Rensch's Rule Crosses the Line: Convergent Allometry of Sexual Size Dimorphism in Hummingbirds and Flower Mites

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ABSTRACT: Hummingbirds demonstrate the full scope of Rensch's rule (females larger than males in small species, males larger than females in large species). The phoretic flower mites that hummingbirds compete with for nectar show the same pattern. An analysis of phylogenetically independent contrasts for 154 hummingbird and 37 mite species confirmed that both small (female-larger) and large (male-larger) species contribute to this result. I propose a common cause for this convergent pattern of sexual size dimorphism, with support from ecological and behavioral data for both groups. When morphology or behavior constrains each species to a limited range of resource densities, natural selection tends to diversify body size among species. If mating is promiscuous or polygynous, sexual selection favors larger males when resources are sufficient. But if male reproductive behavior is energetically costly, smaller males may have an advantage when resources are limiting, producing a pattern of allometry for sexual size dimorphism that conforms with Rensch's rule. Stabilizing selection on female size, if it occurs, amplifies this pattern. When the resource-density spectrum is broad enough, both female-larger and male-larger size dimorphism should occur within the same clade.

Keywords: Rensch's rule, sexual selection, adaptive radiation, energetics, courtship costs, body size.

In the majority of avian and mammalian lineages, males tend to be larger than females. Among most species on Earth, however, including fish, amphibians, reptiles, virtually all invertebrate lineages, and a few groups of birds and mammals, females are generally larger than males—often very much larger (Darwin 1874; Ghiselin 1974; Reiss 1989). Quantitative studies of sexual size di-

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morphism (SSD) within related groups of organisms often reveal allometric trends in SSD, in which proportional size differences either increase or decrease allometrically with overall body size. In other words, larger species in these groups tend to be either more dimorphic (hyperallometry) or less dimorphic (hypoallometry) than smaller species.

Fairbairn (1997) and Abouheif and Fairbairn (1997) have shown that the overwhelming majority of such cases follow a pattern that has become known as "Rensch's rule": in clades in which females tend to be larger than males, the difference diminishes in larger species, whereas in clades in which males tend to be larger than females, the difference increases in larger species (fig. 1; Rensch 1960). As figure 1 shows, in a clade that follows Rensch's rule, female size varies less than male size among species. After reviewing the literature, performing additional statistical tests on published and new data sets, and carrying out a meta-analysis, Abouheif and Fairbairn (1997) and Fairbairn (1997) concluded that Rensch's rule is quite general and highly significant overall. For most groups these authors examined, however, SSD does not cross the line of gender size equality—either all species in a clade have males as large or larger than females (e.g., gamebirds, primates) or the reverse (e.g., water striders; Fairbairn and Preziosi 1994), suggesting the possibility that different explanations account for the two kinds of allometry.

On the other hand, based on a rigorous, phylogenetically corrected statistical analysis, Abouheif and Fairbairn (1997) documented a few cases of statistically significant "mixed" allometry for sexual size dimorphism within a clade (e.g., colubrid snakes and a small sample of hummingbirds). In these examples, the raw data points (species) can be roughly divided into two classes: larger species, in which males tend to be the larger sex and smaller species, in which females tend to be the larger sex. Abouheif and Fairbairn (1997) did not report, in these mixed cases, whether both size classes equally contribute to the significant allometric regression, but they note that statistical support for allometry in SSD is considerably stronger for

clades with exclusively male-biased SSD than for clades with exclusively female-biased SSD.

Fairbairn proposed that the seemingly opposite patterns of hyper- and hypoallometry for SSD may have a common explanation in sexual selection on male size, either alone or combined with stabilizing selection on female size (Fairbairn 1997). But the paucity of large, well-studied single clades known to cross the line of sexual size equality makes it difficult to evaluate this explanation. Indeed, Fairbairn's hypothesis was not based on an analysis of mixed allometry within clades.

I will show that both hummingbirds and hummingbird flower mites demonstrate mixed allometry for SSD, with significant statistical support for Rensch's rule in both clades for both kinds of allometry, based on phylogenetically corrected tests. That flower mites and hummingbirds share a similar social system and a common resource base, despite their obvious and profound biological differences, suggests that there, indeed, may be a common cause for this convergent pattern.

Material and Methods

Hummingbirds and Flower Mites

Hummingbirds (Trochilidae), a strictly New World family of more than 300 species, breed from Alaska to Tierra del Fuego. Hummingbird species vary 10-fold in body size, from the tiny 2 g *Calypte helenae* (Cuba), *Acestrura bombus* (Ecuador and Peru) and *Thaumastura cora* (Peru) to the 20 g *Patagona gigas* (Ecuador to Chile)—although the second largest species, *Ensifera ensifera* (Venezuela to Bolivia), weighs only 11 g. At tropical latitudes, wet lowland rain forest typically supports 10–25 sympatric hummingbird species feeding on the nectar of dozens of species of plants, most of which are obligately pollinated by the birds (Feinsinger and Colwell 1978; Colwell and Coddington 1994). Bill length is a key component of niche differentiation among coexisting hummingbirds through its correlation with the corolla length of food plants (e.g., Feinsinger and Colwell 1978) and figures prominently in the adaptive radiation of the family. Most local assemblages of hummingbirds include species representing widely divergent lineages within the family (Bleiweiss 1998a).

Hummingbird flower mites are obligate inhabitants of the flowers of hummingbird-pollinated plants. Both sexes are transported between inflorescences in the nasal cavities of hummingbirds (Colwell 1973, 1981, 1985, 1986b, 2000; Dobkin 1990; Colwell and Naeem 1999). Courtship, mating, and oviposition occur on the host plant. Sister genera *Rhinoseius* and *Tropicoseius* (Baker and Yunker 1964 sensu Naskrecki and Colwell 1998), together with an ecologically and behaviorally convergent lineage within the genus *Proc-*
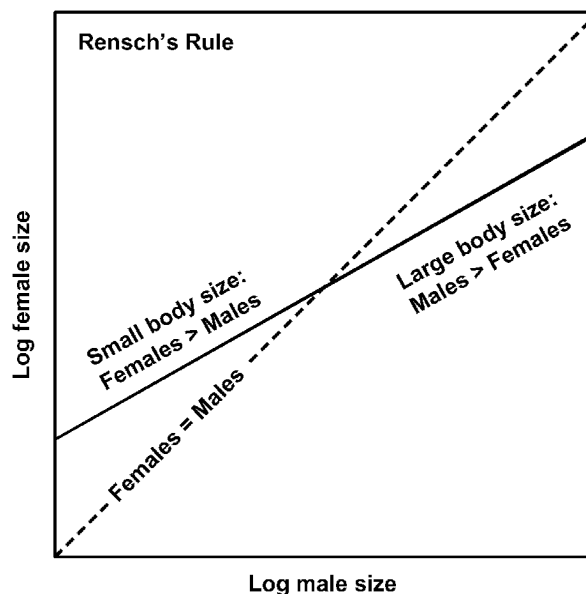

Figure 1: Rensch's rule for allometry of sexual size dimorphism. Species with males and females of equal size lie along the broken line (slope = 1, no size dimorphism). Above the broken line, females are larger than males; below it, males are larger than females. If the slope of the relationship between the log of female size and the log of male size is <1 in such a plot, as shown by the solid line, then in smaller species females are larger than males, whereas in larger species males are larger than females, a relationship known as Rensch's rule. (Figure modeled after Abouheif and Fairbairn 1997.)

tolaelaps comprise this ecologically defined group of some 70 known species in the family Ascidae (Mesostigmata). Among the flower mites in this study, body size (measured as length of the dorsal shield) varies from 0.48 mm (*Tropicoseius kressi*) to 0.73 mm (*Tropicoseius colwelli*); in mass equivalents, the largest species is about 3.5 times as large as the smallest.

