



Mating system, male territoriality and agility as predictors of the evolution of sexual size dimorphism in hummingbirds (Aves: Trochilidae)

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Abstract

Male and female animals often exhibit differences in body size; this difference is known as sexual size dimorphism (SSD). Hummingbirds are an excellent model system to test functional hypotheses of SSD because they exhibit a wide range of body sizes and reproductive behaviour between the sexes. Here, using phylogenetic comparative methods, we tested whether mating system, male territoriality and agility predicted the evolution of SSD in this avian family. Our results first suggest that evolutionary increases in male-biased SSD are related to increases in lekking behaviour. Second, we found that male agility is positively related to increases in male biased-SSD albeit this is only likely to occur in males of territorial species. Finally, we found an allometric pattern for SSD consistent with Rensch's rule that was not explained by our estimates of male competition and agility.

Keywords

sexual size dimorphism, mating competition, male agility, Rensch's rule, hummingbirds.

1. Introduction

In certain animal taxa, for instance, males are typically larger than females (e.g., birds and mammals; male-biased sexual size dimorphism (SSD)), whereas females are larger than males in others (e.g., fish, snakes and turtles; female-biased SSD) (Ghiselin, 1974; Reiss, 1989; Fairbairn, 2007). The magnitude of SSD varies widely across animal taxa, from species exhibiting moderate (5–10%), to those showing extreme differences (49,999,900%; see Fairbairn (2013) for extreme examples of SSD in fish). Not surprisingly, this extraordinary variation in the morphology of males and females has inspired a number of functional hypothesis that aim to explain the evolution and maintenance of SSD (Jehl & Murray, 1986; Hedrick & Temeles, 1989; Shine, 1989; Andersson, 1994; Fairbairn, 2007; Székely et al., 2007). To date, four major functional hypotheses have received the greatest attention (e.g., Székely et al., 2007).

First, the sexual segregation hypothesis suggests that differences in body size amongst males and females are likely to evolve when competition over resources between the sexes is high (Darwin, 1871; Shine, 1989; Stephens & Wiens, 2009). The rationale is that if food is scarce, the members of a pair may exploit different feeding sources (Shine, 1989), thus reducing intersexual competition (Shine, 1989, 1991; Butler et al., 2007; Stephens & Wiens, 2009). The exploitation of different resources, in turn, is expected to enhance SSD (Selander, 1972; Székely et al., 2007).

Second, the fecundity selection hypothesis is usually put forward to explain the evolution of female-biased SSD, via the increase of female body size relative to male body size. This may occur if females gain more in fecundity per unit body size than males (reviewed by Andersson, 1994). Thus, larger-than-average females could be expected to produce larger eggs, larger clutch sizes, or to have a higher ability of raising the offspring to independence (Darwin, 1871; Trivers, 1972; Ridley & Thompson, 1979; Honěk, 1993). Relationships between egg and clutch sizes have been documented in several taxa, including frogs, insects and spiders (Shine, 1979; Head, 1995; Prenter et al., 1999; Legaspi & Legaspi, 2005). In the dance fly *Rhaphomyia tarsata*, for instance, where males and females lek in mixed sex swarms, females obtain nuptial gifts from males, who usually select large females as mates. The males benefit from selecting such females because these invest more in fecundity (i.e., large females produce more eggs; LeBas et al., 2003).

Third, the mating-competition hypothesis predicts an increase in the body size of the most competitive sex (usually the males) (Székely et al., 2000). This may be particularly true in taxa with polygynous mating systems (Owens & Hartley, 1998; Lindenfors et al., 2007; Székely et al., 2007) where increases in male body mass typically enhance the chances of obtaining copulations. This has been documented in birds (bustards: Raihani et al., 2006; New world blackbirds: Webster, 1992; shorebirds, gulls and alcids: Székely et al., 2000; see also Székely et al., 2007), insects (e.g., damselflies: Serrano-Meneses et al., 2008), mammals (primates: Clutton-Brock & Harvey, 1977, Clutton-Brock, 1985; Mitani et al., 1996; Lindenfors & Tullberg, 1998; ungulates: Pérez-Barbería et al., 2002; Loison et al., 1999; pinnipeds: Lindenfors et al., 2002) and reptiles (lizards: Cox et al., 2003, Jiménez-Arcos et al. 2017).

Finally, the display-agility hypothesis predicts increases in female-biased SSD, given that several aspects of male displays are enhanced by small body size, which increases the agility and manoeuvrability of males (Andersson & Norberg, 1981; Payne, 1984; Jehl & Murray, 1986; Figuerola, 1999; Székely et al., 2007). In flying animals small body size enhances angular and linear accelerations, as well as horizontal and ascending speeds, whilst it also reduces the turn radius. In contrast, large body size increases the maximum speed in diving flights (Andersson & Norberg, 1981; Hedenström, 1992). Thus, in males that compete over females or territories in the air, small body size may be particularly advantageous (Székely et al., 2000, 2007). In the dunlin (*Calidris alpina*) the display rates of males, as well as their duration are known to be higher in small males, which confers them an advantage over large males (Blomqvist et al., 1997). Studies in other birds (*Sturnus vulgaris*, Witter et al., 1994; *Taeniopygia guttata*, Metcalfe & Ure, 1995) and bats (Hughes & Rayner, 1991) have further shown that increasing body mass reduces flight speed and manoeuvrability. The expected relationship between male agility and female-biased SSD has been documented by numerous studies (e.g., Figuerola, 1999; Székely et al., 2004; Raihani et al., 2006; Serrano-Meneses & Székely, 2006).

A number of taxonomic groups exhibit a puzzling relationship between overall body size and SSD. In such groups, the magnitude of SSD increases with body size when males are larger than females, but it decreases with body size when females are larger than males (Rensch, 1950; Abouheif & Fairbairn, 1997; Fairbairn, 1997). This macro-evolutionary pattern is known

as Rensch's rule (Rensch, 1950) and has been observed in several taxonomic groups, including insects (e.g., Blanckenhorn et al., 2007; Serrano-Meneses et al., 2008), reptiles (turtles: Stephens & Wiens, 2009), birds (bustards: Raihani et al., 2006; hummingbirds: Colwell, 2000; Székely et al., 2007; shorebirds: Székely et al., 2004) and primates (Clutton-Brock et al., 1977). Interestingly, Rensch's rule appears to be relatively common in birds. Székely et al. (2007) tested for allometry consistent with Rensch's rule in 146 avian families and detected it in 125 families, whilst Dale et al. (2007) found evidence for the pattern in 110 (60.4%) out of 182 avian subfamilies. Although there are several explanations for Rensch's rule, the evolution of social mating systems with high levels of mate competition, as well as the evolution of male displays with high levels of agility predicted allometry consistent with Rensch's rule. Dale et al. (2007) found that social mating system and the evolution of polygynous mating systems correlate with the evolution of male-biased SSD, whilst the evolution of agile aerial male displays correlate with the evolution of female-biased SSD.

Hummingbirds are excellent model organisms to study the evolution of SSD, given that (i) the pattern of SSD in this family ranges from female-biased to male-biased SSD, (ii) the males exhibit non-lekking and lekking mating systems, (iii) the males of certain species establish and defend feeding territories that in some taxa are also used to attract females (e.g., Temeles et al., 2000) and (iv) male agility can be estimated from morphological parameters available in literature (see Materials and methods). Furthermore, potential explanations to the patterns of SSD and Rensch's rule in hummingbirds have not been thoroughly tested. Here, using a recent molecular phylogeny (McGuire et al., 2014) and phylogenetic comparative methods (Harvey & Pagel, 1991) we tested whether SSD and Rensch's rule could be explained by the intensity of male competition and male agility in hummingbirds.

2. Materials and methods

2.1. Data

From published sources and theses we collected the following: (i) body mass for males and females of 200 hummingbird taxa, (ii) wing chord for the males and females of 147 taxa, (iii) information on the mating systems (lekking or non-lekking) of 123 taxa and (iv) data on whether the males

established feeding territories (territoriality) or not (non-territoriality) (see Appendix A) for 139 taxa. Note that sample sizes in the Results section vary according to availability of data for a given variable. Body mass was used as a measure for body size since it was highly correlated to wing length in both males (Pearson's product-moment correlation, $r = 0.915$, $df = 145$, $p = 0.001$) and females ($r = 0.880$, $df = 145$, $p = 0.001$). Nonetheless, given that the body mass of birds is highly variable (i.e. it depends on the condition of individuals), we repeated our analyses using wing length as a measure of body size. The results are consistent with the findings presented here, with the exception of the results in which we investigate SSD in wing length as a function of male competition and male agility (see Appendix B). We argue that the differences between the results obtained with these different datasets are driven by the autocorrelation between SSD in wing length and male agility. Note that this statistical violation of the assumptions of linear models is not exhibited by the relationship between body mass SSD and male agility (see Appendix B). Also, since data on the body mass of 29 taxa is represented by few individuals ($N = 1$; see Appendix A), we carried out a set of analyses excluding these species. We then compared these results with another set of analyses excluding 29 taxa represented by the largest sample sizes. The results of both sets of analyses are consistent with each other (see Appendix C), which suggests that the results presented here may be more dependent on overall sample size than on the number of individuals representing each sex across taxa.

Mating system was used as a *proxy* for the intensity of male competition over females (see similar approaches by Székely et al., 2000 and Dunn et al., 2001) (we assumed male-male competition to be more intense in lekking species), whilst territoriality was used a *proxy* for the intensity of male competition over nectar feeding resources. For statistical analyses, mating system was scored as (0) non-lekking species or (1) lek-forming species; territoriality was scored as (0) non-territorial ("traplining", a foraging strategy in which individuals exploit but do not defend dispersed flowers), or (1) territorial, based on whether the males predominantly established feeding territories or not (as described in literature: e.g., Janzen, 1971 & Feinsinger & Chaplin, 1975).

