general trend, was not supported by the data. Finally, the species with less than 5% variation in SSD included a small number of mid-size species (n = 6), and these were *Threnetes ruckeri*, *Glaucis aeneus*, *Microchera albocoronata*, *Chlorestes candida*, *Heliothryx barroti* and *Saucerottia hoffmanni*. Our second prediction that the smallest species will show less variation in SSD was not supported by the data either. This was also evident when plotting the body mass of males and females vs. the absolute value of Lovich-Gibbons ratio. This relationship was not significant, neither for males (Pearson coefficient = 0.2, P = 0.20) nor for females (r = 0.02, P = 0.88). We excluded *C. hemileucurus* from this analysis because it was an outlier that drove the correlation for males to 0.34, and although statistically significant (P = 0.02), the scatter plot showed wide variation, with species of different sizes overlapping in relation to SSD. The average absolute value of the Lovich-Gibbons ratio was 0.12 ± 0.08 (12% variation in SSD across the 45 species).

In the small dataset, we found small variation in SSD for the wing chord (absolute average value of Lovich-Gibbons ratio = 10.89 ± 4.26), although the wing area showed a higher average variation (22% ± 11.22). None of the morphological traits examined here showed a significant relationship between the magnitude (or size) of the character and SSD. Regarding the extent of intraspecific and intersexual variation in morphological traits, we found significant and positive correlations between the average and SD of body mass (r = 0.92, p = 0.001), wing chord (r = 0.78, p = 0.04), and wing area (r = 0.82, p = 0.01) in males. In these cases, SD increased with trait magnitude (i.e., species with larger males had greater variation). None of the correlations between the mean trait value and its SD were significant for females. Although the sample size was small (n = 9 species), and species varied greatly, average trait magnitude and SD scaled positively with size in males.

**Discussion**

Hummingbirds represent a special case of Rensch's rule, as they display mixed allometries and a predominance of male-biased body mass, which is the general trend for most bird groups (Székely et al. 2007). Using a similar analysis for 154 hummingbird species, Colwell (2000) reports mixed allometry and a slope value (0.84) nearly identical to the one found here (0.8630). Abouheif and Fairbairn (1997) propose that if 80% or more of the species in a group have males larger than females, the taxon could be characterized as male biased, which applies in this study since 80% of the 45 hummingbird species examined here showed male-biased SSD in body mass.

**Does SSD vary with body size?**

In contrast to our hypothesis, our analysis did not follow a trend of increasing variation in SSD from small to large hummingbirds. We expected that greater SSD would be more common in large species. The smaller and more energetically limited species would show a lower capacity for high variation in SSD. Implicit in our hypothesis was the expectation that high variation in SSD could foster a higher differentiation in intersexual niche divergence. In contrast, we observed a relatively modest variation in SSD (Székely et al. 2007). Although we might expect differences in SSD to translate into changes in functional performance, such as competition for resources (Maglianesi et al. 2022) and in the intensity of intersexual and intrasexual selection (Payne 1984), hummingbirds can show highly plastic behavior buffering the effects of morphological differences. Intra and interspecific differences in size, while important in determining competitive hierarchies and resource access, can be buffered through behavioral changes reflected in opportunistic foraging as well as nectar robbing (Ornelas 1994; Boehm 2018). Behavioral plasticity makes it possible to circumvent morphological limitations in accessing resources and this takes place across the whole range of body mass.

However, in the small dataset, the magnitude of the SD in body mass, wing chord, and wing area increased with trait magnitude and hummingbird size only in males. This suggests that selective pressures act differentially on the sexes and potentially influence sexual niche segregation. The primary causes of this variation need to be further explored through field studies that quantify intraspecific and intersexual morphological variation. SSD has been analyzed using the ratio of average values ​​of morphological characters for males and females, usually obtained from museum specimens and very small samples, which ignores the intraspecific and intersexual variation of the actual character. This flaw has been pointed out before (Smith 1999), and as found here, the variation associated to one trait and sex is lost when the analysis is done using the ratio of average values, which does not incorporate the variation around the mean.