The affiliation of hummingbird flower mites with their host plants is quite specific and typically exclusive (Colwell 1986a, 1986b; Heyneman et al. 1991). The mites prefer the nectar of their own characteristic host species to the nectar of the hosts of other hummingbird flower mite species in the same assemblage (Heyneman et al. 1991). In contrast, the mites that any given individual hummingbird carries generally represent whatever mixture of flowers the bird is currently visiting (Colwell 1973, 1986a).

Despite their great difference in size (the smallest hummingbird weighs 10^5 times the largest flower mite), hummingbirds and flower mites compete intensely for nectar (Colwell 1995). Typically, each local mite breeding group is founded by a few adult mites disembarking from hummingbirds into the first flowers of an inflorescence. The group quickly grows to dozens or hundreds of mites, de-

pending on mite and host species (Colwell and Naeem 1994)—numbers sufficient to threaten the entire nectar production of an inflorescence. Although dispersal on hummingbirds is an essential component of flower mite fitness, most individuals probably spend their entire life (about 2 wk) on their natal inflorescence.

Specimens and Measurements

Mite body size data for this study were measurements of the length of the dorsal shield from mounted specimens of both sexes for 37 of the ∼70 known species of hummingbird flower mites. Mean values of log-transformed lengths were used for analysis, based on two to 10 specimens per sex per species (app. A).

Hummingbird body size data for this study were field weights or weights from museum leg tags for 154 of the ∼330 known species of hummingbirds. Mean values of log-transformed weights were used for analysis, based on one to 15 specimens per sex per species (app. B). I obtained bill length (exposed culmen) data (app. B) from the same specimens using electronic calipers.

Phylogenies

A phylogeny is required to correct for phylogenetic nonindependence. For the mites, I relied on the phylogenetic hypothesis of Naskrecki and Colwell (1998), a well-supported, fully resolved cladogram based on morphological features.

No phylogenetic hypothesis has been published for the family Trochilidae (hummingbirds) as a whole. For purposes of phylogenetic correction, I structured a partially resolved, approximate phylogeny around the major clade phylogenetic hypothesis of Bleiweiss et al. (1997), who based their study on DNA hybridization data for 26 species of 25 representative genera. Hummingbirds are placed in two subfamilies, with strong morphological and molecular support. For the small subfamily Phaethorninae (hermits), I relied on the phylogenetic hypothesis of Gill and Gerwin (1989), based on protein electrophoresis. For the subfamily Trochilinae, I added additional genera to the Bleiweiss et al. (1997) phylogeny based on shared anatomical characters (presumed synapomorphies of musculature) reported by Zusi and Bentz (1982). Genera of the subfamily Trochilinae that were not treated by either Bleiweiss et al. or Zusi and Bentz were placed as basal soft polytomies in the subfamily Trochilinae. Species of *Amazilia* and *Hylocharis* were placed in subgenera according to the classifications of Peters (1945) and Morony et al. (1975). Phylogeny within the genus *Heliodoxa* follows the hypothesis of Gerwin and Zink (1989), based on protein electrophoresis. Within all genera not otherwise resolved, congeneric
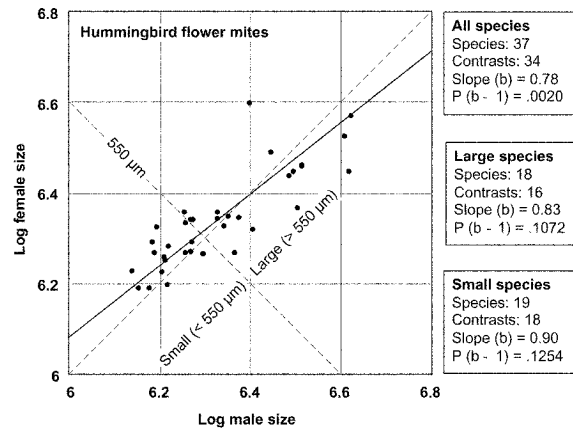

Figure 2: Female size (length of dorsal shield in μm) versus male size for hummingbird flower mites (both variables natural log transformed). Points represent species means for males and females of 37 species of mites (app. A). Positive-slope broken line represents size equality for males and females within species. Solid line is the major axis fitted to these data (all species) with the slope (0.78) determined by phylogenetically independent contrasts. Rensch's rule is thus strongly supported for hummingbird flower mites. The negative-slope broken line labeled 550 μm separates smaller from larger species for testing the contribution of these classes to the overall pattern. Further statistical details appear in table 1.

species were placed as soft polytomies. To assess the sensitivity of the analysis to the numerous soft polytomies in the hummingbird cladogram, a second cladogram was produced using only fully resolved clades (51 species vs. 154 for the full data set). (The cladograms are available from the author, but it must be understood that they are intended for statistical use only and are in no way claimed to advance our understanding of trochilid evolution.)

Statistical Methods

The best way to visualize data for allometry in SSD is to plot female size versus male size, as in figure 1. Plotting the logarithms of size normalizes the size distributions. A slope less than unity indicates conformity with Rensch's rule. The statistical significance of this deviation from a slope of unity, however, cannot be legitimately assessed for raw, species-level data points. Nearby points are likely to represent closely related species whose common ancestor shared a similar pattern of sexual dimorphism. Thus, the "tip" data (one point for each species) may inflate the true sample size for independent evolutionary events. Moreover, large, morphologically conservative radiations may bias the slope in either direction by pseudoreplicating evolutionary events in particular regions of the plot.

A number of methods exist to reduce the effect of phy-

logenetic autocorrelation in data such as the morphological measurements in this study. For consistency with the SSD studies of Abouheif and Fairbairn (1997), I used Felsentein's method of phylogenetically independent contrasts (Felsenstein 1985; Grafen 1989; Garland et al. 1992; Pagel 1992), setting initial branch lengths by Grafen's (1989) method since no independent information on branch lengths was available. Logarithmic transformation of these initial branch lengths, before computing contrasts, successfully removed heterogeneity of variance and correlation between node values and contrasts (Garland et al. 1992; Purvis and Rambaut 1995; Abouheif and Fairbairn 1997). To compute the contrast values and Grafen branch lengths, I used the application CAIC of Purvis and Rambaut (1995).

To assess the relationship between male and female contrasts, lines were fitted by major axis (model 2) regression through the origin, following Garland et al. (1992). Phylogenetically corrected regressions can be meaningfully plotted in the same graph as the raw species points since the slopes for the corrected regressions estimate the slopes in the same units as an uncorrected major axis fitted through the tip values themselves (Garland et al. 1992). Although it is informative to examine the 95% confidence intervals (CIs) for these slopes (which are reported for this study), Abouheif and Fairbairn (1997) devised a statistically more powerful alternative for testing the statistical significance of support for allometry of SSD. Because Rensch's rule predicts greater evolutionary divergence in male size than in female size for sister taxa, a paired *t*-test on male versus female contrasts provides a direct assessment of statistical significance. To be conservative about a priori hypotheses, all *t*-tests in this study were two tailed.