The distinctive, sustained hovering flight of hummingbirds requires a different approach when investigating how male agility relates to body size (and SSD), given that the display agility hypothesis was originally proposed to

account for female-biased SSD in birds which are characterised by flapping flight (Andersson & Norberg, 1981). Thus, the wing disc loading of males (WDL) was used as a *proxy* for male agility. WDL is defined as the ratio of a bird's body weight to a disc whose diameter is wing span (Feinsinger & Chaplin, 1975) and it is therefore expressed as the ratio between g/cm^2 . WDL was estimated from data on the wing chord length of males of 147 hummingbird taxa. WDL is calculated as $W/\pi(l + 0.404l^{0.6})^2$ (Feinsinger et al. 1979), where W is body weight in g and l in wing chord in centimetres. High values of WDL denote high turning speed, acceleration and other components of manoeuvrability (Feinsinger et al., 1979; Moore, 1997). The estimated values of WDL for males are shown in Appendix A.

The following criteria was used to include a particular species in our study: (i) data on the body size and wing chord was available, (ii) data on the mating system and/or territoriality was available, and (iii) the species was included in the phylogeny used to carry out comparative analyses (see below).

Prior to analyses, data on the body size of males and females were \log_{10} transformed. SSD was thus calculated as $\log_{10}(\text{male body size}) - \log_{10}(\text{female body size})$ (Smith, 1999; Székely et al., 2004).

2.2. Phylogeny

We used the multilocus phylogeny estimate for hummingbirds of McGuire et al. (2014). This phylogeny is based on a rich sample of hummingbird taxa (284 taxa and 436 exemplars) and loci. For hummingbirds (and most of the outgroup taxa), McGuire et al. (2014) collected 6461 alignment positions of DNA sequence data representing six genes (four nuclear and two mitochondrial, plus flanking tRNAs). The nuclear genes include intron 7 of beta fibrinogen (FGB), intron 5 of the adenylate kinase gene (AK1), a segment of the ornithine decarboxylase gene extending from the end of exon 6 to the beginning of exon 8 (ODC), and a segment of the Z-linked muscle skeletal receptor tyrosine gene including parts of exon 4 and 5 and the intervening intron (MUSK). The mitochondrial gene sequences include the complete NADH dehydrogenase subunit 2 (ND2), approximately half of NADH dehydrogenase subunit 4 (ND4), and tRNAs flanking each of these protein-coding genes.

The phylogeny included branch lengths as calculated by McGuire et al. (2014). We used Mesquite version 3.04 (Maddison & Maddison, 2015) to

prune taxa with no data from the phylogeny (84 taxa). The phylogenetic comparative analyses (see below) were carried out in R (ver. 3.4.0; R Core Team, 2017) using the package *caper* (Orme et al., 2013).

2.3. Statistical analyses

We tested whether the overall pattern of SSD in hummingbirds was different from monomorphism using a Wilcoxon one-sample test. Thus, the distribution of SSD was tested against a hypothesised median = 0.

2.4. Phylogenetic comparative analyses

In order to test Rensch's rule in hummingbirds, we first obtained the phylogenetic independent contrasts (Felsenstein, 1985) resulting from the regression of male body size as a function of female body size. The phylogenetic independent contrasts method was used to control for the phylogenetic non-independence of species (Harvey & Pagel, 1991). Since outliers can seriously affect the parameter estimates for any regression model, we removed two outliers with studentised residuals $> \pm 3$ (Jones & Purvis, 1997). A key assumption of the contrasts method is that the standardised contrasts are independent from their estimated nodal values (Felsenstein, 1985). The assumption was verified by plotting the standardised contrasts against their estimated nodal values using the *plot* function provided by *caper* (Orme et al., 2013). We then fitted one major axis regression (model II regression, MA; Sokal & Rohlf, 2012) to the phylogenetic independent contrasts of male body size as a function of female body size (Garland et al., 1992). Rensch's rule predicts the slope of male on female size to be significantly larger than unity (Fairbairn, 1997). Since we used phylogenetically independent contrasts, the MA regression was forced through the origin (Harvey & Pagel, 1991; Garland et al., 1992). We provided the slope of the major axis regression (β) as well as its 95% confidence intervals (lower CI–upper CI), which were calculated using the R package *smatr* (Warton et al., 2012). We compared the fitted slope against $\beta = 1$ using the procedure described in Warton et al. (2006), as implemented in the *smatr* package (“slope.test”).

To test the effect mating system, territoriality and display agility on the SSD of hummingbirds, we used the Phylogenetic Generalised Least Squares method (PGLS; Pagel, 1997, 1999; Garland & Ives, 2000; Freckleton et al., 2002). PGLS is a comparative method that incorporates the phylogenetic autocorrelation of the data in the structure of errors (variance-covariance

matrix), which is specified by the phylogeny (Martins & Hansen, 1997; Freckleton et al., 2002). PGLS was used to test the maximum-likelihood of the evolutionary regression coefficient between traits (Pagel, 1997, 1999). We also estimated the weighting parameter λ in order to improve the fit of the data to the model and to correct for phylogenetic effects in all PGLS models (Pagel, 1997, 1999). λ measures phylogenetic dependence of observed trait data (Pagel, 1999; Freckleton et al., 2002): it approaches unity when related species resemble each other more than they resemble species drawn at random from a phylogenetic tree (Blomberg & Garland, 2002). Thus the relationship between SSD (dependent variable) and mating system, territoriality and male agility (independent variables) was investigated in a series of PGLS models. We started from a saturated model that included all independent variables and their first order interaction terms. The model was then reduced using backward elimination, and we stopped when only significant interactions terms were included in the model. Here, since our final model retained two significant interaction terms (see Results and Table 1), we carried out two further analyses in order to inspect these.

Finally, we tested whether Rensch's rule could be explained by our estimates of male competition and agility. To this end, we built a series of PGLS models. We started with a saturated model that included SSD as the dependent variable and mating system, territoriality, male agility and male body size as independent variables. We then reduced the model using backward elimination and stopped when only significant terms were included in the final model. We acknowledge that SSD and male body size are correlated, thus, by including in the models estimates of male competition and male agility, we sought to reduce the predictive power of male body size on SSD. In this way, we tested whether male competition and agility could account for Rensch's rule and not body size per se (see similar procedures in Székely et al., 2004; Dale et al., 2007; Serrano-Meneses et al., 2008).

3. Results

3.1. Distribution of SSD

Hummingbirds exhibit both male- and female-biased SSDs, although male-biased SSD is predominant (body mass: Wilcoxon one-sample test, $V = 13632$, $p = 0.001$; Figure 1).

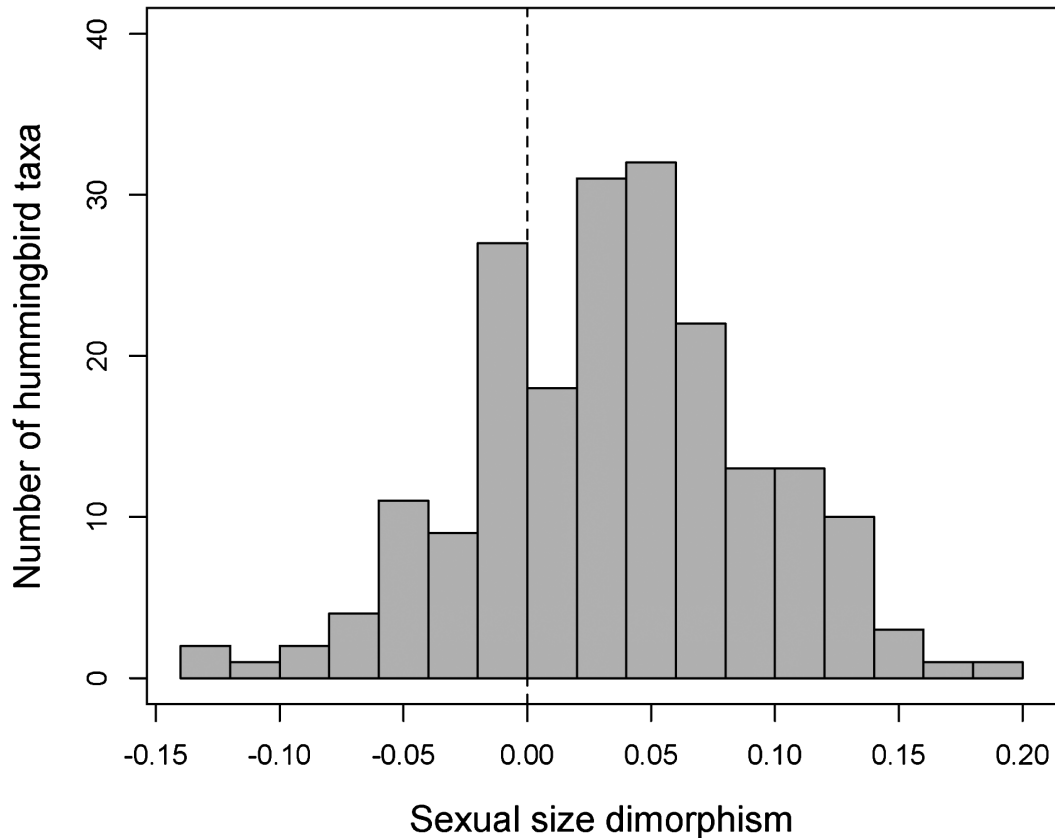


Figure 1. Distribution of sexual size dimorphism in hummingbirds. Positive SSD values denote species in which males are larger than females, whereas negative SSD values indicate species in which females are the larger sex. The dashed line denotes the division between female-biased and male-biased SSD.

3.2. Rensch's rule

Our results confirm that the relationship between male and female body size in hummingbirds is consistent with Rensch's rule (MA regression; $\beta = 1.104$, lower–upper confidence intervals: 1.037–1.177, $p = 0.001$, $N = 199$ phylogenetically independent contrasts; slope comparison test $p = 0.002$; Figure 2): the degree of SSD decreased with overall body size when females were the larger sex, whereas it increased when males were larger than females.