**Causes of variation in SSD**

Although hummingbird species fit Rensch's rule by showing mixed allometry, 48% of the species displayed a modest variation in SSD for body mass (less than 10%). Only 5 species, including the small bees and coquettes, and the Stripe-throated Hermit, *Phaethornis striigularis* (mean body mass 2.6 g), showed female-biased SSD, or reverse sexual size dimorphism (RSD), ranging 10 to 17 %. The largest species, *C. hemileucurus*, exhibited a large variation in SSD biased towards males. In this species, the male is, on average, 36% heavier than the female. Body size in this case provides a competitive advantage to access food resources. We have observed that male *C. hemileucurus* dominate competitive interactions around artificial feeders (displacing *C. hemileucurus* females, as well as males and females from other 6 species).

However, the average variation in the absolute value of SSD for body mass across species was 12%, which we considered moderate (Fairbairn 2007). Instead of scaling with body size, the hypothesis of physiological limits to SSD could apply to hummingbirds as a group, regardless of body size. This is because the high metabolic rates of hummingbirds in general, their high dependence on access to high-energy food (which must be supplied almost constantly), and the high energy costs imposed by a small size and hovering flight, may limit the range of variation in body size altogether, as well as between sexes, despite of different selective pressures leading to SSD in males and females.

**Mating competition and Aerial agility hypotheses**

Eighty percent of the hummingbird species examined here showed male-biased SSD. Large males are usually better competitor for food resources and are better in combat for access to females. However, for the rest of the species with RSD, aerodynamics, and maneuverability (aerial agility) could affect SSD and favor intersexual niche divergence since these characters are subject to different selective pressures between males and females. Males of smaller species do complex, acrobatic displays for females, and thus, morphological characters related to aerodynamics, such as wing area and wing loading, could determine their reproductive sucess in small species such as *S. flammula* and *S. scintilla* (Clark et al. 2011) and could affect SSD in these species. In small species, the cost of reproduction (e.g., egg production) would be higher for females, favoring larger size in this sex relative to males (Wheeler and Greenwood 1983).

As in hummingbirds, bustards (Otididae) display mixed allometries, with species having species in which males can be three times heavier than females, species that are monomorphic (isometry), and species showing RSD (i.e., males < females). In this group, smaller males are common in species showing more agile sexual displays, supporting the aerial agility hypothesis (Raihani et al. 2006). This is also the case of *Falco tinnunculus* where males perform complex acrobatics to attract females and are 10% smaller than females (Hakkarainen et al.1996). In shorebirds and gulls where males do more acrobatic displays, males are smaller than females (Székely et al. 2000).

Other alternative explanations, such as the intersexual niche divergence hypothesis, where sexes have evolved different sizes to lessen intersexual competition for food, and the small-male hypothesis, where small males are more efficient foragers (Krüger 2005), could combine to explain the differences in SSD observed here for large and small hummingbird species. There is a dearth of field experiments necessary to test these hypotheses, but the results found here could orient future research to examine the causes of SSD in species of hummingbirds showing large and small variation in SSD. For instance, in small species such as *S. flammula* (SSD = 9.6%), we have observed habitat segregation. Males are more common in the Páramo whereas females prefer forest edges and the interior of oak forests. Intersexual habitat segregation has been reported in *S. sasin* and *S. rufus* in California, United States, where males and females forage in different habitats (Howell and Gardali 2003).