Allometry between log bill length and log body size in hummingbirds was also assessed using major axis regression through the origin, based on the intersexual mean of phylogenetically independent contrasts for bill length and weight, and 95% CIs were computed. (Paired *t*-tests make no sense in this case.) The relationship between sexual dimorphism in bill length and sexual dimorphism in body size was assessed by plotting the intersexual difference between independent contrasts for bill length against the corresponding intersexual difference between independent contrasts for body size, testing with simple product-moment correlation statistics.

Results

Rensch's Rule: Allometry for SSD

Male and female body size data for mites are plotted in figure 2, and the data for hummingbirds are in figure 3. In these plots, each point represents the mean among in-
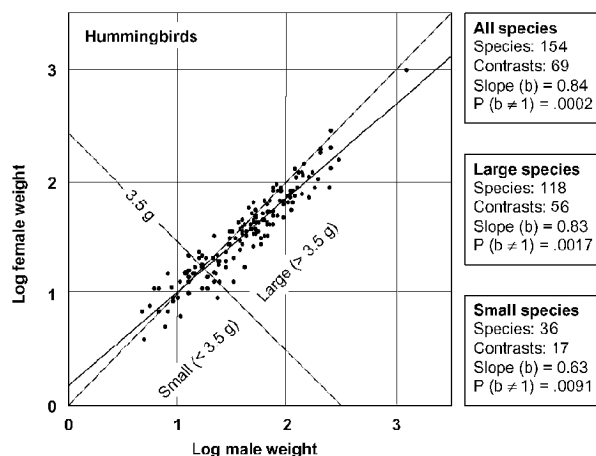

Figure 3. Female weight (mass in g) versus male weight for hummingbirds (both variables natural log transformed). Points represent species means for males and females of 154 species of hummingbirds (app. B). Positive-slope broken line represents size equality for males and females within species. Solid line is the major axis fitted to these data (all species) with the slope (0.84) determined by phylogenetically independent contrasts. Rensch's rule is thus strongly supported for hummingbirds. The negative-slope broken line labeled 3.5 g separates smaller from larger species for testing the contribution of these classes to the overall pattern. Further statistical details appear in table 1.

dividuals for an individual species (a "tip value," in phylogenetic terms). The major axis regression lines plotted in figures 2 and 3, however, are based on the results for phylogenetically independent contrasts. For both mites and hummingbirds, the regression slope is less than unity, indicating conformity with Rensch's rule (table 1, rows labeled "All"). The slope for mites was 0.78 (fig. 2), compared with 0.72 for uncorrected tip values. For hummingbirds, the slope for independent contrasts was 0.84 (fig. 3), compared with 0.90 for tip values. Thus, phylogenetic correction somewhat strengthened support for Rensch's rule for hummingbirds and weakened support slightly for the mites. Because both regression lines cross the line of sexual size equality within the body-size range of the data, both taxa demonstrate "mixed" allometry.

Significance levels for the phylogenetically corrected results, based on paired *t*-tests, show strong support for Rensch's rule (mites: $P = .0020$, hummingbirds: $P = .0002$; table 1). For hummingbirds, the phylogenetic hypothesis used to compute the contrasts necessarily includes many polytomies. To test the sensitivity of the results to this limitation, the analysis for hummingbirds was repeated using the subset of hummingbird species placed in fully resolved clades. Results did not differ appreciably; the slope using resolved clades was 0.86 ($P = .0049$, df = 50) versus 0.84 ($P = .0020$, df = 68) for the full clado-

Table 1: Allometric slopes and significance levels of support for Rensch's rule for independent contrasts

Taxon/body size	Slope	Slope 95% CI		Student's *t*	df	*P* (*b* ≠ 1) (two-tailed)
		L1	L2			
Mites:						
Small	.90	.62	1.27	1.61	17	.1254
Large	.83	.41	1.57	1.71	15	.1072
All	.78	.63	.96	3.36	33	.0020
Hummingbirds:						
Small	.63	.19	1.36	2.97	16	.0091
Large	.83	.73	.93	3.30	55	.0017
All	.84	.76	.94	3.98	68	.0002

Note: An allometric slope significantly less than unity indicates support for Rensch's rule.

gram. Because the size outlier *Patagona gigas* was not in a resolved clade and, in any case, shows male-biased sexual dimorphism considerably less pronounced than predicted by the regression, it can safely be inferred that this species is not driving the results for the full data set.

This pattern has not been previously noted for any other group of mites to the best of my knowledge. For hummingbirds, however, Lasiewski and Lasiewski (1967) were apparently the first to note that males are larger than females in larger species and females larger than males in smaller species, although they provided only anecdotal data to support this observation. Payne (1984) appears to have been the first to publish data, for 32 species, showing that size dimorphism in hummingbirds depends on body size, but he did not perform any statistical tests or correct for phylogenetic autocorrelation. Abouheif and Fairbairn (1997) found statistical support for Rensch's rule for 14 species of North American hummingbirds, using independent contrasts based on a "highly tentative" (Johnsgard 1983) phylogenetic hypothesis.

Contribution of Small versus Large Species

Because both mites and hummingbirds show mixed allometry, we may inquire whether support for Rensch's rule is equally strong for the female-larger fraction (smaller species) and for the male-larger fraction (larger species) in each taxon. To do this, it is necessary to partition species into "small-bodied" and "large-bodied" fractions in some reasonable way. Regardless of how this is done, there inevitably will be a mix of male-larger and female-larger species in both groups, due to the scatter about the regression lines in figures 2 and 3, so any partition is somewhat arbitrary. One approach is to find the body size at which male size equals female size for the (phylogenetically corrected) major axis regression for species (the regression

lines in figs. 2, 3—a value interesting in its own right) and assign all species smaller than that value to the small-bodied fraction and all those larger to the large-bodied fraction. I tried this, using the grand means from the species data (tip values) with the slope from the independent contrasts to obtain the critical size and then assigning species according to the intersexual mean size for each species (the antilog of the mean of the logarithms for male and female size).

For mites, the regression predicts that male size should equal female size at 594 μm. Of the 37 species, 26 are smaller than this size, and only 11 are larger. Since the significance of the paired *t*-test for allometry depends on sample size for a given mean difference and pattern of variation, sample sizes for the two groups of species need to be relatively similar to make the comparison sensible. To equalize the sample sizes (and thus equalize statistical power), I lowered the critical size to 550 μm, yielding samples of 19 and 18 species. For hummingbirds, the regression predicts that male size and female size should be equal at 2.97 g. Because only 11 of the 154 species are smaller than this value, I chose, as a somewhat arbitrary compromise, to use 3.5 g as the critical size instead, yielding samples of 36 and 118 species. Table 2 shows that the number of species in each category of dimorphism in the two fractions for mites and for hummingbirds is suitably distributed to provide the desired contrast.

The results of independent contrasts for size-partitioned data appear in table 1 ("small" and "large" rows). For the mites, the slope increases from 0.78 for all species to 0.90 (small) and 0.83 (large) for the partitioned data. Although the slope does remain less than unity, the *t*-test is not significant for either the small-body or the large-body species fraction for the mites. Nevertheless, the reduced data sets have very similar slopes, *P* values (.1072 and .1254), and sample sizes (18 and 19), so it seems appropriate to conclude that the significant result for all mite species considered together is driven by both fractions. In the hummingbird case, this conclusion is firmly supported. The *t*-tests for the hummingbirds remain highly significant for each fraction considered separately; the slope remains virtually unchanged for larger species (0.83) and actually decreases (to 0.63) for smaller species. Again, because male-biased sexual dimorphism in the size outlier *P. gigas* is considerably less pronounced than predicted by the regression for large species, this species cannot be driving the result.

