RESEARCH ARTICLE

Becoming Different But Staying Alike: Patterns of Sexual Size and Shape Dimorphism in Bills of Hummingbirds

Chelsea M. Berns · Dean C. Adams

Abstract Hummingbirds are known for their distinctive patterns of sexual dimorphism, with many species exhibiting sex-related differences in various ecologically-relevant traits, including sex-specific differences in bill shape. It is generally assumed that such patterns are consistent across all hummingbird lineages, yet many taxa remain understudied. In this study we examined patterns of sexual size and sexual shape dimorphism in bills of 32 of 35 species in the monophyletic *Mellisugini* lineage. We also compared patterns of bill size dimorphism in this group to other hummingbird lineages, using data from 219 hummingbird species. Overall, the presence and degree of sexual size dimorphism was similar across all hummingbird lineages, with the majority of *Mellisugini* species displaying female-biased sexual size dimorphism, patterns that remain unchanged when analyzed in a phylogenetic context. Surprisingly however, we found that sexual dimorphism in bill shape was nearly absent in the *Mellisugini* clade, with only 3 of the 32 species examined displaying bill shape dimorphism. Based on observations in other hummingbird lineages, the lack of sexual shape dimorphism in *Mellisugini* is particularly unusual. We hypothesize that the patterns of sexual size dimorphism observed here may be the consequence of differential selective forces that result from competition for ecological resources. We further propose that an influential mechanism underlying shape dimorphism is competition and niche segregation. Taken together, the evolutionary changes in patterns of sexual shape dimorphism observed in *Mellisugini* suggest that the evolutionary trends of sexual dimorphism in the *Trochilidae* are far more dynamic than was previously believed.

Introduction

Understanding the origin of phenotypic diversity is a major focus of evolutionary research, and patterns of sexual dimorphism represent a particularly intriguing component of this diversity. Sexual dimorphism is exhibited throughout the animal kingdom (see e.g., Butler et al. 2000) and is displayed in a myriad of ways, including sex-specific behavior and vocalizations (Potter et al. 2005), sexual differences in body size (Fairbairn 1997), coloration (Stuart-Fox and Ord 2004), and other morphological traits (Berns and Adams 2010; Butler et al. 2007; Worthington et al. 2012). Darwin (1871) drew attention to these patterns and suggested that morphology can vary between the sexes due to the action of sexual selection operating in one or more ways, which subsequently enhances sex-specific fitness in relation to reproduction (Darwin 1871; Jones and Ratterman 2009).

A number of mechanisms have been proposed to explain the evolution of sexual dimorphism. For example, sexual selection can generate sex-specific differences as the sexes evolve in distinct directions that maximize their own reproductive success (Darwin 1871; Andersson 1994). Alternatively, ecological mechanisms such as competition for resources, may exert distinct selective forces on the sexes, resulting in the evolution of sexual dimorphism (Selander 1972; Hedrick and Temeles 1989; Slatkin 1984).

C. M. Berns (✉) · D. C. Adams
Department of Ecology, Evolution and Organismal Biology,
Iowa State University, 251 Bessey Hall, Ames, IA 50011, USA
e-mail: cmberns@iastate.edu

Here, intraspecific competition in species-poor communities may allow divergent selection between the sexes (rather than between species) to result in niche segregation between males and females (i.e., intersexual niche packing: sensu Butler et al. 2000). A third possible mechanism that may enhance sexual dimorphism in some species is the influence of sex-specific divergence in response to environmental gradients, where males and females exhibit differential responses to the same environmental selective pressures (Hendry et al. 2006). For instance, in guppies (*Poecilia reticulata*), open canopy sites resulted in selection for smaller heads and distended abdomens in females but not in males, whereas both sexes in high flow sites had small heads and deeper caudal peduncles (Hendry et al. 2006). Likewise, weaker latitudinal clines in male houseflies (*Musca domestica*) but not in females suggest sex-specific responses to food resource abundance which may vary clinally (Alves and Belo 2002).

Hummingbirds (family *Trochilidae*) offer a unique opportunity to study patterns of sexual dimorphism and elucidate the underlying mechanisms responsible for these patterns. This monophyletic lineage of 338 currently recognized species (McGuire et al. 2007, 2009; Birdlife.org 2012) has been a model taxon for the study of sexual dimorphism, as these species exhibit patterns such as dimorphic plumage (Darwin 1871; Bleiweiss 1992, 1997) sex-specific behavior (Feinsinger and Colwell 1978, Kodric-Brown and Brown 1978), and ornamentation (Evans et al. 1995; Zusi and Gill 2009), among others. Several hypotheses have been proposed to explain the evolution of this sexual dimorphism in this group. For example, the remarkable ornamentation that males sometimes exhibit, such as the tail 'boots' of the hummingbird *Ocreatus underwoodii* (Booted Racket-tail) or tail length in *Phaethornis superciliosus* (Long-tailed Hermit) may be due to 'Fisherian runaway selection', where females prefer males that exhibit more extreme phenotypes within a population, which over evolutionary time become increasingly exaggerated despite the potential fitness costs to the males themselves (Andersson 1994). Further, differential plumage coloration between the sexes in some species is thought to be the result of females selecting males that exhibit superior characteristics (i.e., the 'good genes' hypothesis: sensu Darwin 1871).

Hummingbirds also exhibit sexual dimorphism in both body size and bill morphology. For example, in hummingbirds bill morphology is under strong selection pressures due to its role in foraging, and differential foraging among species is thought to be a major cause of diversification in trophic structures among species (Darwin 1871; see also Feinsinger 1978; Brown and Bowers 1985; Collins and Paton 1989; Bleiweiss 1998). Additionally, males and females of some species forage differently (Carpenter et al.

1991; Temeles and Kress 2003) and many of these species also display sexual dimorphism in bill size and bill curvature (Temeles et al. 2010). Recently, quantitative support for Darwin's hypothesis is found in some species where there is a direct link between sexual differences in bill morphology in *Eulampis jugularis* (Purple-throated Carib) and patterns of sex-specific foraging. Here, males and females of this species forage on distinct resources, and the bill morphology of each sex is correlated with the morphology of the flower that each feeds from (the 'ecological causation hypothesis' sensu Temeles et al. 2010). Similar patterns have been observed in other clades of hummingbirds, where differences in bill sexual size and shape dimorphism have a direct link to feeding ecology (Temeles et al. 2010). Together, these findings suggest that, not only is sexual dimorphism in bill morphology the evolutionary result of various ecological processes and sex-specific adaptations to foraging (Temeles et al. 2010), but also that bill size and shape dimorphism is common throughout hummingbirds.

Much of the prior work on sexual dimorphism in *Trochilidae* has focused on species in tropical lineages known to display sexual dimorphism, and have concentrated largely on dimorphism in bill size and bill shape (curvature: see Temeles et al. 2010; Rodríguez-Flores and Stiles 2005). Based on these studies, it has generally been assumed that sexually-dimorphic patterns in bill shape are consistent across *Trochilidae* due to the tight coevolutionary link between bill morphology and flower morphology in this group, yet little work on sexual dimorphism has been performed in taxa outside of a few focal lineages (e.g., Bleiweiss 1999; Temeles et al. 2005). For example, a few studies have examined sexual dimorphism in bill morphology in select species in the *Mellisugini* clade, finding sexual size dimorphism of the bill in *Selasphorus rufus* (Temeles and Roberts, 1993), *S. scintilla* and *S. flammula* (Stiles 1983). However the prevalence of such patterns in bill morphology remains largely unknown, as most of the 35 species in the *Mellisugini* clade have yet to be examined. Recently, it was observed that two sister species within the *Mellisugini* clade, *Archilochus alexandri* and *A. colubris*, differ in their patterns of dimorphism in bill morphology (Berns and Adams 2010), where both species display significant bill size dimorphism, but only *A. colubris* exhibits bill shape dimorphism. These results were surprising, as prior work on *Trochilidae* in other clades suggested that shape dimorphism in bill curvature is common (bill curvature is one aspect of bill shape: Temeles et al. 2010).