**Other morphological traits influencing SSD**

Body mass is not the only morphological trait with a significant effect on competitive performance, foraging behavior, or resource access despite of being the most analyzed morphological character used to summarize differences in SSD (i.e., Fairbairn 1997; Colwell 2000). Body mass is regularly recorded in field studies as well as in museum specimens. The influence of other traits on SSD should be further explored. For instance, the size of the hallux allows mountain gem species with relatively large legs, such as *Panterpe insignis*, to perch while foraging, which saves energy by avoiding hovering flight (R. Colwell, pers. com.) In addition, long-billed hummingbirds could access a wider variety of corolla lengths than short-billed ones, including legitimate and non-legitimate visits. Opportunistic and non-specialized foraging could be common in many pollination networks (Simmons et al. 2019). The length and morphology of the bill can be of great importance affecting foraging for nectar and insects (Feinsinger and Colwell 1978; Rico-Guevara et al. 2019), but so is the presence of bill serrations that favor nectar robbing by piercing corollas, as well as insect foraging (Ornelas 1994). These bill serrations are secondary sexual characters influencing competitive interactions between males (Rico-Guevara and Araya-Salas 2015).

We found significant heterogeneity in the SSD of bill length that was not associated to body mass, and that did not conform to Rensch´s rule, despite that many species were clearly dimorphic in bill length. In addition to bill length, sexual dimorphism in bill curvature was inversely related to the overlap in the use of flower resources in 31 species of hummingbirds (Maglianessi et al. 2022), although the pattern was highly variable and affected by territorial behavior.

**Conclusions**

The mixed allometry for SSD found here demonstrates that males and females are under different selective pressures for multiple morphological traits in addition to body size. This includes sexual selection for larger males in large species and selection towards greater male agility in small species. We expected that physiological constraints related to body mass would explain the variation in SSD, and that larger species would show greater variation in SSD. However, the average SSD variation in body mass was modest (12%) and was not related to body mass. This narrow range of variation accounts for the potential effects of physiological limitations that restrict SSD in hummingbirds as a group, regardless of size. Hummingbird behavioral plasticity circumvents morphological limitations on resource access. Other characters, such as bill length and curvature, and the presence of bill striae, could facilitate nectar theft in some species, as well as insect foraging and competitive interactions between males.

Future research should examine the levels of intraspecific and intersexual variation in SSD, which could be better understood with field data quantifying more traits and increasing the sample size for males and females. Analyzing SSD as a ratio of average values for males and females tells an incomplete story. Since the mixed allometry found in hummingbirds indicate different selective pressures acting on males and females, the variation around the mean of traits for males and females must be measured instead. In addition, field experiments should quantify intersexual habitat use and niche segregation, the nature of sexual displays, and interspecific and intraspecific competitive interactions, at least for the species that lie at the ends of the continuum of the Rensch's rule scatterplot.

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**Table 1.** Summary of morphological character of nine hummingbird species used to analyze Rensch´s rule and variation in SSD. Values are means (± S.D.) of individuals measured between 2012 and 2016 in Costa Rica.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| **Species (abbreviation)** | **Sex** | **N** | **Body mass (g)** | **Bill length (cm)** | **Wing chord (cm)** | **Wing area (cm2)** |
| *Microchera cupreiceps* (MC) | F | 6 | 3.64 (0.87) | 1.82 (0.12) | 4.81 (0.51) | 5.54 (1.92) |
|  | M | 4 | 4.7 (0.1) | 1.66 (0.2) | 5.60 (0.46) | 7.7 (2.5) |
| *Campylopterus hemileucurus* (CH) | F | 3 | 9.18 (0.6) | 3.44 (0.04) | 7.45 (0.04) | 15.06 (1.9) |
|  | M | 11 | 12.41 (1.03) | 3.21 (0.13) | 8.46 (0.13) | 17.49 (3.01) |
| *Heliodoxa jacula* (HJ) | F | 112 | 8.54 (0.74) | 2.54 (0.22) | 6.80 (0.47) | 10.38 (2.06) |
|  | M | 48 | 9.06 (0.86) | 2.42 (0.25) | 7.65 (0.52) | 12.10 (2.22) |
| *Phaetornis guy* (PG) | F | 2 | 5.6 (0.7) | 3.85 (0.07) | 5.85 (0.07) | 9.18 (1.32) |
|  | M | 3 | 5.9 (0.46) | 4.21 (0.08) | 6.76 (0.65) | 10.31 (2.04) |
| *Discosura conversii* (DC) | F | 1 | 2.9 | 1.2 | 4 | 2.72 |
|  | M | 1 | 3.1 | 1.6 | 4.5 | 2.95 |
| *Eugenes spectabilis* (ES) | F | 28 | 9.31 (0.64) | 3.76 (0.26) | 7.26 (0.58) | 12.08 (2.16) |
|  | M | 124 | 10.54 (0.80) | 3.28 (0.52) | 7.72 (0.79) | 14.41 (3.84) |
| *Lampornis calolaemus* (LC) | F | 41 | 5.20 (0.86) | 2.10 (0.25) | 5.62 (0.51) | 7.10 (1.06) |
|  | M | 47 | 5.90 (0.45) | 1.98 (0.18) | 6.13 (0.47) | 8.72 (1.42) |
| *Eupherusa eximia* (EE) | F | 10 | 4.47 (0.73) | 2.04 (0.26) | 5.66 (0.56) | 6.74 (1.7) |
|  | M | 24 | 4.76 (0.46) | 2.03 (0.24) | 6.11 (0.46) | 8.56 (1.22) |
| *Selasphorus flammula* (SF) | F | 34 | 2.74 (0.48) | 1.46 (0.23) | 4.08 (0.46) | 4.18 (1.34) |
|  | M | 4 | 2.5 (0.28) | 1.28 (0.14) | 3.92 (0.37) | 2.97 (0.48) |