Allometry and Dimorphism of Hummingbird Bill Length

In hummingbirds, bill length varies somewhat allometrically with body size (fig. 4), with an exponent (allometric coefficient) of 0.46 (95% CI: 0.35, 0.58). For isometry, the

Table 2: Distribution of size dimorphism between small and large species of mites and hummingbirds

Taxon/body size	Criterion	Female > male	Female = male	Female < male	Total
Mites:					
Small	< 550 μm	17	0	2	19
Large	> 550 μm	4	0	14	18
All	…	21	0	16	37
Hummingbirds:					
Small	< 3.5 g	14	5	17	36
Large	> 3.5 g	18	6	94	118
All	…	32	11	111	154

exponent would be 0.33. In other words, on average, a larger species of hummingbird generally has an even longer bill than a photographic enlargement of a smaller species matched for body size with the larger bird. The relationship between sexual dimorphism in bill length and sexual dimorphism in body size (fig. 5) is decisively nonsignificant ($r = 0.17$, df $= 65$, $P = .17$ for phylogenetically independent contrasts).

Discussion

Body Size Scales with Resource Density

Before asking why sexual size dimorphism varies with body size in hummingbirds and flower mites, we must first inquire why body size itself varies so widely among species within each of these groups. In severely resource-limited species such as these (Suarez et al. 1986; Colwell and Naeem 1994), maximum body size is constrained by the density of resources to which each species has reliable access, producing an evolutionary diversification of body sizes within clades that reflects differential adaptation to the spectrum of resource densities in nature (Brown et al. 1993).

The analysis of bill size versus body size (fig. 4) shows that larger-bodied hummingbirds tend to have longer bills. It is well established that longer-billed hummingbirds tend to feed from larger flowers (flowers with deeper corollas; Grant and Grant 1968; Colwell 1973; Stiles 1975, 1978, 1980; Feinsinger 1976, 1978, 1987; Wolf et al. 1976; Feinsinger and Colwell 1978; Johnsgard 1983) and that larger flowers produce more nectar than smaller flowers (Feinsinger and Colwell 1978; Cruden et al. 1983). Therefore, although the picture is complicated somewhat by scatter around the regression of bill length on body size and by the spatial distribution of flowers, larger hummingbirds tend to feed on richer sources of nectar (Wolf et al. 1976; Brown et al. 1978). Adult hummingbirds also feed on arthropods, but nectar is the principal energy source for adult hummingbirds, as indicated by both behavioral

(Wolf and Hainsworth 1972; Brown et al. 1978) and biochemical (Suarez et al. 1986) studies.

Likewise, mite body size is positively correlated with host flower size (Colwell 1986b; Colwell and Naeem 1994) and thus with nectar production. The number of adult mites per inflorescence also varies with flower size, with more mites on larger flowers (Colwell and Naeem 1994). Thus, total biomass of mites per inflorescence increases with flower size, directly reflecting greater resource supply. Hummingbird flower mites also consume pollen (Paciorek et al. 1995). Pollen production may well be correlated with flower size, like nectar, but I have not been able to find any published data to test this conjecture. Possible evolutionary explanations for the correlation between body size and resource supply among hummingbirds and flower mites are discussed elsewhere (Colwell 2000).
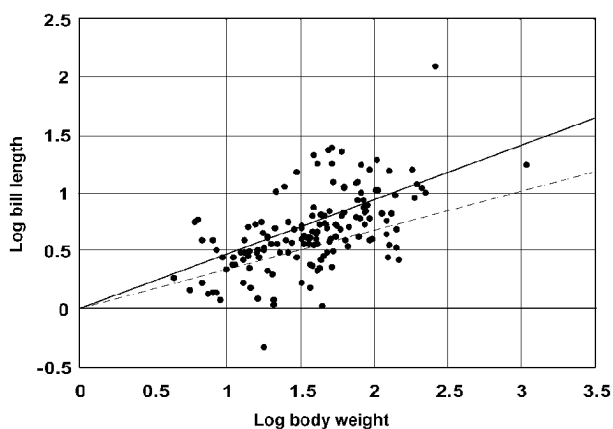
Figure 4: Relationship between bill length (cm of exposed culmen) and body weight (mass in g) for 154 species of hummingbirds. On average, larger hummingbirds have longer bills. The data points represent intersexual means for the individual species in appendix B. Solid line is the major axis (model 2) regression fitted through the origin, based on phylogenetically independent contrasts (df $= 66$). Slope of the major axis is 0.46 (95% CI: 0.35, 0.58), revealing a moderate degree of allometry. Slope would be 0.33 for isometry, shown by the broken line.

Figure 5. Sexual dimorphism in bill length as a function of sexual dimorphism in body size (mass in g) for 154 species of hummingbirds. To the degree that bill length is a proxy for feeding niche, the hypothesis that sexual size dimorphism is correlated with sexual niche differentiation is decisively rejected ($r = 0.17$, df $= 65$, $P = .17$ for phylogenetically independent contrasts).
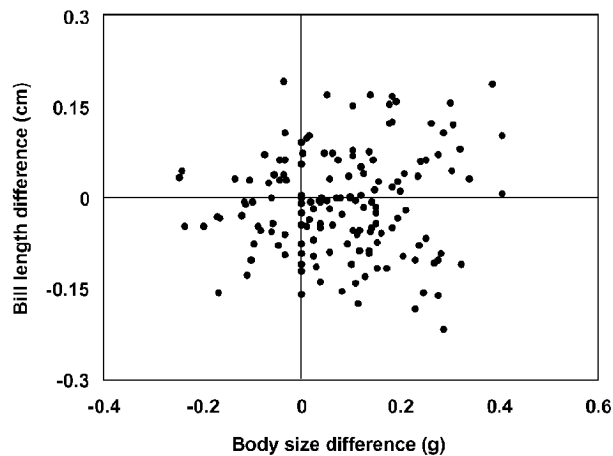
Natural and Sexual Selection for Sexual Size Dimorphism

According to quantitative genetic theory, males and females are expected to adapt independently to net selection acting on each sex (Lande 1980; Fairbairn 1997). Given the pattern of allometry for SSD documented here for both hummingbirds and hummingbird flower mites (figs. 2, 3), it is reasonable to suggest that males and females have been subjected to different patterns of selection in relation to body size.

Natural selection for niche differentiation can, in principle, explain SSD (reviewed by Shine 1989 and Fairbairn 1997), although how it might account for Rensch's rule is obscure. Resource partitioning certainly makes no sense for the mites, since males and females of a given species live together inside the same flowers, sharing the same feeding niche. Because differences in bill length are a key morphological proxy for feeding-niche difference among coexisting hummingbirds (Feinsinger and Colwell 1978), sexual niche differentiation can be nicely assessed by looking for correlation between intersexual difference in bill length and intersexual difference in body size. In fact, the correlation is decisively nonsignificant (fig. 5); there is no evidence that sexual dimorphism in body size has been a prerequisite or a consequence of niche differentiation in either group (see Colwell 1989 for an extreme example).