Given these findings, we conducted a broader study of species in the *Mellisugini* clade with the purpose of addressing the following questions. First, is sexual dimorphism in bill size common across species in the *Mellisugini*

clade? Based on previous studies, we predicted that the majority of species in the *Mellisugini* clade would exhibit primarily female-biased (that is, the bill of females is larger than males) bill size dimorphism. Second, is the presence and pattern of sexual *shape* dimorphism in the *Mellisugini* clade concordant with those found across all *Trochilidae*? Studies of other clades have found sexual curvature dimorphism to be common, therefore we predicted the same pattern would be present in the *Mellisugini* clade. We addressed these questions in a phylogenetic context using both linear measurements and landmark-based geometric morphometric techniques to quantify sexual size and shape dimorphism in the bill morphology in 32 of the 35 *Mellisugini* species (McGuire et al. 2009). We then compared patterns of bill size dimorphism in the *Mellisugini* lineage to those found in other *Trochilidae* lineages, using a dataset collected from prior studies published in the literature (219 species).

Methods

Specimen Information

We measured 1,347 hummingbirds representing 32 of the 35 species in the *Mellisugini* lineage, obtained from 14 museum collections (see "Appendix"). All specimens included in this study were adults of known sexes, and a roughly equal proportion of males and females of each species were examined (722 males, 625 females; see "Appendix").

Morphometrics

We obtained digital images of the left-lateral side of the head and bill of each specimen using a Nikon DXM-1200 digital camera mounted on a Nikon SMZ 1500 stereomicroscope (a Nikon D-90 was used to collect images obtained at museums, as the stereomicroscope system was not easily transportable). Each photograph included a ruler in order to account for size in the analyses, and the birds were placed in the same position on a modeled clay surface. From these images, two sets of data were obtained. First, the exposed culmen was measured on each specimen (culmen length: CL: Fig. 1a; e.g., Bleiweiss 1999; Colwell 2000) and was treated as a measure of bill size for each individual. Culmen length and bill centroid size were highly correlated (r = 0.97), so only CL is used here as a measure of size. To place our findings in a broader phylogenetic context, we combined these linear measurements with additional bill length data that we obtained from the literature, yielding a total dataset of CL from 219 hummingbird species (see "Appendix") across the family

Trochilidae. Second, bill shape was obtained from each image using landmark-based geometric morphometric methods (Rohlf and Marcus 1993; Adams et al. 2004). These methods allow for quantification of shape after the effects of non-shape variation (position, orientation, and scale) have been mathematically held constant. For this approach we first digitized the locations of 10 biologically homologous landmarks from the images of each specimen. Additionally, we included 15 sliding semilandmarks along the boundary curve of each bill to represent its shape and curvature (see Berns and Adams 2010) using TPSDig 2 (Rohlf 2010).

Together, the 25 landmarks and semilandmarks were subjected to a Generalized Procrustes Analysis (GPA: Rohlf and Slice 1990). This least-squares procedure translates all specimens to the origin, scales them to unit centroid size, and optimally rotates them to minimize the total sums-of-squares deviations of the landmark coordinates from all specimens to the average configuration. During this procedure, semilandmarks were allowed to slide along their tangent directions (Bookstein et al. 1999; Gunz et al. 2005) so as to minimize Procrustes distance between specimens (see e.g., Serb et al. 2011). After superimposition, the aligned Procrustes shape coordinates describe the location of each specimen in a curved space related to Kendall's shape space (Rohlf 1999). These were then projected orthogonally into a linear tangent space yielding Kendall's tangent space coordinates (Dryden and Mardia 1993, 1998; Rohlf 1999), which were treated as a set of shape variables for further analyses of shape variation and covariation (e.g., Adams et al. 2007; Adams and Nistri 2010; Adams 2010).

Patterns of Sexual Size Dimorphism

We performed two sets of analyses to assess patterns of sexual dimorphism of bill size. First, to determine whether bill size and size dimorphism differed among species in the *Mellisugini* clade, we used our culmen length data and a two-factor analysis of variance (ANOVA); where variation in bill size (culmen length) was explained by species, sex, and their interaction. A significant species × sex term would imply that there was a significant difference in the degree of sexual size dimorphism among species. Due to the large differences in variance within the species × sex groups, we also ran ANOVAs for each species separately to determine whether sexual dimorphism was present in each species.

Second, we performed a family-wide analysis of bill size dimorphism, using the bill size measurements of the 32 species in the *Mellisugini* clade as above, as well measurements of an additional 187 species obtained from literature (Temeles et al. 2010; Colwell 2000; Bleiweiss 1999). In total, this analysis included 219 of 338