3.3. SSD, male competition and male agility

The parameters of the saturated and the reduced models are shown in Table 1. The reduced model (Model 3) shows that evolutionary increases in

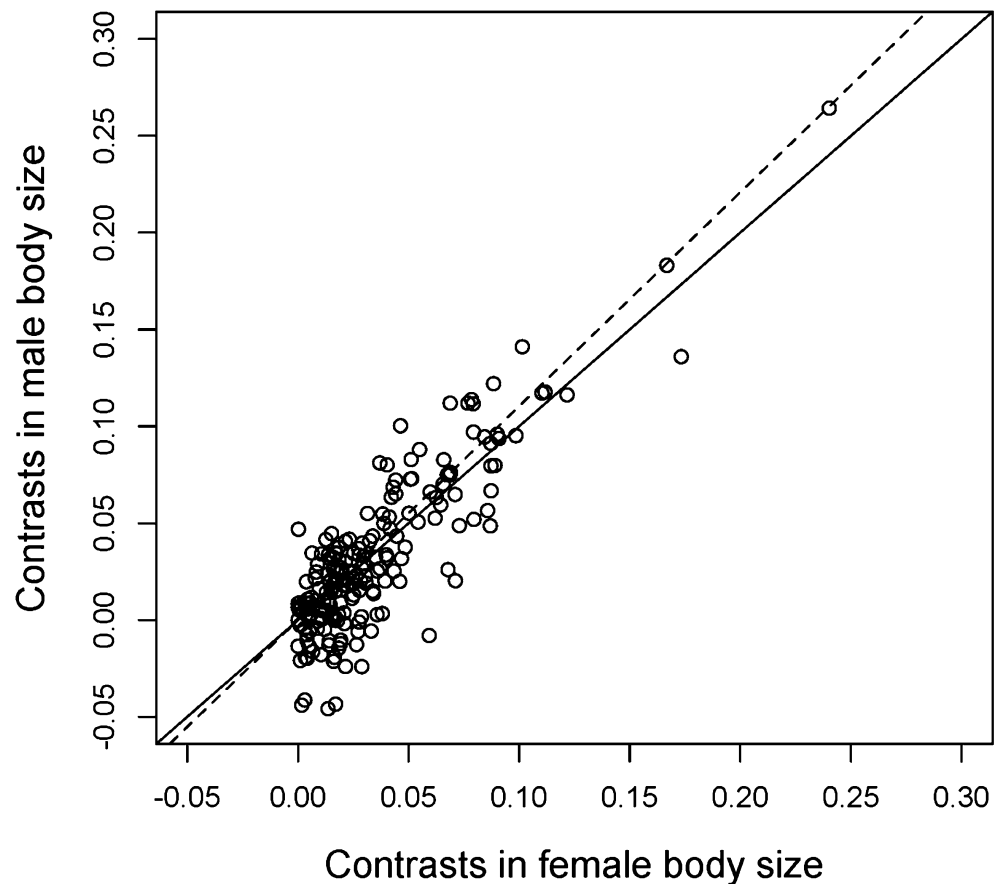


Figure 2. Rensch's rule in hummingbirds. The continuous line indicates the reference isometric relationship ($\beta = 1$) and the dashed line represents the fitted relationship between male body size and female body size by major axis regression for phylogenetically independent contrasts ($\beta = 1.104$, 1.037 – 1.177 , $P = 0.001$, $N = 199$ phylogenetically independent contrasts).

male-biased SSD correlate with evolutionary increases in lek mating systems. Also, Model 3 retained one significant interaction term: territoriality \times male agility. This interaction term suggests that SSD relates differently to male agility when territoriality is considered (Figure 3). Inspection of this interaction revealed that in territorial species, male-biased SSD increased with male agility (estimate \pm SE; 2.982 ± 1.360 , $F_{1,53} = 4.805$, $p = 0.033$, $\lambda = 0.888$), whilst it was unrelated to male agility in non-territorial species (-1.447 ± 1.263 , $F_{1,56} = 1.311$, $p = 0.257$, $\lambda = 0.000$). A further analysis revealed that the males of territorial species were larger than the males of non-territorial ones (0.049 ± 0.018 , $F_{1,137} = 7.058$, $p = 0.009$, $\lambda = 1.000$).

Table 1.

Relationships between body mass SSD (dependent variable) and *proxies* of male competition and agility using Phylogenetic Generalised Least Squares (PGLS) in hummingbirds. λ is the weighting parameter in PGLS (see Freckleton et al., 2002).

Model (Independent variables)	Regression coefficient \pm SE	<i>t</i>	<i>p</i>
Model 1			
Mating system	0.033 \pm 0.075	0.431	0.663
Territoriality	-0.134 \pm 0.070	1.920	0.058
Male agility	-1.970 \pm 2.256	0.874	0.386
Mating system \times Territoriality	0.038 \pm 0.022	1.695	0.094
Mating system \times Male agility	-0.807 \pm 2.261	0.357	0.722
Territoriality \times Male agility	4.007 \pm 2.115	1.894	0.062
Model 2			
Mating system	0.007 \pm 0.017	0.408	0.684
Territoriality	-0.145 \pm 0.062	2.329	0.023
Male agility	-2.641 \pm 1.224	2.156	0.034
Mating system \times Territoriality	0.036 \pm 0.022	1.671	0.098
Territoriality \times Male agility	4.350 \pm 1.874	2.320	0.023
Model 3			
Mating system	0.026 \pm 0.012	2.158	0.034
Territoriality	-0.144 \pm 0.063	2.291	0.025
Male agility	-2.716 \pm 1.238	2.194	0.031
Territoriality \times Male agility	4.680 \pm 1.885	2.482	0.015

The parameters of the full and the reduced models are shown:

Model 1: $\lambda = 0.703$. $r^2 = 0.168$, $F_{6,74} = 2.487$, $p = 0.030$

Model 2: $\lambda = 0.709$. $r^2 = 0.167$, $F_{5,75} = 3.000$, $p = 0.016$

Model 3: $\lambda = 0.711$. $r^2 = 0.136$, $F_{4,76} = 2.984$, $p = 0.024$

3.4. Male competition, male agility and Rensch's rule

The parameters of the models in which we tested for the effect of male competition on Rensch's rule are shown in Table 2. The results suggest that neither mating system, territoriality or male agility (or their first order interactions) contributed to the observed allometric pattern of SSD and overall body size in hummingbirds, given that male size remained the only significant variable in the reduced model.

4. Discussion

In his seminal study, Colwell (2000) showed that hummingbirds exhibit the full scope of Rensch's rule and proposed that both sexual selection and the

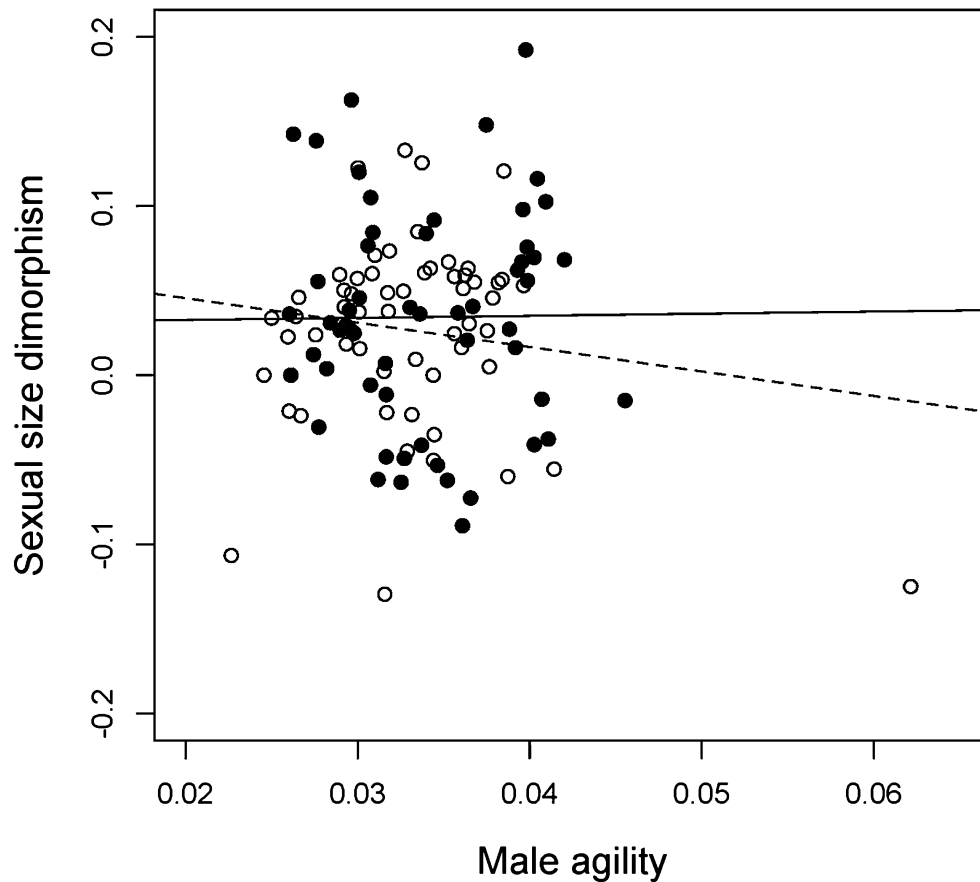


Figure 3. Relationship between SSD and male agility. Wing disc loading (WDL) is used as a *proxy* of male agility (see Methods). Territorial hummingbird species are denoted by closed circles and a continuous line, whilst non-territorial species are denoted by open circles and a dashed line. High WDL values indicate high agility, whereas lower WDL values indicate low agility. The figure is provided for guidance only, given that the data shown are species level, non-phylogenetically corrected values.

costs associated with reproduction shaped the pattern of SSD in hummingbirds. According to Colwell (2000), large male body size could be advantageous in competition for mates, given that the males are highly polygynous. Thus, the distal end of the hyperallometric slope could be explained by the mating advantages of large male body size. However, how could sexual selection account for female-biased SSD? To explain the evolution of female-biased SSD, Colwell (2000) suggested that large male body size could be selected against, given that males must pay high reproductive costs, which are generally greater than those imposed on the females during the mating period (due to the energetically costly aerial displays and the high number of aggressive interactions with other males). In a situation where the males

Table 2.