Conformity with Rensch's rule requires that female size varies less than male size among species (fig. 1). If body size radiated interspecifically in response to the resource spectrum, then either stronger stabilizing selection or

stronger constraints on female size than on male size could produce a pattern that conforms to Rensch's rule (Fairbairn 1997) in the complete absence of sexual selection on male size.

Several facts suggest a role for stronger selection against small females than against small males for both hummingbirds and mites. It has been argued that, in the smallest hummingbirds, reproductive metabolic constraints prevent females from becoming as small as males (Payne 1984). Smaller hummingbirds have a higher metabolism and produce heavier eggs than larger hummingbirds, on a weight-specific basis (Lasiewski and Lasiewski 1967; Brown et al. 1978; Johnsgard 1983). In the case of flower mites, eggs of females in the smallest species are more than one-third the length of the female's body, whereas larger species tend to have proportionally smaller eggs. Perhaps a lower limit on egg size sets a lower limit on female body size in both hummingbirds and mites.

At the other end of the body-size spectrum, it seems possible that constraints on clutch size may make it uneconomic for females to become as large as males. Hummingbird clutch size is constant at two eggs per clutch over the entire family, in spite of a 10-fold range in body mass (Johnsgard 1983). Only limited data are available on clutch sizes for the hummingbird flower mites (Colwell and Naeem 1999), but clutch size is known to be independent of body size in other clades of Mesostigmata (Walter and Proctor 1999). Why clutch size should be constrained in this way in either group is obscure, but females whose body size is larger than necessary for producing a fixed clutch size would likely be at a selective disadvantage in the resource-limited world of hummingbirds and their mites.

Regardless of a probable role for stronger stabilizing selection or greater constraints on female size, male size in both hummingbirds and mites very likely has been shaped by sexual selection. Both hummingbirds and mites present the classic conditions for intrasexual selection among males, as well as the potential for intersexual selection by female choice (Kirkpatrick 1982; Andersson 1994). Both are highly polygynous and pair promiscuously, and males generally have no role in reproduction aside from courtship and mating (Johnsgard 1983; Payne 1984; Colwell 1985; Colwell and Naeem 1994; Colwell and Naskrecki 1999). In the mites, polygyny is reinforced by the sex ratio, which is generally quite female biased (Colwell 1981; Wilson and Colwell 1981; Colwell and Naeem 1994). Promiscuous mating systems may promote speciation and adaptive radiation, with hummingbirds (vs. their non-promiscuous sister group, the swifts) providing perhaps the strongest example (Mitra et al. 1996).

Morphological evidence of sexual selection abounds in both groups, quite apart from SSD. Most hummingbird

species of the large subfamily Trochilinae (nearly 90% of the family) are sexually dimorphic in coloration, and males of many species are famous for their elaborate ornamentation and showy modifications of plumage (Skutch 1973; Payne 1984; Bleiweiss 1998*b*). Male hummingbird flower mites bear elaborate, species-specific patterns of setation quite distinct from their respective females. Among closely related species, the spermatodactyl (male-inseminating apparatus) often differs in striking and seemingly arbitrary ways, and the legs of many species are highly modified for fighting with other males (Naskrecki and Colwell 1998; Colwell and Naskrecki 1999).

Studies of a number of male-larger species in other taxa (Reiss 1989) show that larger males have a mating advantage, both in presenting effective threats and in actual combat. Fairbairn and Preziosi (1994) reviewed the literature on sexual selection for larger males in taxa with female-larger SSD and demonstrated the phenomenon experimentally for water striders, although in this case the greater success of larger males appears to be the result of a greater encounter rate, rather than direct male-male interactions.

Rensch's Rule and Reproductive Costs

The puzzle piece still missing is how to explain female-larger SSD in the context of Rensch's rule. The statistical results for small-bodied (female-larger) hummingbirds and flower mites (figs. 2, 3; table 1) demonstrate that this class contributes just as much to the overall pattern as the large-bodied (male-larger SSD) species for these groups. If larger males tend to have greater mating success, why are they not at least as large as females of the same species since they have access to the same resources?

The answer, I believe, lies in comparing patterns of reproductive costs for males and females. Males of many hummingbird species are famous for their energetically costly aerial displays and aggressive interactions with competing males, including territorial defense (e.g., Wolf and Hainsworth 1972; Kodric-Brown and Brown 1978; Calder et al. 1990). In other species, males display and sing actively on leks many hours per day (Payne 1984 reviewed the literature; see also Tyrrell and Tyrrell 1990; Bleiweiss 1998*b*). Female hummingbirds, in contrast, generally spend much of their time during courtship observing from a perch, although in some species females defend feeding territories (Wolf and Stiles 1970; Stiles 1973; Carpenter 1976; Kodric-Brown and Brown 1978; Colwell 1989). Weight-specific male flight costs are amplified in some species by higher wing loading in males than in females (Feinsinger and Chaplin 1975; Kodric-Brown and Brown 1978; Feinsinger and Colwell 1978). Males do not shift to more efficient strategies at low resource densities; smaller

hummingbird species are just as likely to be territorial as larger species (Payne 1984). Among the mites, males actively court the relatively stationary females, moving rapidly among them, frequently seeking out and grappling frenetically with other males engaged in the same activities. Males persistently tap and stroke each female with the first pair of legs and attempt to mount many times for each successful mating.

In short, in both groups, courtship and mating behavior (the success or failure of which, of course, is crucial to male fitness) and related male-male interactions exact a considerably greater energetic cost on males than on females per unit body weight. Males must pay the greater cost either by maintaining a greater per individual rate of resource consumption during courtship compared with conspecific females or by being smaller than conspecific females. By this reasoning, males of species with access to richer resources (larger hummingbird and mite species) tend to pay the cost by additional consumption, whereas males restricted to poorer resources (smaller species) pay the cost by being smaller than females. The result conforms to Rensch's rule, with or without stabilizing selection on female body size.

At the very lowest resource densities, female body size presumably represents not only the smallest female size for the clade but the largest size those resource densities will support (Brown et al. 1978) at the limit of "energy acquisition" capabilities for the clade (Brown et al. 1993). If so, males must be even smaller than these smallest females. At the high end of the resource-density spectrum, in contrast, females need not reach the maximum size supportable, whereas sexual selection would be expected to push males toward this size to the limit of "energy conversion" capabilities for the clade (Brown et al. 1993). Total lifetime reproductive costs of females may be higher or lower than for males, per unit time, when averaged over the adult lifetime. But, in contrast to males, females may accrue or amortize these costs over longer periods of time. Indeed, incubation and fledging times for hummingbirds are considered quite long for birds of this size and may be adjusted depending on ambient temperature and availability of resources (Johnsgard 1983).

Sexual selection for small males, based on energetic considerations in relation to mating success, has considerable statistical and some experimental support for individual species in which females are larger than males (reviewed by Fairbairn and Preziosi 1994 and Blanckenhorn et al. 1995). In the well-studied North American hummingbirds, there is both ontogenetic and physiological support for this hypothesis. In some female-larger species, both body weight and wing length of juvenile males actually decrease shortly before their first breeding season (reviewed by Payne 1984). Breeding male *Selasphorus platycercus* keep

their body weight low throughout the day, while averaging more than 40 territorial chases and more than 40 courtship climb-dive displays per hour, by feeding only enough to fuel these activities at one-sixth the energy intake rate of females. At dusk, males cease courtship activities and feed voraciously, raising body weight by more than 30% before perching for the night (Calder et al. 1990). Seasonal patterns are also in accord with the hypothesis. Breeding male *Selasphorus rufus* undergo pronounced seasonal weight changes, maintaining minimum weight during the breeding season (Hiebert 1991).