Fig. 1 **a** Exposed culmen representing bill length. **b** Landmark-based geometric morphometrics. *Open circles* designate biologically homologous landmarks and *filled circles* represent sliding semilandmarks. **c** Representative individual from the species with extreme bill curvature (*Calothorax lucifer*), and **d** from the species with the straight bills (*Archilochus colubris*)
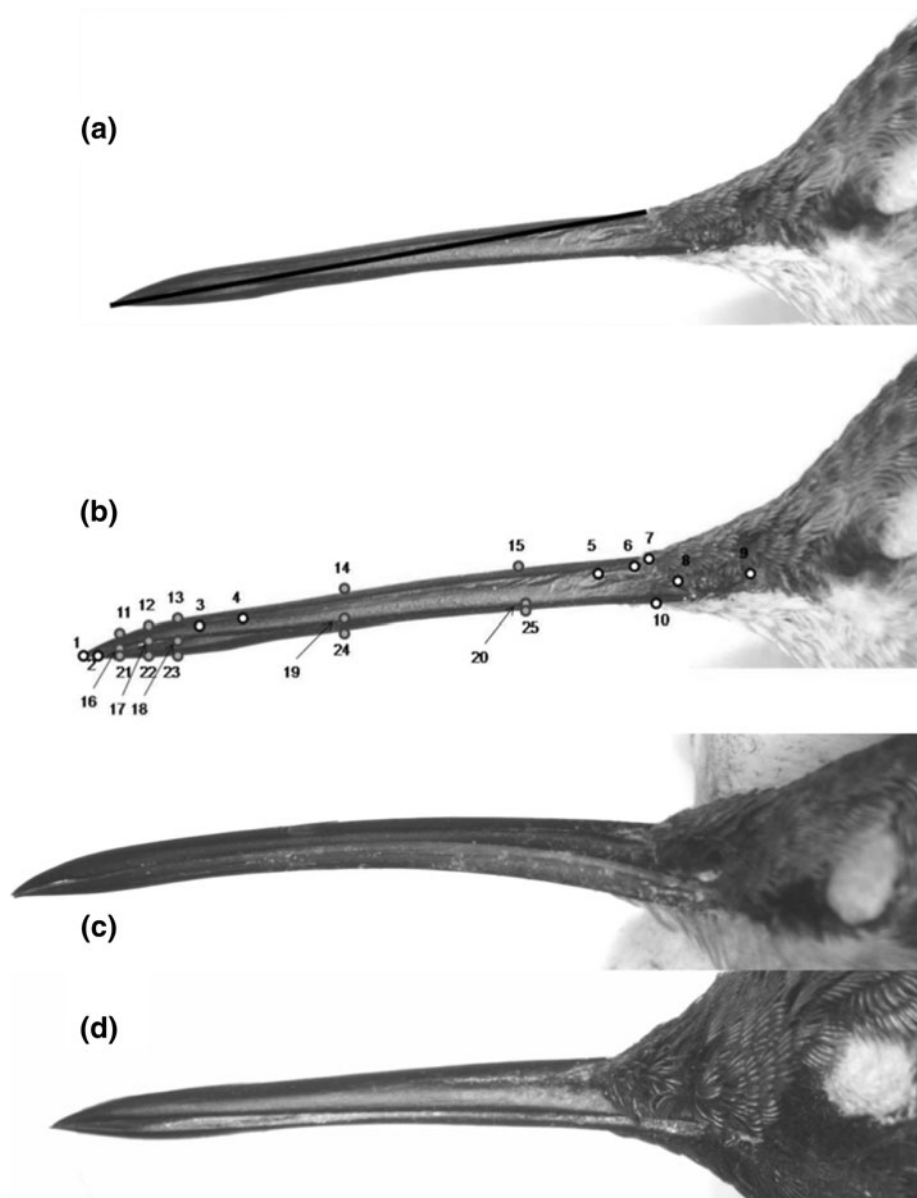
hummingbird species (Birdlife.org), or 65 % of the current diversity of the group. From these measurements, the average male and female bill sizes ($\overline{CL}_M$, $\overline{CL}_F$), were obtained. Next, measures of sexual size dimorphism were estimated as the Lovich-Gibbons ratio (Lovich and Gibbons 1992), which is found as: $(\overline{CL}_F/\overline{CL}_M - 1)*(1)$ for species where the female is the larger sex, and $(\overline{CL}_M/\overline{CL}_F - 1)*(-1)$ when the male is the larger sex (see Stephens and Wiens 2009; Temeles et al. 2010). Using these size-dimorphism ratios, we performed an ANOVA to determine whether the seven major hummingbird clades for which we had information (sensu McGuire et al. 2009) differed in their patterns of sexual size dimorphism. In addition, we performed a phylogenetic ANOVA (Garland et al. 1993) on the same ratio data to account for

non-independence due to shared evolutionary history. For this approach, the evolutionary relationships among species were based on the current molecular phylogeny for hummingbirds (McGuire et al. 2007). Finally, these analyses were repeated on the simple ratio of male to female bill size ($\overline{CL}_M$, $\overline{CL}_F$), from which statistically similar results were obtained (results not shown).

Patterns of Sexual Shape Dimorphism

To determine whether bill shape and shape dimorphism differed among species in the *Mellisugini* clade we performed a two-factor multivariate analysis of variance (MANOVA), where variation in bill shape was explained by species, sex, and species × sex interaction. A significant

species × sex term would imply that there were differences in the degree of sexual shape dimorphism among species. As with the ANOVA, we ran a separate permutational-MA-NOVA with 9,999 iterations (Anderson 2001) for each species to examine the degree of sexual shape dimorphism within each species. We then calculated vectors of sexual shape dimorphism for each species as the difference between

male and female means (see Berns and Adams 2010), and used a permutation procedure with 9,999 iterations to determine whether the degree of sexual shape dimorphism differed between species (for details see Adams and Collyer 2007, 2009; Collyer and Adams 2007). Here, the observed sexual shape dimorphism for each species was quantified as the multivariate vector connecting male and female means

Table 1 (A) Statistical results from ANOVA on culmen length for 32 species of hummingbird in the *Mellisugini* lineage. (B) ANOVA comparing male versus female culmen lengths for each of 32 species of *Mellisugini* hummingbirds

(A) Effects	Mean squares	Approx. F	df	P
Species	493.06	393.3193	31	**<0.001**
Sex	240.74	192.0392	1	**<0.001**
Species × sex	2.66	2.1192	31	**<0.001**
Residuals	1.25		1,283	

(B) Species	Mean squares	Approx. F	df	P	Ratio
Archilochus alexandri	33.165	19.070	1	**<0.001**	0.038
Archilochus colubris	62.972	125.479	1	**<0.001**	0.119
Atthis Heliosa	7.102	20.873	1	**<0.001**	0.086
Calliphlox amethystina	1.144	1.283	1	0.269	0.031
Calliphlox bryantae	3.936	6.626	1	**0.017**	0.053
Calliphlox evelynae	1.616	1.012	1	0.324	−0.008
Calliphlox mitchelli	6.236	9.152	1	**0.005**	0.069
Calothorax lucifer	2.958	2.585	1	0.119	0.032
Calothorax pulcher	25.477	10.599	1	**0.003**	0.123
Calypte anna	7.319	5.563	1	**0.025**	0.086
Calypte costae	4.664	5.128	1	**0.032**	0.051
Chaetocercus astreans	7.459	19.981	1	**<0.001**	0.082
Chaetocercus bombus	2.580	6.552	1	**0.023**	0.064
Chaetocercus heliodor	8.158	7.389	1	**0.011**	0.074
Chaetocercus jourdanii	5.939	6.592	1	**0.016**	0.067
Chaetocercus mulsanti	15.844	13.059	1	**0.001**	0.083
Doricha eliza	2.581	5.664	1	**0.033**	0.041
Doricha enicura	9.781	2.660	1	0.118	0.084
Mellisuga helenae	7.454	11.726	1	**0.002**	0.093
Mellisuga minima	5.451	14.684	1	**0.001**	0.091
Microstilbon burmeisteri	9.615	24.023	1	**<0.001**	0.047
Myrmia micrura	7.351	7.384	1	**0.014**	0.088
Myrtis fanny	0.293	0.197	1	0.660	−0.013
Rhodopis vesper	34.673	3.506	1	0.071	0.080
Selasphorus flammula	4.499	7.610	1	**0.009**	0.062
Selasphorus platycercus	11.400	8.092	1	**0.009**	0.074
Selasphorus rufus	14.766	36.033	1	**<0.001**	0.190
Selasphorus sasin	0.065	0.054	1	0.817	0.005
Stellula calliope	2.443	6.788	1	**0.016**	0.059
Selasphorus scintilla	4.896	5.838	1	**0.021**	0.056
Thaumastura cora	7.753	17.005	1	**<0.001**	0.060
Tilmatura dupontii	3.503	8.499	1	**0.007**	0.057

Size dimorphism ratios for each species (expressed as Lovich-Gibbons ratios) are shown. Significant effects are shown in bold

for each species. The length of this vector (i.e., Euclidean distance) corresponds to the magnitude of sexual shape dimorphism exhibited by each species, which were compared using the permutation procedure above to determine the extent to which the degree of sexual shape dimorphism differed among species (see Berns and Adams 2010).