Relationships between SSD (dependent variable), *proxies* of male competition, and male size using using PGLS in hummingbirds. λ is the weighting parameter in PGLS (see Freckleton et al., 2002).

Model (Independent variables)	Regression coefficient \pm SE	<i>t</i>	<i>p</i>
Model 1			
Mating system	0.010 \pm 0.062	0.170	0.865
Territoriality	-0.041 \pm 0.062	0.665	0.508
Male agility	-2.713 \pm 1.796	1.510	0.135
Mating system \times Male agility	-0.157 \pm 1.868	0.084	0.933
Mating system \times Territoriality	0.030 \pm 0.019	1.601	0.114
Male agility \times Territoriality	1.106 \pm 1.855	0.596	0.553
Male size	0.201 \pm 0.026	7.602	0.001
Model 2			
Mating system	0.005 \pm 0.012	0.436	0.664
Territoriality	-0.043 \pm 0.058	0.741	0.461
Male agility	-2.835 \pm 1.061	2.671	0.009
Mating system \times Territoriality	0.030 \pm 0.019	1.611	0.111
Male agility \times Territoriality	1.162 \pm 1.722	0.675	0.502
Male size	0.201 \pm 0.026	7.671	0.001
Model 3			
Mating system	0.004 \pm 0.013	0.358	0.721
Territoriality	-0.005 \pm 0.012	0.392	0.695
Male agility	-2.388 \pm 0.826	2.890	0.005
Mating system \times Territoriality	0.032 \pm 0.018	1.715	0.090
Male size	0.204 \pm 0.026	7.867	0.001
Model 4			
Mating system	0.021 \pm 0.009	2.111	0.038
Territoriality	0.006 \pm 0.009	0.613	0.542
Male agility	-2.029 \pm 0.839	2.416	0.018
Male size	0.209 \pm 0.027	7.616	0.001
Model 5			
Mating system	0.018 \pm 0.009	2.002	0.047
Male agility	-1.294 \pm 0.704	1.839	0.068
Male size	0.187 \pm 0.027	6.867	0.001

of larger species could monopolise richer resources, these could eventually become larger than females, whilst the males of smaller species, confined to territories with poorer resources, would not be able to attain the resources to become larger than females (Colwell, 2000). Nonetheless, a number of stud-

Table 2.
(Continued.)

Model (Independent variables)	Regression coefficient \pm SE	<i>t</i>	<i>p</i>
Model 6			
Mating system	0.015 \pm 0.009	1.697	0.092
Male size	0.165 \pm 0.025	6.687	0.001
Model 7			
Male size	0.174 \pm 0.022	7.779	0.001

The parameters of all created models are shown:

Model 1: $\lambda = 0.000$. $r^2 = 0.547$, $F_{7,73} = 12.570$, $p = 0.001$

Model 2: $\lambda = 0.000$. $r^2 = 0.546$, $F_{6,74} = 14.870$, $p = 0.001$

Model 3: $\lambda = 0.000$. $r^2 = 0.544$, $F_{5,75} = 17.880$, $p = 0.001$

Model 4: $\lambda = 0.153$. $r^2 = 0.477$, $F_{4,76} = 17.350$, $p = 0.001$

Model 5: $\lambda = 0.320$. $r^2 = 0.347$, $F_{3,103} = 18.200$, $p = 0.001$

Model 6: $\lambda = 0.253$. $r^2 = 0.295$, $F_{2,120} = 25.090$, $p = 0.001$

Model 7: $\lambda = 0.508$. $r^2 = 0.234$, $F_{1,198} = 60.520$, $p = 0.001$

ies carried out after Colwell's (2000) original contribution (e.g., Székely et al., 2004, 2007; Raihani et al., 2006; Serrano-Meneses & Székely, 2006; Dale et al., 2007) suggest that sexual selection may also be related to the evolution of female-biased SSD. Thus, female-biased SSD could result from selection for small male size (relative to female size; e.g., Székely et al., 2007), but also from directional male mate choice. For instance, in the rock sparrow (*Petronia petronia*), males are known to preferentially mate with highly ornamented females (a patch of yellow feathers on the breast) (Griggio et al., 2005, 2009), a trait that is positively correlated with body size in females. By choosing such females, the males may enhance their reproductive output, since the total number of eggs produced in a breeding season is likely to increase with female ornament size (Pilastro et al., 2003). However, whether this occurs in hummingbirds, to our knowledge, remains to be investigated.

In the present study we corroborated Colwell's (2000) findings by showing that hummingbirds exhibit Rensch's rule, and further tested whether the pattern of SSD and Rensch's rule were explained by mating competition (in the context of competition over mates and over resources) and male agility in this avian family. First, we found that increases in male-biased SSD correlate with the evolution of lek mating systems. Oakes (1992) tested the idea that more sexually dimorphic birds could be found amongst lekking species (compared to monogamous or polygynous non-lekking birds), given

that the males of lekking species would probably experience more intense sexual selection (Oakes, 1992; also see Höglund, 1989), and would benefit from achieving larger-than-average body sizes. By categorising mating system similarly to us, Oakes (1992) concluded that the evolution of lekking behaviour may be related to enhanced SSD. Here, since the males of hummingbird species are highly polygynous, we were only able to test the effect of lekking and non-lekking behaviour on SSD, assuming higher levels of male-male competition amongst lekking species. In hummingbirds, the majority of lekking species are characterised by exploded lek systems, in which most displaying males appear to establish and defend territories *via* vocalisations and high speed chases through the forest mid-canopy (Atwood et al., 1991) (e.g., *Amazilia candida* and *Klais guimeti*; Atwood et al., 1991 and Skutch, 1958, respectively). Territoriality, foraging and mate-selection in hummingbirds are behaviours known to be strongly influenced by local energy resources (Carpenter, 1987; Kodric-Brown & Brown, 1978; Temeles & Kress, 2010, Gowda et al., 2012), hence the large males of lek-forming species, with territories rich in nectar may have selective advantages over small, intruding males.

Second, evolutionary increases in male agility are related to increases in male-biased SSD, but only in territorial species. The relationship is more evident on male body size, since territorial males evolved to larger sizes than the males of non-territorial species. To understand this pattern, it is necessary to understand how the males compete over feeding resources. In several hummingbird species, males establish and defend territories characterised by a variable number of flowering plants, which produce the main food resource of hummingbirds, nectar (Wolf & Hainsworth, 1971). Territory owners typically chase away other potential nectarivores (Brown, 1964), because at least two components of fitness may depend on the ability of a male to defend a territory: survival and mating success (Wolf, 1975; Temeles & Kress, 2010). The relationship between territorial defence and foraging behaviour is well established (e.g., Wolf et al., 1972; Powers & McKee, 1994; Bateson et al., 2003; Temeles et al., 2009; Temeles & Kress, 2010), but there is also a relationship between territory defence, foraging behaviour and mating success that has not been studied in detail (Temeles & Kress, 2010). There are, however, some documented cases. The males of the Purple-throated carib *Eulampis jugularis* are known to defend nectar supplies that are up to five times greater than their daily energy needs; these resources are used

to attract intruding females as potential mates (Temeles & Kress, 2010; for similar behaviour in males of *Panterpe insignis* and *Selasphorus rufus* see Wolf & Stiles, 1970 and Paton & Carpenter, 1984, respectively). Variation in male mating success in this species thus depends on territory quality, which in turn is determined by the fighting ability of males and their body sizes. Note that in this species males are approximately 25% heavier than females (Wolf, 1975; Temeles et al., 2000), and there are reasons to believe that sexual selection plays a role in the evolution of male-biased SSD in this and other hummingbird species (Temeles et al., 2000; Temeles & Kress, 2003): success in interspecific aggressive encounters is positively correlated with body size. Large males are potent aerial competitors because they can generate more muscle power than smaller ones (Chai & Millard, 1997), and their relative short wings are likely to increase aerodynamic stability and manoeuvrability (Feinsinger et al., 1979). However, the selective advantage of large male body size must be balanced out by the increased costs for foraging and flying to defend a territory (Wolf et al., 1975). To compensate for this, large territorial males may adopt a sit-and-wait defence strategy that is energetically more economical than active, prolonged hovering (Wolf & Hainsworth, 1971; see also Pearson, 1954 for observations on *Calypte anna*). Such males may also adjust their territory size and foraging time in order to meet the costs of territorial defence (Wolf et al., 1975). This can be achieved because, although the large size and aggressive behaviour of territorial males demands a boosted intake of energy, such males may replenish and maintain their body sizes by exploiting the flowers in their territories (Tiebout, 1993). Conversely, for non-territorial males, small body size may be more advantageous than large size, since their foraging strategy typically demands prolonged hovering flights. Indeed smaller males can generally hover for longer than larger males (e.g., *Archilochus alexandri* and *Selasphorus rufus* vs. *Eugenes fulgens* and *Lampornis clemenciae*; Chai & Millard, 1997), and they are able to do so whilst investing less energy (Powers & McKee, 1994).

Finally, our results suggest that Rensch's rule in hummingbirds is not explained by mating system, territoriality or male agility. What, then, may explain this allometric pattern for SSD? For Rensch's rule to occur it is necessary that female body size varies less than male size, amongst closely related taxa (Fairbairn, 1997). This implies that the body size of males and females may be under different selective pressures. For instance, if hummingbird body size radiated in response to availability of resources, a pattern

consistent with Rensch's rule could arise in the absence of sexual selection (Colwell, 2000). This could occur if female body size is subject to strong stabilising selection (which is likely to occur if egg production sets the lower limits of female body size; Colwell, 2000) and if male body size is subject to a different type of selection, for instance, directional selection. In this context, males could be selected to become smaller than females, if they are subject to lesser reproductive metabolic constraints than females (Colwell, 2000). Nonetheless, other ecological or developmental variables, not investigated here by us, should be investigated.