**Table 2.** Body mass (g) and Lovich-Gibbons sexual dimorphism index of the 45 species considered in this study according to phylogenetic clade and sex. Phylogenetic clades follow the classification of McGuire et al. (2014).

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| **Common name** | **Scientific name** | **Phylogenetic clade** | **Body mass of male** | **Body mass of female** | **Lovich-Gibbons ratio** |
| Magenta-throated Woodstar | *Philodice bryantae* | Bees | 3.3 | 3.5 | 0.061 |
| Ruby-throated Hummingbird | *Archilochus colubris* |  | 2.7 | 3 | 0.111 |
| Scintillant Hummingbird | *Selasphorus scintilla* |  | 2.05 | 2.3 | 0.122 |
| Volcano Hummingbird | *Selasphorus flammula* |  | 2.5 | 2.74 | 0.096 |
| Green-crowned Brilliant | *Heliodoxa jacula* | Billiants | 9.06 | 8.54 | -0.061 |
| Black-crested Coquette | *Lophornis helenae* | Coquettes | 2.15 | 2.52 | 0.172 |
| Green Thorntail | *Discosura conversii* |  | 3.1 | 2.9 | -0.069 |
| Black-bellied Hummingbird | *Eupherusa nigriventris* | Emeralds | 3.425 | 3.25 | -0.054 |
| Blue-chested Hummingbird | *Polyerata amabilis* |  | 4 | 3.8 | -0.053 |
| Blue-throated Goldentail | *Chlorestes eliciae* |  | 3.8 | 3.3 | -0.152 |
| Blue-vented Hummingbird | *Saucerottia hoffmanni* |  | 4.4 | 4.3 | -0.023 |
| Bronze-tailed Plumeleteer | *Chalybura urochrysia* |  | 7.1 | 6.1 | -0.164 |
| Cinnamon Hummingbird | *Amazilia rutila* |  | 4.9 | 4.2 | -0.167 |
| Coppery-headed Emerald | *Microchera cupreiceps* |  | 4.7 | 3.64 | -0.291 |
| Crowned Woodnymph | *Thalurania colombica* |  | 4.5 | 4 | -0.125 |
| Mangrove Hummingbird | *Amazilia boucardi* |  | 4.95 | 4.2 | -0.179 |
| Rufous-tailed Hummingbird | *Amazilia tzacatl* |  | 4.82 | 4.54 | -0.062 |
| Scaly-breasted hummingbird | *Phaeochroa cuvierii* |  | 9.38 | 8.6 | -0.091 |
| Snowcap | *Microchera albocoronata* |  | 2.48 | 2.56 | 0.032 |
| Snowy-bellied Hummingbird | *Saucerottia edward* |  | 5 | 4.3 | -0.163 |
| Stripe-tailed Hummingbird | *Eupherusa eximia* |  | 4.68 | 4.06 | -0.153 |
| Violet Sabrewing | *Campylopterus hemileucurus* |  | 12.42 | 9.18 | -0.353 |
| Violet-headed Hummingbird | *Klais guimeti* |  | 2.9 | 2.7 | -0.074 |
| White-bellied Emerald | *Chlorestes candida* |  | 3.7 | 3.8 | 0.026 |
| White-tailed Emerald | *Microchera chonura* |  | 3.3 | 3.1 | -0.065 |
| Band-tailed Barbthroat | *Threnetes ruckeri* | Hermits | 6.09 | 5.82 | -0.046 |
| Bronzy Hermit | *Glaucis aeneus* |  | 5.08 | 4.9 | -0.037 |