Visualization

Finally, to visualize patterns of bill shape variation, we performed a principal components analysis using the full set of Kendall's tangent space coordinates and plotted the first two PCs, which described the largest amount of shape variation. In this principal components plot we also included vectors connecting male and female means for species that displayed significant sexual shape dimorphism (see "Results" below). We then generated thin-plate spline deformation grids (Bookstein 1991) for phenotypic means of males and females to graphically depict differences in bill shapes for these species, and to facilitate biological interpretation of the observed shape differences within and between them. All analyses were conducted in R version 2.11.1 (R Development Core Team 2010), TpsSpline (Rohlf 2005) and TPSRelW (Rohlf 2004).

Results

Patterns of Sexual Size Dimorphism

Using a two-factor ANOVA on the *Mellisugini* data, we found significant differences in bill size among species, between the sexes, as well as a significant species × sex interaction term (Table 1A). The latter term revealed that the degree of sexual size dimorphism differed significantly among species. When sexual size dimorphism was examined for each species separately, we found that the majority of species (26) displayed significant sexual size dimorphism (Table 1B). Interestingly, we identified considerable variation in the degree of size dimorphism exhibited among species in this group, with a 27-fold difference in the degree of sexual size dimorphism between the species with the least size dimorphism (*Selasphorus sasin*: sexual size dimorphism = 0.0045), and the most dimorphic species (*Calothorax pulcher*: sexual size dimorphism = 0.12257).

When magnitudes of sexual size dimorphism were examined across the entire hummingbird family, we found no difference in the degree of size dimorphism exhibited among clades within *Trochilidae* ($F_{7,211} = 0.632$; $P = 0.7292$), suggesting that all groups displayed a similar degree of size dimorphism. Similarly, no differences among clades were identified when the phylogenetic

relationships among species were taken into consideration ($F_{7,114} = 0.2143$; $P_{rand} = 0.9714$). While all species displayed similar magnitudes of size dimorphism in their bills, overall the majority of species (156 of 219) were female-biased (Fig. 2). Consistent with prior results, some lineages (e.g., *Phaethornithinae*) displayed male-biased size dimorphism for the majority of their species (e.g., Temeles et al. 2010: Fig. 2). However, this was not the case in the *Mellisugini* clade, where 92 % of the species examined (24 of 26) exhibited female-biased size dimorphism (Fig. 2).

Patterns of Sexual Shape Dimorphism

Using a factorial MANOVA, we found that all factors (species, sex, species × sex) explained significant proportions of variation in bill shape (Table 2A). The significant interaction term implied that patterns of sexual shape dimorphism differed among species, and when this was examined separately in each species, we found that only three of 32 species displayed significant shape dimorphism: *Archilochus colubris*, *Selasphorus scintilla*, and *Mellisuga minima* (Table 2B). Thus, in stark contrast to patterns of size dimorphism, and in contrast to patterns of shape dimorphism observed in other hummingbird lineages, very little shape dimorphism is exhibited in the *Mellisugini* lineage. When patterns of sexual shape dimorphism were compared among these three species, *M. minima* exhibited a significantly greater degree of shape dimorphism (Euclidean distance) than the other two species ($D_{M\ minima} = 0.054$, $D_{A\ colubris} = 0.026$, $D_{S\ scintilla} = 0.041$, $P = 0.001$), whereas *A. colubris* and *S. scintilla* did not differ in the amount of shape dimorphism displayed ($P = 0.19$). Further, the direction of shape dimorphism in morphospace also differed between *M. minima* and both *A. colubris* and *S. scintilla*, ($P = 0.001$, Fig. 3). Thin-plate spline deformation grids revealed that in these species, females have longer, more curved bills at both the tip and main body of the bill relative to the mean, while males have straighter and shorter bills and *M. minima* has the largest magnitude of sexual shape dimorphism (Fig. 3). Thus, the significant sexual shape dimorphism in these species can be generally characterized as females having more curved bills, while males have relatively straighter bills.

Discussion

For centuries, evolutionary biologists have been interested in the phenotypic differences between the sexes and the effect that these patterns have on organismal diversity. Many studies have identified patterns of sexual size and sexual shape dimorphism in hummingbird bill morphology,
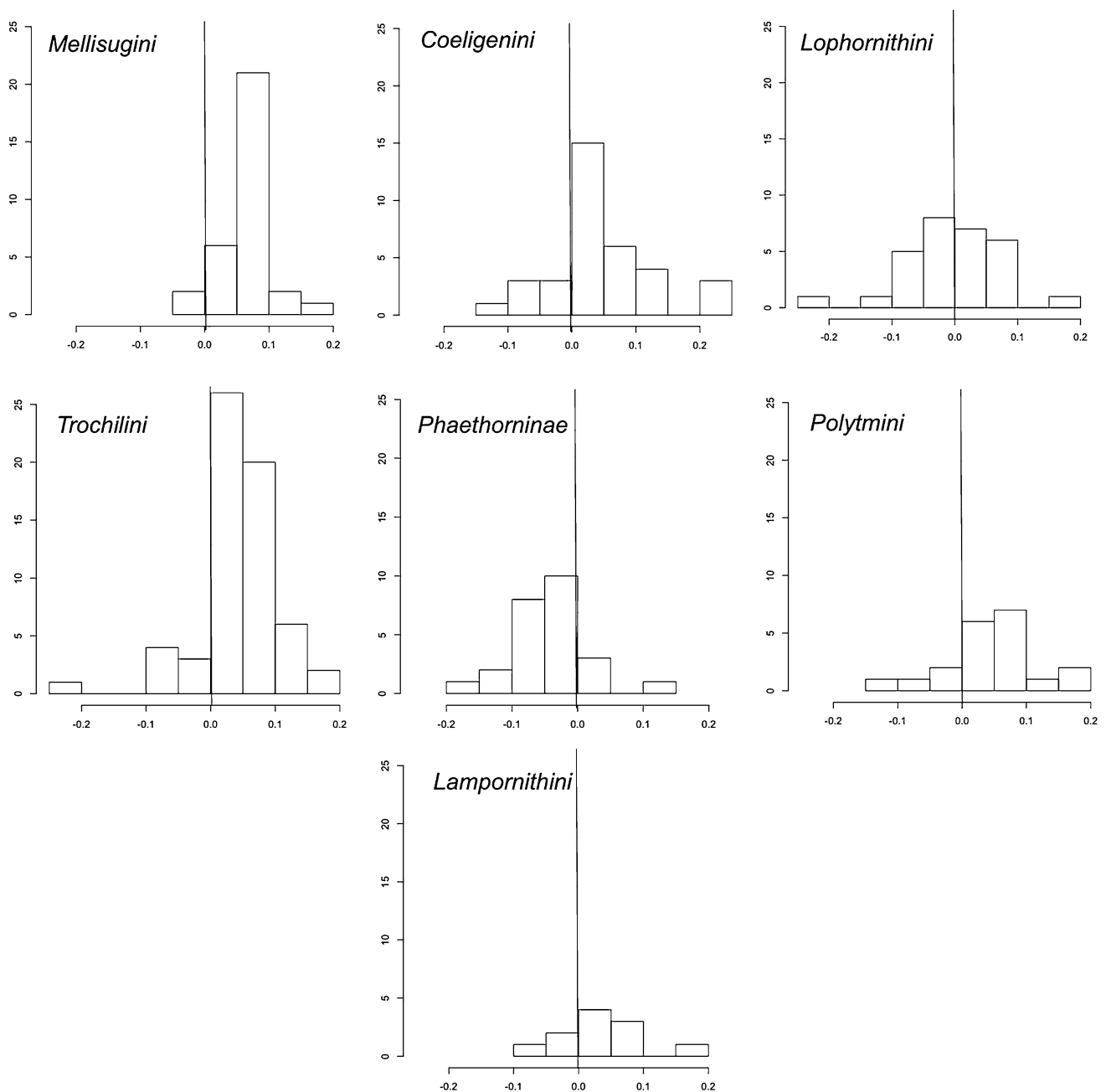
Fig. 2 Histograms displaying the variation of sexual size dimorphism within each clade of hummingbirds. Frequency is on the Y-axis and bill size dimorphism (expressed as the Lovich-Gibbons ratio) is on the X-axis. Those to the left of 0 are male-biased