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Appendix A.
Data used in the study and sources.

Species	Male weight (g)	n	Female weight (g)	n	Male wing length (mm)	n	Female wing length (mm)	n	Mating system	Territoriality	Male agility	References
<i>Abeillia abeillei</i>	2.70	–	2.70	–	47.12	–	43.09	–	–	1	0.02612	14, 33
<i>Adelomyia melanogenys</i>	3.89	13	3.41	8	53.25	20	49.10	20	0	0	0.02998	14, 22
<i>Aglaeactis castelnaudii</i>	7.75	–	7.75	–	–	–	–	–	–	0	–	14
<i>Aglaeactis cupripennis</i>	7.80	–	7.20	–	–	–	–	–	–	1	–	14
<i>Aglaeactis pamela</i>	7.75	–	7.75	–	–	–	–	–	–	–	–	14
<i>Aglatocercus coelestis</i>	6.10	9	4.60	5	67.72	9	56.00	6	0	0	0.03002	14, 22
<i>Aglatocercus kingii</i>	5.50	–	4.70	–	53.50	–	53.50	–	–	1	0.04202	14
<i>Amazilia amabilis</i>	4.13	5	3.80	4	59.34	5	56.60	4	1	1	0.02604	14, 23, 49, 50
<i>Amazilia amazilia</i>	5.00	–	4.50	–	60.81	26	57.56	18	0	1	0.03009	14, 33, 52
<i>Amazilia beryllina</i>	4.54	20	4.14	19	54.90	20	51.72	20	0	1	0.03305	14, 22, 24, 33
<i>Amazilia brevirostris</i>	4.60	–	4.40	–	–	–	–	–	–	–	–	14
<i>Amazilia candida</i>	3.96	20	3.63	17	52.18	20	50.35	20	1	0	0.03178	4, 14, 22, 35
<i>Amazilia chionogaster</i>	5.50	–	4.50	–	57.60	–	55.45	–	–	–	0.03661	14, 33
<i>Amazilia cyanocephala</i>	5.49	19	4.80	17	58.45	20	56.59	20	0	0	0.03562	14, 22, 33, 34
<i>Amazilia edward</i>	5.00	–	4.40	–	–	–	–	–	–	1	–	14
<i>Amazilia franciae</i>	4.93	14	4.64	5	53.67	20	51.17	20	0	0	0.03753	14, 22, 33, 35

Appendix A.
(Continued.)

Species	Male weight (g)	n	Female weight (g)	n	Male wing length (mm)	n	Female wing length (mm)	n	Mating system	Territoriality	Male agility	References
<i>Amazilia lactea</i>	5.40	1	4.60	1	54.20	-	54.20	-	0	1	0.04026	10, 14, 33
<i>Amazilia leucogaster</i>	4.50	-	4.30	-	51.80	-	49.75	-	0	-	0.03651	14, 33
<i>Amazilia rosenbergi</i>	3.40	1	4.10	2	-	-	-	-	0	-	-	10, 14
<i>Amazilia rutila</i>	4.40	19	4.46	19	56.13	20	54.79	20	1	1	0.03074	3, 14, 22
<i>Amazilia saucerrottei</i>	4.88	6	4.70	3	52.10	15	49.54	11	0	1	0.03917	14, 16, 22
<i>Amazilia tobaci</i>	4.60	-	4.20	-	52.44	-	53.66	-	0	-	0.03647	33
<i>Amazilia tzacatl</i>	5.22	10	4.91	9	63.48	10	60.47	9	1	1	0.02898	14, 22, 47, 49
<i>Amazilia versicolor</i>	3.50	-	3.35	-	49.14	-	48.06	-	0	-	0.03132	14, 22, 33
<i>Amazilia violiceps</i>	5.29	17	4.66	16	56.27	20	55.14	20	-	0	0.03678	14, 22, 27, 43
<i>Amazilia viridicauda</i>	6.00	-	5.50	-	-	-	-	-	-	-	-	14
<i>Amazilia viridifrons</i>	5.44	17	5.14	7	58.11	20	55.55	13	1	0	0.03562	14, 22, 33
<i>Amazilia viridigaster</i>	3.87	6	3.37	3	52.30	20	51.22	20	0	0	0.03084	14, 22, 33
<i>Amazilia yucatanensis</i>	4.11	18	3.84	16	55.50	20	51.68	18	0	1	0.02932	14, 22, 33
<i>Androdon aequatorialis</i>	7.37	3	6.47	5	65.67	6	65.50	6	1	0	0.03839	6, 14, 22

Appendix A.
(Continued.)

Species	Male weight (g)	n	Female weight (g)	n	Male wing length (mm)	n	Female wing length (mm)	n	Mating system	Territoriality	Male agility	References
<i>Anthracothorax dominicus</i>	7.10	–	5.50	–	–	–	–	–	–	1	–	14
<i>Anthracothorax nigricollis</i>	6.43	6	7.13	8	66.32	20	64.27	20	0	0	0.03289	11, 14, 22
<i>Anthracothorax prevoostii</i>	6.83	4	6.07	7	65.14	8	61.62	11	0	0	0.03613	14, 22, 33
<i>Anthracothorax viridigula</i>	8.00	–	6.00	–	–	–	–	–	–	1	–	14
<i>Archilochus alexandri</i>	2.55	4	2.95	8	40.59	5	44.99	12	0	1	0.03253	14, 22, 25, 33
<i>Archilochus colubris</i>	2.77	19	3.40	20	40.13	20	43.72	20	0	1	0.03609	14, 16, 17, 22, 25, 33
<i>Atthis heloisa</i>	2.03	3	2.33	4	32.66	3	32.50	2	1	0	0.03873	14, 22, 27, 30, 41
<i>Boissonneaua flavescens</i>	8.60	2	7.90	2	74.00	20	70.73	15	–	1	0.03582	14, 22
<i>Boissonneaua jardini</i>	9.40	4	8.56	4	76.60	5	71.00	6	–	1	0.03669	14, 22
<i>Calliphox bryantae</i>	3.31	5	3.42	5	41.40	5	42.00	5	1	1	0.04071	14, 16
<i>Calliphox evelynae</i>	2.60	13	3.00	3	39.30	39	40.80	43	–	1	0.03521	18
<i>Calothorax lucifer</i>	3.20	13	3.50	19	35.00	–	37.70	–	–	–	0.05366	14, 19, 29, 33

Appendix A.
(Continued.)

Species	Male weight (g)	n	Female weight (g)	n	Male wing length (mm)	n	Female wing length (mm)	n	Mating system	Territoriality	Male agility	References
<i>Calypte anna</i>	4.55	431	4.00	541	49.70	-	49.60	-	1	1	0.03987	1, 14, 21, 25, 33, 35, 37, 47
<i>Calypte costae</i>	3.00	25	3.30	19	43.47	20	44.34	15	0	1	0.03371	14, 22, 25
<i>Campylopterus ensipennis</i>	10.00	-	9.50	-	-	-	-	-	1	1	-	14, 27
<i>Campylopterus falcatus</i>	7.50	8	5.68	5	66.20	20	61.29	16	-	0	0.03849	14, 22
<i>Campylopterus hemileucurus</i>	11.22	14	8.86	17	79.40	13	73.10	17	1	1	0.04094	14, 16, 17, 22, 23, 35, 50
<i>Campylopterus largipennis</i>	9.80	1	7.50	1	74.35	-	71.40	-	1	1	0.04045	10, 14, 33
<i>Campylopterus rufus</i>	9.00	1	6.40	1	74.01	-	72.93	-	1	1	0.03747	10, 14, 33
<i>Campylopterus villaviscensio</i>	8.50	1	6.60	1	-	-	-	-	-	-	-	14
<i>Chalcostigma herrani</i>	6.40	-	5.50	-	-	-	-	-	-	1	-	14
<i>Chalcostigma stanleyi</i>	6.20	-	4.50	-	-	-	-	-	-	1	-	14
<i>Chalybura buffonii</i>	6.18	5	5.67	5	68.10	20	61.92	20	0	0	0.03008	14, 22
<i>Chalybura urochrysa</i>	7.06	15	5.13	6	76.55	15	69.33	6	0	1	0.02759	14, 49

Appendix A.
(Continued.)

Species	Male weight (g)	n	Female weight (g)	n	Male wing length (mm)	n	Female wing length (mm)	n	Mating system	Territoriality	Male agility	References
<i>Chlorostilbon canivetii</i>	2.62	7	2.48	12	45.04	20	43.30	20	0	0	0.02756	3, 14, 17, 22, 27
<i>Chlorostilbon maugaeus</i>	3.00	25	2.90	19	48.50	25	46.90	19	0	–	0.02751	14, 28, 33
<i>Chlorostilbon mellisugus</i>	2.70	18	2.55	17	43.90	–	42.90	–	0	1	0.02979	10, 12, 14
<i>Chlorostilbon notatus</i>	8.85	–	7.50	–	–	–	–	–	–	1	–	11, 14
<i>Chlorostilbon poortmani</i>	8.00	–	7.00	–	–	–	–	–	–	0	–	14
<i>Chlorostilbon ricordii</i>	3.35	–	3.54	–	52.30	–	50.70	–	0	0	0.0267	14, 22, 27, 33
<i>Chrysolampis mosquitus</i>	3.62	3	3.52	4	53.73	15	51.55	9	0	1	0.02743	14, 22, 33
<i>Chrysuronia oenone</i>	5.50	1	4.80	1	–	–	–	–	1	1	–	10, 12, 14
<i>Clytolaema rubricauda</i>	8.10	–	6.50	–	–	–	–	–	–	1	–	14
<i>Coeligena coeligena</i>	7.30	–	6.20	–	73.23	–	68.45	–	0	0	0.031	14, 33
<i>Coeligena helianthea</i>	7.06	–	6.31	–	71.04	–	67.61	–	–	0	0.03174	14, 22
<i>Coeligena lutetiae</i>	7.10	7	6.60	5	74.75	20	70.08	7	0	–	0.02901	14, 33

Appendix A.
(Continued.)