Fairbairn and Preziosi (1994) suggested that female-larger clades may have arisen from selection for larger males alone (rather than a balance of sexual selection for larger and smaller males, as proposed here) if the clade was derived from an even smaller, highly dimorphic (female larger) ancestor. This hypothesis cannot be directly refuted for the mites, since both species of the closest known out-group (*Xanthippe*) are indeed somewhat smaller, and at least one of the two species (*Xanthippe clavisetosa*) is at least as dimorphic (female 469 μm, male 400 μm; Naskrecki and Colwell 1995) as any known *Tropicoseius* or *Rhinoseius*. For hummingbirds, on the other hand, this mechanism cannot account for the pattern since body size among species of the out-group (swifts) is not only larger than the smallest hummingbird but larger than the largest hummingbird—nor are swifts dimorphic in size.

Conclusion

I suggest here that sexual selection on male body size has two opposing components. Sexual selection favoring larger males, based on male-male interactions (and perhaps on female choice), is opposed by the energetic advantage that smaller males gain in requiring a lower total energy output per hour to carry on courtship activities and engage in male-male contests. The balance between these components depends on resource availability, with female-larger and mixed allometry for SSD conforming to Rensch's rule expected only in resource-limited clades. But the energetic advantage of small male size may play a role in Rensch's rule even for clades with exclusively male-larger SSD. The effect should be larger when males have low postmating reproductive costs relative to females.

APPENDIX A

Table A1: Body size (length of dorsal shield in μm) for males and females of 37 species of hummingbird flower mites

Mite species	Male size			Female size		
	Mean	SD	*n*	Mean	SD	*n*
Rhinoseius androdon	629	17	6	660	0	1
Rhinoseius haplophaedia	600	4	6	723	5	6
Rhinoseius luteyni	525.5	23	6	567	6	6
Rhinoseius nadachowskyi	519	26	6	576.5	6	6
Rhinoseius pastorae	580.5	6	2	528	0	1
Rhinoseius rafinskii	487.5	11	2	558	51	2
Rhinoseius richardsoni	484	15	6	540	12	6
Rhinoseius tiptoni	520	27	6	564	13	6
Rhinoseius ucumariensis	462	11	6	506.5	22	6
Tropicoseius analis	527	10	6	540	12	6
Tropicoseius bakeri	480	5	6	487.5	19	6
Tropicoseius berryi	750	0	1	714	32	3
Tropicoseius bisacculatus	495.5	11	6	523	17	6
Tropicoseius cervus	741	8	4	683.5	16	6
Tropicoseius chazdonae	748	56	6	632	40	6
Tropicoseius chiriquensis	604	43	6	556	56	6
Tropicoseius colombiensis	486	16	6	527	11	6
Tropicoseius colwelli	751	55	6	714	17	6
Tropicoseius erioxynon	572.5	18	6	572	15	6
Tropicoseius erro	520	21	6	528	12	6
Tropicoseius fairchildi	529	15	6	567	12	6
Tropicoseius fidelis	567	26	6	559	23	6
Tropicoseius fuentesi	586	30	6	570	43	6
Tropicoseius heliconiae	501	17	6	535	21	6
Tropicoseius kaliszewskii	655	52	6	627	8	6
Tropicoseius klepticos	559	8	6	577	8	6
Tropicoseius kressi	469	14	6	488	15	6
Tropicoseius naeemi	674	3	3	642	12	6
Tropicoseius ochoai	500	11	6	492	21	6
Tropicoseius ornatus	559	32	6	569	27	6
Tropicoseius phoreticus	668	6	6	582	15	6
Tropicoseius rowelli	674	44	6	640	17	6
Tropicoseius steini	661.5	30	6	633	7	6
Tropicoseius trinitatis	494	16	6	506	15	6
Tropicoseius uniformis	497	25	6	519	16	6
Tropicoseius venezuelensis	526	9	6	529	20	6
Tropicoseius wetmorei	541	15	6	526	21	6

Note: Tabled values are arithmetic means and standard deviations.

APPENDIX B

Table B1: Body size (mass in g) and bill length (exposed culmen in cm) for males and females of 154 species of hummingbirds

| Hummingbird species | Male[a] | | | | | Female[a] | | | | |
| | Weight | | Bill | | | Weight | | Bill | | |
	Mean	SD	Mean	SD	*n*	Mean	SD	Mean	SD	*n*
Doryfera johannae	4.1	.0	2.68	.00	1	3.5	.0	2.82	.00	1
Doryfera ludovicae	6.0	1.0	3.42	.19	2	5.2	.0	3.59	.00	1
Glaucis hirsuta	7.7	.0	3.25	.00	1	5.7	.0	2.78	.00	1
Threnetes leucurus	6.5	.0	2.77	.00	1	5.7	.5	2.93	.04	2
Threnetes ruckeri	6.3	.0	2.84	.00	1	5.0	.0	3.15	.00	1
Phaethornis yaruqui	6.1	.1	4.33	.04	2	5.1	.0	3.71	.00	1
Phaethornis guy	4.9	.5	3.92	.21	6	4.9	.5	3.65	.29	6
Phaethornis syrmatophorus	5.4	.2	4.02	.06	2	5.6	1.1	3.86	.51	2
Phaethornis superciliosis	6.6	.6	4.21	.20	2	5.4	.0	3.59	.00	1
Phaethornis bourcieri	4.2	.0	2.98	.00	1	3.9	.0	2.80	.00	1
Phaethornis koepckeae	5.5	.0	3.72	.00	1	4.6	.0	3.29	.00	1
Phaethornis philippi	4.8	.0	3.46	.00	1	4.0	.0	3.05	.00	1
Phaethornis subochraceus	4.0	.0	2.99	.00	1	3.6	.0	2.57	.00	1
Phaethornis ruber	2.1	.0	2.20	.00	1	2.4	.0	2.13	.00	1
Phaethornis longuemareus	2.4	.0	2.32	.00	1	2.0	.0	1.96	.00	1
Eutoxeres aquila	10.0	.7	2.86	.49	2	9.5	.0	2.41	.00	1
Eutoxeres condamini	11.0	.0	2.79	.00	1	10.0	.0	2.69	.00	1
Phaeochroa cuvierii	9.3	1.0	1.98	.10	2	8.0	.0	2.03	.00	1
Campylopterus curvipennis	6.7	.0	2.36	.00	1	7.1	.0	2.46	.00	1
Campylopterus largipennis	9.8	.0	2.54	.00	1	7.5	.0	2.83	.00	1
Campylopterus rufus	9.0	.0	2.83	.00	1	6.4	.0	2.74	.00	1
Campylopterus hemileucurus	11.8	.6	2.73	.33	5	8.9	1.1	2.99	.18	4
Campylopterus villaviscencio	8.5	.0	2.70	.00	1	6.6	.0	2.89	.00	1
Florisuga mellivora	7.6	.4	1.83	.27	2	6.8	.7	1.82	.16	3
Colibri delphinae	7.2	.0	1.84	.00	1	5.3	.0	1.63	.00	1
Colibri thalassinus	5.3	.1	2.16	.17	2	5.0	.0	2.36	.00	1
Colibri coruscans	8.0	.0	2.24	.00	1	6.5	.0	2.15	.00	1
Anthracothorax prevostii	7.0	.0	2.42	.00	1	6.8	.0	2.71	.00	1
Anthracothorax nigricollis	7.6	.0	2.67	.00	1	6.6	.0	2.25	.00	1
Klais guimeti	2.5	.7	1.13	.01	2	2.3	.0	1.16	.00	1
Paphosia helenae	2.6	.0	1.14	.00	1	2.5	.0	1.19	.00	1
Popelairia langsdorffi	2.8	.0	1.19	.00	1	2.2	.0	1.12	.00	1
Chlorostilbon mellisugus	3.0	.0	1.62	.00	1	2.7	.0	1.51	.00	1
Chlorostilbon aureoventris	3.4	.0	1.84	.00	1	2.8	.0	1.79	.00	1
Chlorostilbon canivetii	2.6	.0	1.43	.00	2	2.9	.1	1.39	.16	2
Chlorostilbon gibsoni	2.8	.2	1.44	.16	2	3.0	.0	1.51	.00	1
Cynanthus sordidus	4.2	.0	2.00	.00	1	3.4	.0	2.04	.00	1
Cynanthus latirostris	3.2	.0	2.09	.00	1	3.4	.0	2.09	.00	1
Thalurania furcata	4.9	.0	1.98	.00	1	4.2	.0	2.13	.00	1
Panterpe insignis	6.1	.4	1.84	.06	7	5.0	.0	1.82	.00	1
Damophila julie	3.3	.0	1.29	.00	1	3.9	.0	1.51	.00	1
Hylocharis xantusii	3.1	.0	1.69	.00	1	3.2	.0	1.70	.00	1
Hylocharis leucotis	4.6	.0	1.76	.00	1	3.5	.0	1.57	.00	1
Hylocharis eliciae	4.2	.0	1.55	.00	1	3.6	.0	1.74	.00	1
Hylocharis cyanus	3.4	.0	1.84	.00	1	3.8	.0	1.86	.00	1
Hylocharis chrysura	4.3	.0	1.77	.00	1	4.2	.0	1.80	.00	1
Hylocharis grayi	5.9	.0	2.08	.00	1	5.5	.0	2.08	.00	1