particularly in species from tropical lineages. However, none have used a phylogenetic context to study sexual shape dimorphism within an entire hummingbird lineage, nor compared patterns of sexual size dimorphism across all hummingbird clades in a phylogenetic context. Based on existing studies of sexual dimorphism in other species, it is generally assumed that the presence of sexual size and sexual shape dimorphism will be found throughout all hummingbird clades. However, while this appears to be the case for sexual size dimorphism of hummingbird bills, our

results show that shape dimorphism in the *Mellisugini* lineage does not follow this general pattern.

Using bill size data for 219 species of Trochilidae, we found that the majority of the species in the *Mellisugini* clade exhibited sexual size dimorphism in similar magnitudes as was observed in other groups (Temeles et al. 2010; Colwell 2000; Bleiweiss1999). Our findings also revealed that the *Mellisugini* lineage is decidedly female-biased in bill sexual size dimorphism, with 92 % of the species examined (24 of 26) displaying larger bills in females as

Table 2 (A) MANOVA analysis of bill shape (Kendall's tangent space coordinates) for 32 species in the *Mellisugini* clade. (B) Results of permutational-MANOVA for those species displaying significant sexual shape dimorphism (*A. colubris*, *S. scintilla* and *M. minima*)

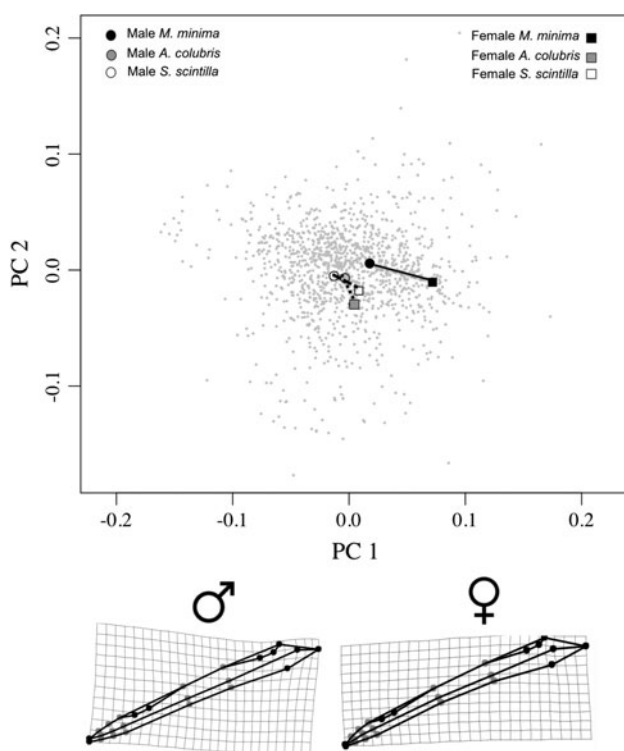| (A) Effects	Pillai's trace	Approx. F	df	P
Species	208.95	160.167	35, 1,167	**<0.001**
Sex	470.97	361.009	1,085, 37,107	**<0.001**
Species × sex	2.24	1.715	1,085, 37,107	**<0.001**
(B) Species		Mean squares	Approx. F	P
Archilochus colubris		0.0137	2.944	**0.04**
Selasphorus scintilla		0.0146	3.005	**0.032**
Mellisuga minima		0.0208	4.965	**0.006**

Significant effects shown in bold

Fig. 3 Principal components plot of bill shape data based on Kendall's tangent space coordinates. Here, all individuals are shown, as well as the male and female means for the three species displaying significant sexual shape dimorphism (*A. colubris*, *S. scintilla and M. minima*). *Lines* connecting *symbols* represent the magnitude of sexual shape dimorphism in each of the 3 species. Thin-plate spline deformation grids of the average female and male bill shape relative to the mean are also presented and have been scaled to a factor of 2 to enhance biological interpretation

compared to males. Thus, the patterns of sexual size dimorphism in *Mellisugini* are concordant with what is observed in other lineages within *Trochilidae* except *Phaethornithinae,* which is male-biased (Fig. 2; also Bleiweiss 1999; Temeles et al. 2010).

The presence and magnitudes of sexual size dimorphism observed here may be the consequence of differential selective forces that result from competition for ecological resources. For example, Bleiweiss (1999) hypothesized that feeding ecology may influence the evolution of male- or female-biased sexual size dimorphism in hummingbirds. In hummingbirds, a longer bill allows feeding from a wide variety of resources whereas a short bill is more efficient in a patch of the same flower. In species where the males are the dominant sex and defend territories, females tend to have longer bills, allowing them to feed from more dispersed resources, whereas males tend to have shorter bills, increasing foraging efficiency in small territories (Bleiweiss 1999). By contrast, in species with lekking mating systems males no longer hold territories, and must instead compete with other hummingbirds. In this case, the male bill tends to be longer to allow them to feed from a wider variety of flowers due to competitive forces, whereas females feed from small patches outside the lekking grounds and have smaller bills better suited to feeding in small patches. Thus in both cases, there is a direct relationship between sexual social interactions, foraging, and bill morphology (see Bleiweiss 1999). Our results are concordant with Bleiweiss' hypothesis, as species in the *Mellisugini* clade do not lek, and the majority display female-biased sexual size dimorphism. By contrast, species in the *Phaethornithinae* clade exhibit primarily male-biased sexual size dimorphism of bill morphology, and the majority of these species indeed have lekking behavior. It is therefore reasonable to hypothesize that the presence of female-biased sexual size dimorphism in the *Mellisugini* clade is a reflection of the non-lekking and male territorial behavior in these species, which subsequently affects differential foraging between males and females of these species.

The most surprising result of our study is that in stark contrast to other *Trochilidae* lineages, only three species (*A. colubris*, *S. scintilla* and *M. minima*) in the *Mellisugini* exhibited significant sexual shape dimorphism in bill morphology. *Trochilidae* are generally considered to be dimorphic in both bill size and bill shape, as the majority of species in some lineages display differences in bill curvature (e.g., *Phaethornithinae*: Temeles et al. 2010; Stiles 1995). Further, individual species in many other groups, such as *E. jugularis* in the *Polytmini* clade (Temeles et al. 2005) and *Oreotrochilus estella* in the *Lophornithini* clade (Bleiweiss 1999) have also been shown to exhibit significant sexual dimorphism of both bill size and bill curvature. Together, these patterns have been interpreted as evidence that hummingbirds generally display sexual shape dimorphism in their bill morphology. However, in contrast to this general pattern, we found that nearly all species in the *Mellisugini* clade (29 of 32 species examined) displayed no significant dimorphism in bill shape.