Species	Male weight (g)	n	Female weight (g)	n	Male wing length (mm)	n	Female wing length (mm)	n	Mating system	Territoriality	Male agility	References
<i>Coeligena torquata</i>	7.53	–	6.74	–	76.27	–	70.30	–	–	0	0.02963	14, 22
<i>Coeligena violifer</i>	8.95	6	7.10	4	79.07	9	74.50	7	0	–	0.03291	14, 33
<i>Coeligena wilsoni</i>	6.91	6	9.31	8	70.44	12	65.57	12	–	0	0.03157	14, 22
<i>Colibri coruscans</i>	7.86	10	6.59	9	76.70	20	69.07	20	1	1	0.0306	14, 22
<i>Colibri delphinae</i>	7.20	1	5.30	1	70.60	–	66.80	–	1	0	0.03275	10, 14, 33
<i>Colibri serrirostris</i>	6.20	–	6.20	–	70.82	–	63.91	–	1	–	0.02804	14, 33
<i>Colibri thalassinus</i>	5.68	20	4.46	20	64.33	20	61.56	20	1	1	0.03075	8, 14, 22, 25, 32, 35
<i>Cynanthus doubledayi</i>	2.30	19	2.94	9	46.67	19	47.01	10	–	0	0.02265	22
<i>Cynanthus latirostris</i>	3.55	20	3.81	17	52.85	20	52.19	20	0	1	0.02774	14, 22, 24, 35
<i>Cynanthus sordidus</i>	3.86	18	3.70	15	53.64	20	52.58	20	0	0	0.02934	33
<i>Discosura langsdorffi</i>	2.80	1	2.20	1	–	–	–	–	–	–	–	10, 14
<i>Doricha eliza</i>	2.30	1	2.60	3	37.10	2	38.70	–	–	1	0.03464	14, 15, 22, 27, 36
<i>Doryfera johannae</i>	6.17	6	6.10	7	60.35	20	64.55	20	0	0	0.03765	14, 22
<i>Doryfera ludovicae</i>	6.00	2	5.20	1	58.11	–	56.12	–	0	1	0.03929	10, 14, 33
<i>Elvira chionura</i>	3.30	–	3.10	–	–	–	–	–	1	–	–	14
<i>Elvira cupreiceps</i>	3.40	3	3.10	–	–	–	–	–	1	–	–	14, 17

Appendix A.
(Continued.)

Species	Male weight (g)	n	Female weight (g)	n	Male wing length (mm)	n	Female wing length (mm)	n	Mating system	Territoriality	Male agility	References
<i>Ensifera ensifera</i>	13.00	–	13.00	–	–	–	–	–	0	–	–	33
<i>Eriocnemis cupreiventris</i>	5.37	6	4.94	9	59.53	13	57.27	13	–	1	0.03361	14, 22
<i>Eriocnemis luciani</i>	6.30	1	6.20	1	67.00	–	67.00	–	0	1	0.03161	14
<i>Eriocnemis vestita</i>	4.46	5	4.58	9	55.65	10	57.36	10	–	1	0.03166	14, 22
<i>Eugenes fulgens</i>	7.83	19	6.34	19	71.88	20	67.17	20	0	1	0.03444	7, 14, 22, 25, 41
<i>Eulampis holosericeus</i>	6.70	–	5.25	–	–	–	–	–	0	0	–	14, 33
<i>Eulampis jugularis</i>	9.90	13	7.90	20	75.60	15	69.60	33	0	1	0.03961	14, 20, 22, 33, 57
<i>Eupetomena macroura</i>	8.85	–	6.50	–	–	–	–	–	1	1	–	14, 39
<i>Eupherusa cyanophrys</i>	4.69	16	4.09	16	59.98	16	54.96	16	–	0	0.02895	14, 22
<i>Eupherusa eximia</i>	4.54	10	4.50	5	59.77	11	54.38	7	0	1	0.0282	14, 22, 23, 33
<i>Eupherusa nigriventris</i>	3.70	–	3.30	–	49.50	–	46.50	–	1	0	0.03266	14, 33
<i>Eupherusa politocerca</i>	4.14	19	3.83	20	60.69	20	54.74	20	0	0	0.025	14, 22, 33
<i>Eutoxeres aquila</i>	11.92	9	10.40	6	87.48	9	81.55	6	1	0	0.03624	14, 22, 49, 50

Appendix A.
(Continued.)

Species	Male weight (g)	n	Female weight (g)	n	Male wing length (mm)	n	Female wing length (mm)	n	Mating system	Territoriality	Male agility	References
<i>Eutoxeres condamini</i>	11.00	1	10.00	1	68.10	-	68.10	-	1	-	0.05354	10, 14, 33
<i>Florisuga fusca</i>	9.00	-	7.00	-	-	-	-	-	-	1	-	14
<i>Florisuga mellivora</i>	7.02	5	6.48	5	78.12	5	72.76	5	0	0	0.02641	14, 22, 23, 27, 49
<i>Glaucis aeneus</i>	5.46	11	5.16	8	63.89	11	60.05	8	0	-	0.02995	14, 49
<i>Glaucis hirsutus</i>	6.35	12	5.62	6	59.61	51	54.47	17	1	0	0.03965	12, 14, 35, 42, 46
<i>Goethalsia bella</i>	4.00	-	3.00	-	-	-	-	-	-	-	-	14
<i>Goldmania violiceps</i>	4.40	-	3.50	-	-	-	-	-	-	-	-	14
<i>Haplophaedia aureliae</i>	4.60	2	4.21	5	58.75	8	55.22	9	1	1	0.02951	14, 22
<i>Haplophaedia lugens</i>	5.50	-	5.50	-	65.10	6	61.90	8	-	-	0.02912	14, 44
<i>Helictin bilophus</i>	2.15	-	2.15	-	-	-	-	-	-	-	-	14
<i>Helangelus amethysticollis</i>	5.70	-	5.30	-	65.90	-	59.10	-	0	-	0.0295	33
<i>Helangelus exortis</i>	4.86	9	3.50	2	64.40	10	56.00	7	-	1	0.02626	14, 22
<i>Heliodoxa aurescens</i>	6.11	5	5.50	3	59.86	7	56.80	5	-	0	0.03785	14, 22
<i>Heliodoxa imperatrix</i>	7.71	7	8.36	5	71.28	7	62.90	10	-	0	0.03445	6, 14, 22

Appendix A.
(Continued.)

Species	Male weight (g)	n	Female weight (g)	n	Male wing length (mm)	n	Female wing length (mm)	n	Mating system	Territoriality	Male agility	References
<i>Heliodoxa jacula</i>	7.60	6	6.61	4	71.35	10	62.90	10	1	0	0.03389	6, 14, 22
<i>Heliodoxa leadbeateri</i>	8.00	-	7.05	-	70.12	-	62.71	-	0	-	0.03686	6, 14, 33
<i>Heliodoxa rubinoides</i>	8.20	-	8.70	-	69.86	-	68.06	-	0	-	0.03804	6, 14, 33
<i>Heliodoxa schreibersii</i>	9.90	-	7.80	-	66.07	-	64.07	-	-	-	0.05099	14, 33
<i>Heliomaster constantii</i>	7.07	16	6.64	2	63.85	20	63.63	6	-	1	0.03882	14, 28, 22
<i>Heliomaster furcifer</i>	5.75	-	5.75	-	-	-	-	-	-	1	-	14
<i>Heliomaster longirostris</i>	6.25	-	5.25	-	58.94	-	60.21	-	-	1	0.03985	14, 22, 33
<i>Heliomaster squamosus</i>	5.75	-	5.75	-	-	-	-	-	-	1	-	14
<i>Heliothryx auritus</i>	5.15	-	5.15	-	68.60	-	68.60	-	-	-	0.02472	14
<i>Heliothryx barroti</i>	5.60	2	5.55	3	74.80	2	73.97	3	0	-	0.02286	14, 49
<i>Hylocharis chrysura</i>	4.30	1	4.20	1	52.90	-	52.10	-	0	-	0.03355	10, 14, 33
<i>Hylocharis cyanus</i>	3.40	1	3.80	1	48.10	-	44.79	-	0	1	0.03166	10, 14, 33
<i>Hylocharis eliciae</i>	4.20	1	3.60	1	47.82	-	46.63	-	1	1	0.03954	10, 14, 16, 33
<i>Hylocharis grayi</i>	5.90	1	5.50	1	59.92	-	55.89	-	0	0	0.03648	10, 14, 33

Appendix A.
(Continued.)

Species	Male weight (g)	n	Female weight (g)	n	Male wing length (mm)	n	Female wing length (mm)	n	Mating system	Territoriality	Male agility	References
<i>Hylocharis leucotis</i>	3.78	159	3.40	27	55.93	165	52.91	28	1	0	0.02658	14, 22, 30
<i>Hylocharis sapphirina</i>	4.30	–	4.10	–	50.65	–	49.87	–	–	1	0.03637	14, 33
<i>Hylocharis xantusii</i>	2.99	16	3.14	7	49.88	18	49.68	8	–	0	0.02602	14, 22
<i>Juliamyia julie</i>	3.30	1	3.90	1	43.80	–	42.90	–	0	1	0.03656	10, 14, 33
<i>Klais guimeti</i>	2.95	15	2.80	18	49.60	–	44.90	–	1	0	0.02595	10, 14, 33
<i>Lafresnaya lafresnayi</i>	5.40	–	5.40	–	–	–	–	–	–	1	–	14
<i>Lampornis amethystinus</i>	5.92	19	5.71	18	66.51	20	60.35	20	1	0	0.03012	14, 22, 35
<i>Lampornis castaneovenstris</i>	5.95	–	4.90	–	65.80	–	58.50	–	–	1	0.03088	14, 33
<i>Lampornis cinereicauda</i>	5.90	–	4.90	–	–	–	–	–	–	1	–	14
<i>Lampornis clemenciae</i>	7.91	16	6.00	18	77.68	20	69.89	20	0	1	0.03007	14, 22
<i>Lampornis hemileucus</i>	6.20	–	5.10	–	64.40	–	58.30	–	0	0	0.0335	14, 33
<i>Lampornis viridipallens</i>	6.37	11	4.77	18	65.09	14	58.70	20	–	0	0.03374	14, 22

Appendix A.
(Continued.)