| Green Hermit | *Phaetornis guy* |  | 5.9 | 5.6 | -0.054 |
| Long-tailed Hermit | *Phaethornis superciliosus* |  | 6.04 | 5.65 | -0.069 |
| Stripe-throated Hermit | *Phaethornis striigularis* |  | 2.43 | 2.69 | 0.107 |
| White-tipped Sicklebill | *Eutoxeres aquila* |  | 10.80 | 10.11 | -0.068 |
| Brown Violet-ear | *Colibri delphinae* | Mangoes | 8 | 6.1 | -0.311 |
| Green-breasted Mango | *Anthracothorax prevostii* |  | 6.90 | 6.15 | -0.122 |
| Green-fronted Lancebill | *Doryfera ludovicae* |  | 5.9 | 5.5 | -0.073 |
| Lesser Violetear | *Colibri cyanotus* |  | 5.3 | 4.8 | -0.104 |
| Purple-crowned Fairy | *Heliothryx barroti* |  | 5.5 | 5.63 | 0.024 |
| Canivet's Emerald | *Cynanthus canivetii* | Mountain Gems | 2.5 | 2.3 | -0.087 |
| Fiery-throated Hummingbird | *Panterpe insignis* |  | 5.9 | 4.9 | -0.204 |
| Gray-tailed Mountain-gem | *Lampornis castaneoventris* |  | 5.86 | 4.35 | -0.347 |
| Long-billed Starthroat | *Heliomaster longisrostris* |  | 6.04 | 5.65 | -0.069 |
| Plain-capped Starthroat | *Heliomaster constantii* |  | 8.2 | 7.15 | -0.147 |
| Purple-throated Mountain-gem | *Lampornis calolaemus* |  | 5.9 | 5.2 | -0.135 |
| Talamanca Hummingbird | *Eugenes spectabilis* |  | 10.54 | 9.31 | -0.132 |
| White-bellied Mountain-gem | *Lampornis hemileucus* |  | 6.2 | 5 | -0.240 |
| White-necked Jacobin | *Florisuga mellivora* | Topazes | 7.4 | 6 | -0.233 |

Chart, scatter chart

Description automatically generated

**Figure 1. (A)** RMA regression between Ln male body mass and Ln female body mass in 45 species of Costa Rican hummingbirds. **(B)** RMA regression between Ln male body mass and Ln female body mass in eight clades of Costa Rican hummingbirds.

Chart, box and whisker chart

Description automatically generated

**Figure 2.** 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 female-biased allometry.

Chart, scatter chart

Description automatically generated

**Figure 3.** RMA regressions between the log10 transformed values of (A) bill length, (B) wing chord, (C) wing area and (D) body mass in 9 species of Costa Rican hummingbirds. Species abbreviations follow Table 1.

Chart, bar chart, surface chart

Description automatically generated

**Figure 4.** Variation in the Lovich-Gibbons ratio for SSD in (A) bill length, (B) wing chord, (C) wing area, and (D) body mass in nine hummingbird species from Costa Rica (abbreviations follow Table 1). Values are sorted from lowest to highest, which varies the species order in each panel.