Fig. 4 Current phylogeny of *Trochilidae* indicating presence of sexual size dimorphism throughout all *Trochilidae*, presence of sexual shape dimorphism throughout all *Trochilidae* and the loss of sexual shape dimorphism in the *Mellisugini* clade
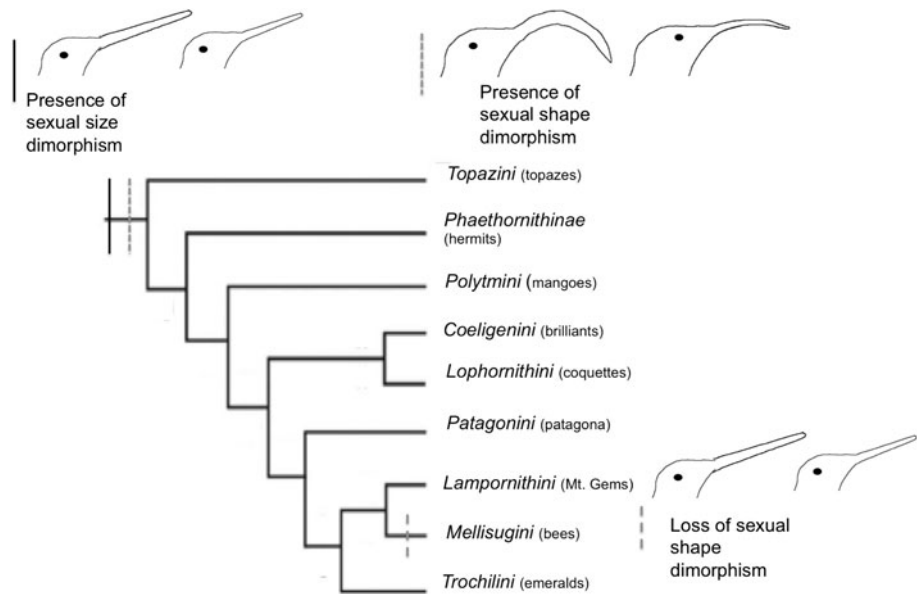
One possible explanation for these patterns is that hummingbird species in species-poor environments may have increased intraspecific competition, as the lack of interspecific competitors would allow the sexes to utilize distinct niches that would otherwise be occupied by congenerics. Indeed, this scenario would facilitate niche separation between the sexes, which would provide possible divergent selection on bill morphology between the sexes. While this hypothesis may hold true for *A. colubris*, which breeds allopatric with respect to other hummingbird species, neither *S. scintilla* nor *M. minima* live in species-depauperate communities. Therefore, this hypothesis alone is insufficient to explain the few instances of sexual shape dimorphism displayed in *Mellisugini*. Interestingly however, *S. scintilla* is the smallest hummingbird in its range (Wood 1983) and *M. minima* is the second smallest hummingbird species in *Trochilidae* (Bird 2004). Thus, niche segregation may still be a major mechanism driving the evolution of sexual dimorphism in these taxa, as these tiny hummingbird species may not have selective pressures because larger species are not able to feed from the resources the smallest hummingbirds can feed from.

Finally, it is of interest to examine the observed patterns in the *Mellisugini* in light of their phylogenetic placement within the *Trochilidae*. Phylogenetically, *Mellisugini* are a recently diverged lineage nested deeply within *Trochilidae* (Fig. 4), and are part of a radiation that includes the evolution of several species of neotropical migrants with nearly all species within this lineage displaying little to no sexual shape dimorphism in their bills. By contrast, lineages more basal to the *Mellisugini* display strong patterns of bill shape dimorphism, as well as bill size dimorphism.

Therefore, the available data suggest the hypothesis that both bill size dimorphism and bill shape dimorphism arose early in the diversification of *Trochilidae*, and that the lack of sexual shape dimorphism presently displayed in the *Mellisugini* lineage is a derived trait.

Taken together, the evolutionary changes in patterns of sexual size and shape dimorphism observed in *Mellisugini* suggest that the trends of sexual dimorphism in the *Trochilidae* are far more varied than was previously believed. It is possible that a combination of environmental and evolutionary factors leads to these patterns of sexual dimorphism, and further analyses examining phenotypic and environmental variation in light of phylogenetic history may reveal further insight into the underlying mechanisms driving the evolution of sexual dimorphism in the bills of hummingbirds.

Appendix

See Tables 3 and 4.

Table 3 Number of males and females in each species of the 32 hummingbirds in the Mellisugini clade with the sexual size dimorphism ratio (negative numbers indicate male-biased SSD) and magnitude of sexual shape dimorphism

Species	Females	Males	SSD ratio	SShD Magnitude
Archilochus alexandri	155	124	0.038	0.009
Archilochus colubris	35	42	0.119	0.026
Atthis heliosa	13	21	0.086	0.018
Calliphlox amethystina	11	14	0.031	0.017
Calliphlox bryantae	12	13	0.053	0.016
Calliphlox evelynae	13	15	−0.008	0.021
Calliphlox mitchellii	8	30	0.069	0.032
Calothorax lucifer	14	16	0.032	0.017
Calothorax pulcher	8	20	0.123	0.036
Calypte anna	13	18	0.086	0.035
Calypte costae	15	13	0.051	0.015
Chaetocercus astreans	12	12	0.082	0.022
Chaetocercus bombus	7	9	0.064	0.048
Chaetocercus heliodor	15	16	0.074	0.018
Chaetocercus jourdanii	15	13	0.067	0.036
Chaetocercus mulsanti	17	17	0.083	0.022
Doricha eliza	6	9	0.041	0.026
Doricha enicura	5	18	0.084	0.019
Mellisuga helenae	17	15	0.093	0.018
Mellisuga minima	14	13	0.091	0.058
Microstilbon burmeisteri	44	64	0.047	0.019
Myrmia micrura	8	12	0.088	0.023
Myrtis fanny	8	21	−0.013	0.019
Rhodopis vesper	10	22	0.080	0.023
Selasphorus flammula	20	18	0.062	0.025
Selasphorus platycercus	15	12	0.074	0.016
Selasphorus rufus	13	15	0.190	0.025
Selasphorus sasin	23	26	0.005	0.019
Selasphorus scintilla	12	13	0.059	0.044
Stellula calliope	15	21	0.056	0.030
Thaumastura cora	17	57	0.060	0.037
Tilmatura dupontii	14	13	0.057	0.027

Table 4 Species sexual size dimorphism ratios from literature (negative numbers indicate male-biased SSD)