Species	Male weight (g)	n	Female weight (g)	n	Male wing length (mm)	n	Female wing length (mm)	n	Mating system	Territoriality	Male agility	References
<i>Lepidopyga goudoti</i>	3.97	4	3.50	3	47.28	9	46.57	7	0	0	0.03817	14, 22, 33
<i>Lesbia victorinae</i>	5.10	1	4.50	1	59.90	94	55.30	46	0	-	0.03155	14, 53
<i>Leucippus baeri</i>	4.40	1	4.20	1	-	-	-	-	-	-	-	10
<i>Leucippus chlorocercus</i>	5.30	1	4.80	1	-	-	-	-	-	-	-	10
<i>Leucippus taczanowskii</i>	7.20	1	6.00	1	-	-	-	-	-	-	-	10
<i>Leucochloris albicollis</i>	6.50	-	4.50	-	-	-	-	-	-	-	-	14
<i>Lophornis chalybeus</i>	3.00	-	2.40	-	43.83	-	40.96	-	-	-	0.0332	14, 33
<i>Lophornis delattrei</i>	3.00	1	2.60	1	38.10	-	36.90	-	0	-	0.04302	14, 22, 27
<i>Mellisuga minima</i>	2.70	-	3.00	-	-	-	-	-	-	-	-	14
<i>Metallura williami</i>	4.55	-	4.55	-	-	-	-	-	-	1	-	14
<i>Microchera albocoronata</i>	2.52	14	2.55	12	-	-	-	-	1	1	-	14
<i>Myrtis fanny</i>	2.35	-	2.35	-	-	-	-	-	0	-	-	14
<i>Ocreatus underwoodii</i>	2.83	3	2.77	2	42.35	10	40.30	10	-	0	0.03337	14, 22
<i>Oreotrochilus estella</i>	8.80	-	8.00	-	-	-	-	-	0	0	-	14

Appendix A.
(Continued.)

Species	Male weight (g)	n	Female weight (g)	n	Male wing length (mm)	n	Female wing length (mm)	n	Mating system	Territoriality	Male agility	References
<i>Orthorhynchus cristatus</i>	2.90	6	2.70	7	46.80	6	46.50	7	0	1	0.02841	14, 28, 57
<i>Oxypogon guerinii</i>	5.55	-	4.80	-	-	-	-	-	0	-	-	14
<i>Panterpe insignis</i>	6.15	7	5.00	1	-	-	-	-	0	1	-	14, 47, 56, 58
<i>Phaethornis anthophilus</i>	5.32	8	4.60	2	56.75	10	54.10	10	1	0	0.03641	14, 22, 33
<i>Phaethornis atrimentalis</i>	2.48	2	2.75	2	39.67	5	38.00	5	-	-	0.03301	42
<i>Phaethornis augusti</i>	5.25	-	5.00	-	-	-	-	-	1	-	-	14, 22, 33, 40
<i>Phaethornis bourcieri</i>	4.37	6	3.69	5	54.87	8	50.83	6	1	0	0.03185	14, 22
<i>Phaethornis eurynome</i>	5.30	-	4.50	-	59.94	-	51.28	-	1	-	0.03275	14, 33
<i>Phaethornis griseogularis</i>	2.20	7	2.50	4	32.87	8	34.28	7	1	0	0.04142	14, 22, 33
<i>Phaethornis guy</i>	4.90	6	4.90	6	61.02	-	60.31	-	1	-	0.02929	10, 14, 24, 31, 33
<i>Phaethornis hispidus</i>	4.90	6	5.17	5	57.10	10	52.85	10	1	0	0.03315	14, 22, 44
<i>Phaethornis koepeckeae</i>	5.50	1	4.60	1	64.60	1	58.30	6	1	-	0.02955	10, 14, 33, 54

Appendix A.
(Continued.)

Species	Male weight (g)	n	Female weight (g)	n	Male wing length (mm)	n	Female wing length (mm)	n	Mating system	Territoriality	Male agility	References
<i>Phaethornis longirostris</i>	5.98	14	5.17	3	62.46	15	59.88	5	1	0	0.03422	14, 50
<i>Phaethornis longuemareus</i>	2.49	9	2.62	7	40.64	9	42.79	7	1	0	0.03169	14, 22, 23, 49, 55
<i>Phaethornis malaris</i>	5.99	9	5.80	5	52.92	26	57.50	20	1	-	0.0467	14, 33, 42
<i>Phaethornis mexicanus</i>	5.95	19	5.92	19	65.07	20	64.55	20	-	0	0.03153	14, 22
<i>Phaethornis philippii</i>	4.80	1	4.00	1	61.20	18	56.40	17	1	-	0.02853	10, 14, 33, 54
<i>Phaethornis pretrei</i>	4.50	-	4.10	-	58.37	-	56.44	-	1	0	0.02922	2, 14, 33
<i>Phaethornis ruber</i>	2.25	3	3.00	3	26.67	3	28.20	5	1	0	0.06215	12, 14, 23, 24, 37, 42
<i>Phaethornis rufurumii</i>	2.75	-	2.75	-	-	-	-	-	-	-	-	14, 46
<i>Phaethornis strigularis</i>	2.50	-	2.60	-	-	-	-	-	-	-	-	14
<i>Phaethornis subochraceus</i>	4.00	1	3.60	1	-	-	-	-	-	-	-	10
<i>Phaethornis superciliosus</i>	6.19	17	5.82	12	68.78	17	65.28	12	1	0	0.02957	11, 12, 14, 27, 46, 49

Appendix A.
(Continued.)

Species	Male weight (g)	n	Female weight (g)	n	Male wing length (mm)	n	Female wing length (mm)	n	Mating system	Territoriality	Male agility	References
<i>Phaethornis symmatophorus</i>	5.40	2	5.60	2	59.27	-	57.91	-	1	-	0.03408	10, 14, 33
<i>Phaethornis yaruqui</i>	6.10	2	5.10	1	59.49	-	55.18	-	1	-	0.03823	10, 14, 33
<i>Phlogophilus harterti</i>	2.45	-	2.45	-	-	-	-	-	-	-	-	14
<i>Polytmus guainumbi</i>	5.43	3	5.23	2	57.70	5	54.80	5	-	0	0.03603	14, 22
<i>Polytmus milleri</i>	5.60	-	4.40	-	-	-	-	-	-	-	-	14
<i>Polytmus theresiae</i>	3.45	-	3.45	-	55.57	-	55.24	-	-	0	0.02455	14, 33
<i>Pterophanes cyanopterus</i>	10.70	-	10.05	-	-	-	-	-	-	0	-	14
<i>Ramphodon naevius</i>	7.30	-	7.30	-	69.29	-	63.59	-	0	0	0.03439	14, 33
<i>Selasphorus calliope</i>	2.52	46	2.83	26	39.12	8	40.71	7	0	0	0.03441	14, 25, 30, 33, 51
<i>Selasphorus flammula</i>	2.50	-	2.80	-	40.04	34	41.95	22	0	1	0.03271	14, 33, 48
<i>Selasphorus platycercus</i>	3.21	68	3.70	65	47.02	6	48.62	3	0	1	0.03118	5, 14, 22, 25, 30
<i>Selasphorus rufus</i>	3.30	46	3.60	83	41.13	-	45.08	-	0	1	0.04108	14, 22, 25, 26, 28

Appendix A.
(Continued.)

Species	Male weight (g)	n	Female weight (g)	n	Male wing length (mm)	n	Female wing length (mm)	n	Mating system	Territoriality	Male agility	References
<i>Selasphorus sasin</i>	3.13	38	3.24	18	37.80	-	41.60	-	-	1	0.04554	14, 33
<i>Selasphorus scintilla</i>	2.12	8	2.33	7	32.71	46	35.82	39	0	1	0.04027	14, 33, 48
<i>Sephanoides fernandensis</i>	10.90	15	7.00	2	79.40	35	68.80	15	-	1	0.03977	9, 14
<i>Sephanoides sephanioides</i>	5.70	15	4.70	12	61.10	18	56.00	12	-	1	0.03398	9, 14
<i>Stephanoxis lalandi</i>	3.20	-	2.20	-	48.25	-	46.71	-	1	1	0.02963	14, 33, 38
<i>Thalurania colombica</i>	4.59	13	4.04	9	60.72	13	56.59	9	0	1	0.02769	14, 49
<i>Thalurania furecata</i>	4.90	1	4.20	1	55.23	-	50.73	-	0	0	0.03528	10, 12, 14, 33, 47
<i>Thalurania glaucopsis</i>	5.00	-	4.00	-	56.48	-	43.61	-	0	-	0.03452	14, 33
<i>Thalurania ridgwayi</i>	3.84	5	3.42	6	53.63	5	54.24	6	-	0	0.0292	14, 22
<i>Thalurania watertoni</i>	4.80	-	4.80	-	-	-	-	-	1	1	-	14
<i>Threnetes leucurus</i>	5.56	5	5.00	2	60.60	10	54.43	7	1	-	0.03366	14, 42, 50
<i>Threnetes ruckeri</i>	6.01	9	5.92	9	65.78	9	64.13	9	1	-	0.03121	14, 23, 49
<i>Topaza pella</i>	14.00	-	10.76	-	-	-	-	-	1	1	-	13, 14, 23

Appendix A.
(Continued.)