Table B1: (*Continued*)

| | Male[a] | | | | | Female[a] | | | | |
| | Weight | | Bill | | | Weight | | Bill | | |
Hummingbird species	Mean	SD	Mean	SD	n	Mean	SD	Mean	SD	n
Chrysuronia oenone	5.5	.0	1.99	.00	1	4.8	.0	2.18	.00	1
Goethalsia bella	3.0	.0	1.64	.00	1	3.8	.0	1.72	.00	1
Trochilus polytmus	5.2	.0	1.83	.00	1	4.1	.0	1.98	.00	1
Polytmus guainumbi	5.6	.0	2.32	.00	1	5.4	.0	2.33	.00	1
Leucippus baeri	4.4	.0	2.08	.00	1	4.2	.0	1.93	.00	1
Leucippus taczanowskii	7.2	.0	2.17	.00	1	6.0	.0	2.28	.00	1
Leucippus chlorocercus	5.3	.0	1.77	.00	1	4.8	.0	1.77	.00	1
Taphrospilus hypostictus	7.4	.0	1.95	.00	1	6.5	.0	2.22	.00	1
Amazilia viridicauda	6.2	.0	1.88	.00	1	5.6	.0	2.10	.00	1
Amazilia candida	4.5	.0	1.77	.00	1	3.0	.0	1.76	.00	1
Amazilia fimbriata	5.1	.1	1.81	.14	2	4.7	.0	2.11	.00	1
Amazilia lactea	5.4	.1	1.87	.01	2	4.6	.0	1.98	.00	1
Amazilia amabilis	3.9	.0	1.75	.00	1	2.6	.0	1.58	.00	1
Amazilia rosenbergi	3.4	.0	2.16	.00	1	3.5	.0	2.10	.00	1
Amazilia franciae	4.7	.0	2.18	.00	1	5.1	.0	2.30	.00	1
Amazilia cyanocephala	6.5	.0	1.99	.00	1	5.0	.0	1.76	.00	1
Amazilia beryllina	4.8	.0	1.77	.00	1	4.8	.0	1.94	.00	1
Amazilia saucerrottei	4.5	.5	1.70	.11	5	4.7	.0	1.84	.00	1
Amazilia tobaci	4.9	.0	1.83	.00	1	4.6	.0	1.70	.00	1
Amazilia rutila	5.0	.0	2.34	.00	1	3.4	.0	1.94	.00	1
Amazilia yucatanensis	4.5	.0	1.78	.00	1	3.7	.0	1.84	.00	1
Amazilia tzacatl	5.3	.2	1.95	.14	6	4.8	.5	1.96	.13	6
Amazilia amazilia	3.9	.0	1.68	.00	1	3.8	.0	1.85	.00	1
Amazilia viridifrons	5.5	.0	1.88	.00	1	5.3	.0	2.16	.00	1
Eupherusa eximia	4.6	.1	1.83	.07	5	4.4	.0	1.84	.00	1
Eupherusa cyanophrys	5.4	.0	1.76	.00	1	4.1	.0	1.95	.00	1
Chalybura buffonii	6.5	.0	2.28	.00	1	7.0	.0	2.12	.00	1
Lampornis clemenciae	7.8	.0	2.24	.00	1	6.1	.0	2.62	.00	1
Lampornis amethystinus	6.1	.0	2.26	.00	1	6.0	.0	2.34	.00	1
Lampornis viridipallens	6.2	.0	2.20	.00	1	4.5	.7	2.03	.16	2
Lampornis castaneoventris	5.6	.0	2.01	.00	1	5.1	.0	2.17	.00	1
Lamprolaima rhami	9.5	.0	1.60	.00	1	7.0	.0	1.53	.00	1
Adelomyia melanogenys	3.6	.6	1.47	.21	2	2.8	.0	1.38	.00	1
Phlogophilus hemileucurus	2.3	.0	1.63	.00	1	2.8	.0	1.71	.00	1
Phlogophilus harterti	2.7	.0	1.57	.00	1	2.6	.0	1.58	.00	1
Heliodoxa aurescens	5.4	.0	2.03	.00	1	6.1	.0	2.09	.00	1
Heliodoxa rubinoides	8.0	.4	2.24	.08	5	7.6	.3	2.34	.10	6
Heliodoxa leadbeateri	7.6	.0	2.17	.00	1	6.4	.0	2.44	.00	1
Heliodoxa jacula	8.2	.0	2.07	.00	1	8.0	.0	2.22	.00	1
Heliodoxa schreibersii	9.0	.0	2.32	.00	1	7.7	.0	2.26	.00	1
Heliodoxa gularis	6.5	.0	2.64	.00	1	6.8	.0	2.48	.00	1
Heliodoxa branickii	5.4	.0	2.19	.00	1	5.2	.0	2.30	.00	1
Eugenes fulgens	11.0	.0	3.08	.00	1	8.3	1.1	3.62	.17	3
Oreotrochilus estella	8.5	2.1	1.72	.15	5	8.0	.0	1.75	.00	1
Patagona gigas	22.0	.0	3.63	.00	1	19.8	.0	3.36	.00	1
Aglaeactis cupripennis	7.9	.8	1.82	.04	3	8.2	.0	2.00	.00	1
Aglaeactis castelnaudii	7.2	.0	1.87	.00	1	6.2	.0	1.90	.00	1
Aglaeactis pamela	5.2	.0	1.69	.00	1	5.8	.0	1.92	.00	1
Lafresnaya lafresnayi	4.9	.0	2.26	.00	1	4.9	.6	2.56	.01	2
Pterophanes cyanopterus	10.0	.0	2.92	.00	1	9.8	.0	2.94	.00	1

Table B1: (*Continued*)

Hummingbird species	Male[a] Weight Mean	SD	Bill Mean	SD	n	Female[a] Weight Mean	SD	Bill Mean	SD	n
Coeligena coeligena	7.5	.0	2.60	.00	1	6.1	.0	2.86	.00	1
Coeligena torquata	7.6	.3	3.19	.14	6	6.8	.5	3.48	.16	6
Coeligena phalerata	6.8	.0	2.63	.00	1	5.4	.0	3.16	.00	1
Coeligena lutetiae	8.6	.0	3.30	.00	1	7.8	.0	3.29	.00	1
Coeligena violifer	8.1	.0	3.75	.00	1	7.0	.0	3.52	.00	1
Coeligena iris	7.0	1.5	2.71	.13	2	6.2	.0	3.23	.00	1
Ensifera ensifera	11.0	.7	8.26	2.26	2	11.5	.0	8.02	.00	1
Sephanoides sephaniodes	5.7	.4	1.48	.79	15	4.7	.4	1.60	1.20	12
Sephanoides fernandensis	10.9	.6	1.54	.49	15	7.0	.0	1.55	.27	2
Boissonneaua flavescens	8.7	.0	1.80	.00	1	8.6	.0	1.63	.00	1
Boissonneaua matthewsii	7.8	.0	1.76	.00	1	6.8	.0	1.92	.00	1
Heliangelus amethysticollis	5.7	.0	1.59	.00	1	5.1	.1	1.69	.01	2
Heliangelus exortis	4.4	.0	1.45	.00	1	4.4	.0	1.70	.00	1
Heliangelus viola	5.8	.0	1.45	.00	1	4.4	.0	1.35	.00	1
Eriocnemis vestitus	5.0	.0	1.77	.00	1	5.0	.0	1.91	.00	1
Eriocnemis luciani	6.3	.0	2.14	.00	1	6.2	.0	1.93	.00	1
Haplophaedia aureliae	5.9	.0	1.83	.00	1	5.2	.0	1.86	.00	1
Ocreatus underwoodii	3.0	.0	1.30	.00	1	3.1	.0	1.22	.00	1
Lesbia victoriae	5.1	.0	1.50	.00	1	4.5	.0	1.44	.00	1
Lesbia nuna	3.9	.0	1.04	.00	1	3.6	.0	1.04	.00	1
Sappho sparganura	6.3	.3	2.17	.35	2	5.6	.0	2.29	.00	1
Polyonymus caroli	4.4	.0	2.05	.00	1	4.7	.0	2.00	.00	1
Ramphomicron microrhynchum	3.8	.2	.73	.03	3	3.3	.4	.72	.02	2
Metallura odomae	5.4	.0	1.61	.00	1	5.1	.0	1.56	.00	1
Metallura phoebe	5.5	.0	1.82	.00	1	5.7	.0	1.50	.00	1
Metallura theresiae	4.9	.1	1.22	.05	2	4.7	.0	1.21	.00	1
Metallura aeneocauda	4.9	.4	1.71	.03	2	5.2	.1	1.81	.06	2
Metallura eupogon	5.5	.0	1.49	.00	1	4.8	.0	1.38	.00	1
Metallura williami	4.8	.0	1.18	.00	1	4.3	.0	1.36	.00	1
Metallura tyrianthina	3.8	.2	1.06	.06	5	3.7	.6	1.11	.11	5
Chalcostigma ruficeps	3.8	.0	1.12	.00	1	3.0	.0	1.08	.00	1
Chalcostigma stanleyi	6.0	.0	1.09	.00	1	4.5	.0	.98	.00	1
Chalcostigma herrani	6.0	.0	1.44	.00	1	5.2	.0	1.45	.00	1
Aglaiocercus kingi	5.1	.8	1.41	.05	2	4.7	.6	1.52	.01	2
Oreonympha nobilis	7.0	.0	2.34	.00	1	7.0	.0	2.33	.00	1
Schistes geoffroyi	4.0	.4	1.39	.08	2	3.5	.0	1.32	.00	1
Heliothryx aurita	6.0	.0	1.76	.00	1	6.2	.0	1.87	.00	1
Heliomaster longirostris	6.8	.0	3.63	.00	1	6.8	.0	3.31	.00	1
Rhodopis vesper	4.0	.0	1.74	.00	1	3.0	.0	2.16	.00	1
Thaumastura cora	2.0	.0	1.28	.00	1	1.8	.0	1.35	.00	1
Philodice bryantae	3.3	.0	1.67	.00	1	3.7	.0	1.68	.00	1
Calothorax lucifer	3.1	.0	2.15	.00	1	3.2	.0	1.93	.00	1
Calothorax pulcher	2.2	.0	1.85	.00	1	2.8	.0	1.77	.00	1
Archilochus colubris	2.9	.3	1.55	.06	6	3.2	.4	1.72	.10	6
Archilochus alexandri	3.5	.0	1.92	.00	1	3.7	.0	1.85	.00	1
Calliphlox amethystina	3.0	.0	1.64	.00	1	3.0	.0	1.64	.00	1
Calypte anna	5.8	.0	1.65	.00	1	4.2	.0	1.84	.00	1
Calypte costae	3.4	.0	1.54	.00	1	3.4	.0	1.61	.00	1

Table B1: (*Continued*)

Hummingbird species	Male[a]					Female[a]				
	Weight		Bill			Weight		Bill		
	Mean	SD	Mean	SD	*n*	Mean	SD	Mean	SD	*n*
Stellula calliope	2.5	.0	1.50	.00	1	3.2	.0	1.45	.00	1
Myrtis fanny	2.3	.0	1.72	.00	1	2.3	.0	1.92	.00	1
Acestrura mulsant	3.8	.0	1.62	.00	1	4.5	.0	1.67	.00	1
Selasphorus platycercus	3.0	.0	1.53	.00	1	3.3	.0	1.65	.00	1
Selasphorus rufus	3.6	.0	1.60	.00	1	3.9	.0	1.67	.00	1
Selasphorus sasin	2.9	.0	1.54	.00	1	3.2	.0	1.55	.00	1
Selasphorus flammula	2.6	.0	1.12	.00	1	2.6	.0	1.06	.00	1
Selasphorus simoni	3.2	.0	1.20	.00	1	3.2	.0	1.21	.00	1
Selasphorus scintilla	2.0	.0	1.17	.00	1	2.3	.0	1.21	.00	1

[a] Tabled values are arithmetic means and standard deviations. Because sample sizes are small for most species in this data set, these data should be used only for the study of broad statistical patterns. Reliability of means for individual species should be judged according to sample size. The sequence of genera and species follows Peters (1945).

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