Species	Male weight (g)	n	Female weight (g)	n	Male wing length (mm)	n	Female wing length (mm)	n	Mating system	Territoriality	Male agility	References
<i>Topaza pyra</i>	10.75	-	10.75	-	-	-	-	-	-	-	-	13, 14, 23
<i>Trochilus polytmus</i>	5.20	1	4.10	1	63.82	-	55.97	-	-	-	0.02858	10, 14, 33
<i>Trochilus scitulus</i>	5.30	-	4.30	-	-	-	-	-	-	-	-	14

Mating system was scored as: 0, non-lekking; 1, lekking species. Territoriality was scored as: 0, nonterritorial; 1, territorial. Agility refers to wing disc loading (see Materials and methods). Sources: (1) Aldrich (1945); (2) Araújo et al. (2011); (3) Arizmendi (1986); (4) Atwood et al. (1991); (5) Barash (1972); (6) Bleiweiss (1998); (7) Chai & Millard (1997); (8) Colwell (1973); (9) Colwell (1989); (10) Colwell (2000); (11) Cotton (1998a); (12) Cotton (1998b); (13) Davis (1958); (14) del Hoyo et al. (2015); (15) Diaz-Valenzuela et al. (2011); (16) Feinsinger (1976); (17) Feinsinger & Colwell (1978); (18) Feo et al. (2015); (19) Fox (1954); (20) Gowda et al. (2012); (21) Hamilton (1965); (22) Hernández-Vega (2014); (23) Höglund (1989); (24) Höglund & Alatalo (1995); (25) Howell (2003); (26) Hurly et al. (2001); (27) Johnsgard (1997); (28) Kodric-Brown et al. (1984); (29) Lara (pers. comm); (30) López-Segoviano (2012); (31) MacDougall-Shackleton & Harbison (1998); (32) Martínez-García et al. (2013); (33) Ornelas (1995); (34) Ornelas (2010); (35) Ornelas et al. (2002); (36) Ortiz-Pulido et al. (2002); (37) Payne (1984); (38) Pizo (2012); (39) Pizo and Silva (2001); (40) Ramjohn et al. (2003); (41) Rodríguez-Flores (2009); (42) Rodríguez-Flores & Stiles (2005); (43) Rowley (1966); (44) Schuchman et al. (2000); (45) Skutch (1964); (46) Snow (1973); (47) Stiles (1982); (48) Stiles (1983); (49) Stiles (1995); (50) Stiles and Wolf (1979); (51) Tamm et al. (1989); (52) Weller (2000); (53) Weller & Schuchmann (2004); (54) Weske & Terborgh (1977); (55) Wiley (1971); (56) Wolf (1969); (57) Wolf (1975); (58) Wolf & Stiles (1970).

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Appendix B: Analyses using wing length as an estimator of body size

- (i) Rensch's rule is exhibited by hummingbirds (MA regression; $\beta = 1.095$, lower–upper confidence intervals: 1.026–1.169, $P = 0.001$; slope comparison test $P = 0.007$; 145 taxa).
- (ii) The reduced PGLS model of sexual size dimorphism (SSD) in wing length as a function of proxies of male competition (Table B1) suggests that in species in which males are smaller than females, the latter tend to exhibit low agility.
- (iii) The reduced model of SSD in wing length as a function of proxies of male competition (Table B2), as well as wing length, suggests that SSD in hummingbirds is not explained by our estimates of male competition, given that only male size (wing length) remains in the model (see main text).

Results one and three are consistent with the results using SSD in body mass; however, result number two differs from those results presented in the main text. We argue that the difference between the results presented in Table B1 and the ones presented in the main text may be driven by the autocorrelation between SSD in wing length and male agility (linear re-

Table B1.

Reduced PGLS model of SSD in wing length (dependent variable) as a function of estimates of male competition.

Model: independent variable		Regression coefficient \pm SE	t	P
Variable	Mating system	0.006 \pm 0.004	1.517	0.133
	Male territoriality	-0.002 \pm 0.004	0.594	0.553
	Male agility	-0.770 \pm 0.332	2.314	0.023

Model: $\lambda = 0.894$. $r^2 = 0.090$, $F_{3,77} = 2.547$, $P = 0.062$.

Table B2.

Reduced PGLS model of SSD in wing length (dependent variable) as a function of estimates of male competition and male wing length.

Model: independent variables		Regression coefficient \pm SE	t	P
Variable:	Male size	0.133 \pm 0.022	6.037	0.001

Model: $\lambda = 0.537$. $r^2 = 0.202$, $F_{1,144} = 36.440$, $P = 0.001$.

gression; $\beta = -1.424$, $r^2 = 0.118$, $F_{1,144} = 19.220$, $P = 0.001$). Note that SSD in body mass is not related to male agility ($\beta = -0.322$, $r^2 = 0.001$, $F_{1,145} = 0.167$, $P = 0.684$).

Appendix C

C.1. Set 1: excluding taxa represented by one individual per sex (data on body mass)

The following 29 taxa were excluded from analyses: *Amazilia lactea*, *A. rosenbergi*, *Campylopterus largipennis*, *C. rufus*, *C. villaviscensio*, *Chrysura oenone*, *Colibri delphinae*, *Discosura langsdorffi*, *Doricha eliza*, *Dorifera ludovicae*, *Eriocnemis luciani*, *Eutoxeres condensini*, *Hylocharis chrysura*, *H. cyanus*, *H. eliciae*, *H. grayi*, *Juliamyia julie*, *Lesbia victoricae*, *Leucippus baeri*, *L. chlorocercus*, *L. taczanowskii*, *Lophornis delattrei*, *Panterpe insignis*, *Phaethornis koepckeae*, *P. philippii*, *P. subochraceus*, *P. yaruqui*, *Thalurania furcata* and *Trochilus polytmus*. Thus, 171 taxa were used in the analyses of Rensch's rule, and 70 for the analyses of male competition.

The new results suggest that Rensch's rule is not exhibited by hummingbirds (MA regression; $\beta = 1.019$, lower–upper confidence intervals: 0.943–1.102, $P = 0.001$, $N = 170$ phylogenetically independent contrasts; slope comparison test $P = 0.631$). This result contradicts the results of Payne (1984), Colwell (2000) and Dale et al. (2007), which all have documented Rensch's rule in hummingbirds.

Finally, the reduced model of male competition (Table C1) was marginally consistent with the results presented in the main text (Table 1). The interaction term Male territoriality \times Male agility was retained in this set of

Table C1.

Reduced PGLS model of sexual size dimorphism in body mass (dependent variable) as a function of estimates of male competition. The dataset excluded 29 taxa that were $N = 1$.

Model: independent variable	Regression coefficient \pm SE	<i>t</i>	<i>P</i>
Variable: Mating system	0.016 \pm 0.013	1.241	0.219
Territoriality	−0.121 \pm 0.068	1.775	0.081
Male agility	−2.937 \pm 1.227	2.394	0.019
Territoriality \times Male agility	4.127 \pm 2.084	1.980	0.051

Model: $\lambda = 0.642$. $r^2 = 0.118$, $F_{4,65} = 2.183$, $P = 0.080$.

analyses, although it marginally exceeds $P = 0.050$. The rationale is that phylogenetic comparative analyses deal with data varying in scales of millions of years, so we believe it would not be appropriate to dismiss this result as non-significant. Note that sample size was reduced by 29 taxa, which may cause a bias in our results (see below).

C.2. Set 2: excluding taxa represented by the largest sample sizes (e.g. $N > 10$) per sex (data on body mass)

The following 29 taxa were excluded from analyses: *Amazilia beryllina*, *A. candida*, *A. cyanocephala*, *A. rutila*, *A. violiceps*, *A. yucatanensis*, *Archilochus colubris*, *Calothorax lucifer*, *Calypte anna*, *Campylopterus hemileucurus*, *Chlorostilbon maugaeus*, *C. mellisugus*, *Colibri thalassinus*, *Cyananthus doubledayi*, *Cyn. latirostris*, *Cyn. sordidus*, *Eupherusa polioerca*, *Hylocharis leucotis*, *Lampornis amethystinus*, *L. clemenciae*, *Microchera albocoronata*, *Phaethornis mexicanus*, *P. superciliosus*, *Selasphorus calliope*, *S. platycercus*, *S. rufus*, *S. sasin*, *Sephanoides sephaniodes* and *Thalurania colombica*. 171 taxa were used in the analyses of Rensch's rule, and 60 for the analyses of male competition.

These results also suggest that Rensch's rule is not exhibited by hummingbirds (MA regression; $\beta = 0.996$, lower–upper confidence intervals: 0.915–1.082, $P = 0.001$, $N = 170$ phylogenetically independent contrasts; slope comparison test $P = 0.920$). This result is similar to the set of analyses above, and also contradicts the results of Payne (1984), Colwell (2000) and Dale et al. (2007), which all have documented Rensch's rule in hummingbirds.

Finally, the reduced model of male competition (Table C2) was consistent with the results presented in the main text (Table 1 in the main text). The

Table C2.

Reduced model of sexual size dimorphism in body mass (dependent variable) as a function of estimates of male competition. The dataset excluded 29 taxa represented by the largest sample sizes.

Model: independent variable	Regression coefficient \pm SE	t	P
Variable: Mating system	0.142 \pm 0.052	2.732	0.008
Territoriality	−0.165 \pm 0.081	2.037	0.046
Male agility	−3.484 \pm 1.439	2.420	0.019
Territoriality \times Male agility	5.186 \pm 2.380	2.179	0.034

Model: $\lambda = 0.582$. $r^2 = 0.154$, $F_{4,55} = 2.496$, $P = 0.053$.

interaction term Male territoriality \times Male agility was retained in this set of analyses.

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