Species	SSD ratio
Abeillia abeillei	0.085
Adelomyia melanogenys	−0.065
Aglaeactis castelnaudii	0.016
Aglaeactis pamela	0.136
Agliocercus kingi	0.078
Amazilia amabilis	0.043
Amazilia amazilia	0.101
Amazilia beryllina	0.096
Amazilia boucardi	0.041
Amazilia candida	0.075
Amazilia cyanocephala	0.050
Amazilia cyanura	0.024
Amazilia decora	0.043
Amazilia edward	0.023
Amazilia fimbriata	0.166
Amazilia franciae	0.055
Amazilia lactea	0.059
Amazilia rosenbergi	−0.029
Amazilia rutila	−0.206
Amazilia saucerrottei	0.082
Amazilia tobaci	−0.076
Amazilia tzacatl	0.005
Amazilia violiceps	0.008
Amazilia viridicauda	0.117
Amazilia viridifrons	0.149
Amazilia yucatanensis	0.034
Androdon aequatorialis	0.017
Anthracothorax dominicus	0.054
Anthracothorax mango	0.030
Anthracothorax nigricollis	0.036
Anthracothorax prevostii	0.062
Anthracothorax viridis	0.070
Boissonneaua flavescens	−0.104
Boissonneaua mathewsii	0.091
Campylopterus curvipennis	0.042
Campylopterus excellens	−0.063
Campylopterus falcatus	0.102
Campylopterus largipennis	0.070
Campylopterus villavicencio	0.070
Chalcostigma herrani	0.007
Chalcostigma ruficeps	−0.037
Chalcostigma stanleyi	−0.112
Chalybura buffonii	−0.012
Chalybura urochrysia	0.010
Chlorostilbon aureoventris	−0.028
Chlorostilbon auriceps	0.076
Chlorostilbon canivetii	0.070

Table 4 continued

Species	SSD ratio
Chlorostilbon gibsoni	0.049
Chlorostilbon maugaeus	0.088
Chlorostilbon melanorhyncus	0.040
Chlorostilbon mellisugus	−0.073
Chlorostilbon ricordii	0.058
Chlorostilbon swainsonii	0.071
Chrysolampis mosquitus	0.080
Chrysuronia oenone	0.095
Clytolaema rubricauda	0.025
Coeligena bonapartei	0.225
Coeligena coeligena	0.100
Coeligena helianthea	0.106
Coeligena iris	0.121
Coeligena lutetia	0.047
Coeligena phalerata	0.202
Coeligena torquata	0.055
Coeligena violifer	−0.065
Coeligena wilsoni	0.068
Colibri coruscans	−0.042
Colibri delphinae	−0.129
Colibri thalassinus	0.093
Cyanthus latirostris	0.069
Cynanthus sordidus	0.025
Damophila julie	0.077
Discosura conversii	0.027
Doryfera johannae	0.052
Doryfera ludovicae	0.050
Elvira chionura	0.013
Elvira cupreiceps	0.035
Ensifera ensifera	−0.030
Eriocnemis alinae	0.014
Eriocnemis cupreoventris	0.026
Eriocnemis derbyi	0.048
Eriocnemis luciana	−0.003
Eriocnemis mosquera	0.012
Eriocnemis nigrivestis	0.037
Eriocnemis vestitus	0.079
Eugenes fulgens	0.050
Eulampis holosericeus	0.152
Eulampis jugularis	0.180
Eupherusa cyanophrys	0.108
Eupherusa eximia	0.012
Eutoxeres aquila	−0.040
Eutoxeres condamini	0.010
Florisuga mellivora	0.010
Glaucis aenea	−0.020
Glaucis hirsutus	−0.003
Haplophaedia aureliae	0.016

Table 4 continued

Species	SSD ratio
Heliangelus amethysticollis	0.063
Heliangelus exortis	−0.060
Heliangelus viola	−0.074
Heliodoxa aurescens	0.030
Heliodoxa branickii	0.006
Heliodoxa gularis	−0.065
Heliodoxa imperatrix	0.040
Heliodoxa jacula	0.047
Heliodoxa leadbeateri	0.069
Heliodoxa rubinoides	0.045
Heliodoxa schreibersii	−0.027
Heliodoxa xanthogonys	0.208
Heliomaster constantii	0.009
Heliothryx aurita	0.062
Heliothryx barroti	0.013
Hylocharis chrysura	0.017
Hylocharis cyanus	0.011
Hylocharis eliciae	0.042
Hylocharis grayi	0.033
Hylocharis leucotis	0.048
Hylocharis xantusii	0.006
Klais guimeti	0.015
Lafresnaya lafresnayi	0.133
Lampornis amethystinus	0.035
Lampornis calolaema	0.074
Lampornis castaneoventris	0.080
Lampornis cinereicauda	0.057
Lampornis clemenciae	0.170
Lampornis rhami	−0.046
Lampornis sybillae	0.043
Lampornis viridipallens	−0.084
Lesbia nuna	>0.000
Lesbia victoriae	−0.042
Leucippus baeri	−0.078
Leucippus chlorocercus	>0.000
Leucippus hypostictus	0.138
Leucippus taczanowskii	0.051
Loddigesia mirablis	0.103
Lophornis adorabilis	0.035
Lophornis delattrei	0.073
Lophornis ornatus	0.031
Metallura aeneocauda	0.058
Metallura eupogon	−0.080
Metallura iracunda	−0.004
Metallura odomae	−0.032
Metallura phoebe	−0.213
Metallura tyrianthina	0.047
Metallura williami	0.153

Table 4 continued

Species	SSD ratio
Oreonympha nobilis	−0.004
Oreotrochilus estella	−0.031
Orthrorhyncus cristatus	0.185
Panterpe insignis	−0.013
Phaeochroa cuvieri	0.033
Phaethornis anthophilus	−0.100
Phaethornis astrimentalis	−0.008
Phaethornis augusti	−0.005
Phaethornis bourcieri	−0.040
Phaethornis griseogularis	0.150
Phaethornis guy	−0.080
Phaethornis hispidus	−0.070
Phaethornis koepckae	−0.090
Phaethornis longirostris	−0.060
Phaethornis longuemareus	0.020
Phaethornis malaris	−0.050
Phaethornis philippii	−0.090
Phaethornis pretrei	−0.053
Phaethornis ruber	−0.006
Phaethornis striigularis	−0.079
Phaethornis subochraceus	−0.163
Phaethornis superciliosus	−0.029
Phaethornis syrmatophorus	−0.030
Phaethornis yaruqui	−0.120
Phlogophilus harterti	0.006
Polyonymus caroli	−0.025
Polytmus guainumbi	0.004
Polytmus theresiae	−0.008
Popelairia langsdorffi	−0.063
Pterophanes cyanopterus	0.007
Ramphomicron microrhynchum	−0.014
Sappho sparganura	0.055
Schistes geoffroyi	−0.053
Sephanoides fernandensis	0.006
Sephanoides sephanoides	0.081
Thalurania colombica	0.018
Thalurania furcata	0.076
Thalurania glaucopis	0.072
Threnetes leucurus	0.006
Threnetes ruckeri	−0.020
Topaza pella	0.020
Topaza pyra	−0.055
Trochilus polytmus	0.030
Urosticte benjamani	−0.066

Specimens Examined to Quantify Morphological Variation

We examined the left lateral side of bills from collections at Carnegie Museum of Natural History (CM), Cornell University Museum of Vertebrates (CUMV), Delaware Museum of Natural History (DMNH), Field Museum of Natural History (FMNH), Los Angeles County Museum (LACM), Museum of Comparative Zoology (MCZ), Museum of Southwestern Biology (MSB), Museum of Vertebrate Zoology (MVZ), San Diego Natural History Museum (SDNHM), University of Michigan Museum of Zoology (UMMZ), National Museum of Natural History (NMNH), Western Foundation of Vertebrate Zoology (WFVZ), and Yale Peabody Museum (YPM). Specific specimens, listed by institution, include the following:

AMNH: 100678, 109537, 117704, 124278, 124279, 124280, 124281, 13002, 131195, 145839, 151434, 151437, 151458, 151459, 170352, 171148, 171149, 171157, 179065, 181241, 182361, 229094, 234478, 235492, 235680, 235859, 305591, 305592, 229094, 234478, 235492, 235680, 235859, 305591, 305592, 326286, 326287, 326290, 326292, 326293, 326295, 326296, 361892, 361894, 337924,61896, 361897, 361898, 37784, 37893, 37894, 37896, 37903, 37905, 37911, 37938, 37941, 37945, 37947, 37949, 37950, 37952, 37953, 37957, 37981, 38004, 38715, 389741, 394200, 394202, 394204, 394206, 394208, 394215, 394217, 394218, 394219, 394220, 394222, 437741, 46310, 46608, 46631, 46634, 46636, 46637, 46655, 46659, 46713, 46736, 484400, 484402, 484403, 484407, 484408, 484409, 484525, 484529, 484547, 484550, 484551, 484553, 484554, 484555, 484564, 484580, 484597, 484598, 484599, 484600, 484601, 484602, 484603, 484607, 484613, 484620, 484628, 484629, 484630, 484631, 484632, 484710, 484791, 484794, 484802, 484817, 484818, 484821, 484824, 484826, 484828, 484829, 484831, 484832, 484833, 484836, 484837, 484838, 484840, 484841, 484842, 484842, 484843, s484845, 484846, 484850, 484872, 484929, 484930, 484935, 484938, 484945, 484948, 484949, 484950, 484951, 484956, 484958, 484960, 484984, 484986, 484988, 54154, 60746, 71312, 73093, 73094, 78956, 793430, 806281, 812050, 824739, 99115, 99116.

CM: 67643, 101705, 101706, 113457, 113462, 124330, 125660, 125728, 128495, 138725, 142822, 142892, 155017, 158840, 159356, 159357, 159358, 159359, 159389, 159362, 159365, 159390, 159391, 162238, 162240, 162248, 19584, 19585, 19586, 19587, 19586, 19587, 19588, 19601, 19602, 19603, 19604, 19605, 19608, 19609, 19647, 19648, 19650, 19651, 19655, 19662, 19666, 19671, 19675, 19676, 19680, 19681, 19688, 19689, 19694, 19695, 19696, 19698, 19699, 19707, 19708, 19709, 19710,

19712, 19713, 19714, 28207, 29271, 29322, 30567, 30574, 30591, 30765, 30811, 30838, 30847, 30854, 30861, 30854, 30861, 30862, 30970, 31079, 31087, 33480, 33974, 34185, 34186, 34206, 34207, 34209, 34210, 34213, 34224, 34261, 48058, 81925, 81939, 95191, 106686, 106837, 119903, 119978, 120388, 135818, 141455, 141457, 141465, 141466, 142891, 142893, 143338, 144792, 144797, 35046, 37817, 37863, 37869, 37870, 37871, 37872, 41264, 42503, 42504, 43719, 51309, 51310, 79155, 79156, 79159, 80549, 85050, 85320, 85465, 85498, 85499 125705, 125706, 125710, 141875, 142477, 151407, 152912, 153151, 153802, 154036, 154146, 154621, 158828, 1588289, 158830, 158831, 158832, 158833, 158834, 158836, 158837, 159323, 159324, 159325, 159327, 159328, 159329, 159330, 159331, 159332, 159333, 159334, 159335, 159336, 159337, 159338, 159339, 159340, 159342, 159343, 159345, 159346, 159347, 159348, 159349, 159350, 166922, 167457, 168761, 169649, 170846, 170867, 95217.

CUMV: 12030, 5428 14986, 21604, 23717, 24397, 37009, 44079, 44128, 44129, 44130, 44131, 44171, 49013, 50001, 50780, 51239, 5352, 5355, 5357, 5358, 5361, 5362, 5363, 5364, 5365, 5367, 5382.

DMNH: 6273, 12401, 12402, 12403, 12404, 12405, 18677, 18678, 18679, 18681, 18685, 22409, 22419, 22423, 24683, 24687, 24690, 24691, 24692, 24693, 24694, 24695, 24696, 24697, 24698, 24700, 24701, 24702, 24704, 24705, 24706, 24709, 59797, 59813, 59814, 59815 1400, 1426, 1436, 19019, 19025, 59806.

FMNH: 138884, 138887, 42934, 120625, 12692, 1279, 1280, 1281, 1283, 1284, 138877, 138879, 138882, 138883, 138885, 138888, 179490, 179491, 179494, 186014, 186015, 186016, 207017, 207019, 207024, 207028, 207029, 207030, 207031, 207032, 207033, 207035, 207036, 207037, 207038, 207039, 207040, 207041, 207043, 208746, 208747, 208748, 208749, 208750, 215969, 21940, 24234, 24235, 275613, 285092, 285093, 285094, 293745, 299872, 302753, 32014, 36108, 36113, 36610, 372482, 372483, 372485, 372486, 42822, 42824, 42826, 42931, 42932, 42935, 45528, 45549, 45550, 46407, 46410, 46411, 46417, 46419, 46420, 46461, 46462, 46463, 47104, 47106, 47108, 47109, 47111, 53307, 53873, 56771, 56773, 56774, 61598, 61599, 61714, 61715, 61716, 61719, 61720, 65515, 65517, 65519, 66328, 67764, 67767, 67769, 67770, 67771, 72207, 72209, 72212, 72213, 91943, 91944, 138705, 138720, 138723, 138725, 14653, 14654, 14655, 14656, 14657, 14658, 14659, 14661, 14662, 14663, 14666, 14667, 14668, 14670, 14672, 14673, 14674, 14675, 14676, 14678, 159838, 159839, 161019, 16575, 16576, 93036, 93037, 93038, 93039, 93040.

LACM: 14115, 15187, 15641, 15643, 15645, 21992, 24216, 24218, 24453, 32465, 32467, 3377, 4521, 50712, 6529, 6530, 6596, 73865, 73867, 77860, 78165, 103469,

107665, 111607, 111608, 14107, 15560, 15562, 15563, 15565, 15566, 15642, 15644, 15646, 15646, 15647, 15649, 15650, 15651, 1766, 1793, 18004, 18381, 19821, 21993, 21994, 2416, 2417, 2423, 2424, 2426, 25430, 25432, 25434, 25435, 3045, 3046, 3047, 3048, 3051, 3053, 3055, 3072, 3128, 3129, 3130, 3204, 32466, 32468, 4069, 85325, 85326, 14127, 14138, 14139, 1927, 3381, 78618, 78619, 78621, 78623, 78624, 78625, 78626, 78627, 78632, 78643, 78646, 78652, 78653, 78654, 78656, 78659, 78661, 78662, 78663, 78664, 78668, 78669, 78671, 78677, 78678, 78683, 78684, 78688, 78691, 78694.

LSU: 91976, 143500, 143507, 143510, 35139, 64031, 64032, 64033.

MCZ: 100182, 103286, 100182, 103286.

MSB: 14801, 22663, 22665, 22668, 22670, 22671, 22677.

MVZ: 138272, 138273, 109221, 110077, 110078, 110079, 110080, 11860, 139415, 139415, 139417, 139418, 153271, 153272, 156457, 157758, 157759, 160840, 163525, 107024, 116741, 12811, 19920, 19921, 19922, 19923, 19925, 22484, 22704, 26729, 26730, 27927, 27928, 27929, 27930, 27931, 3192, 3194, 3197, 32864, 32870, 32875, 32878, 32880, 32881, 32882, 32883, 32884, 32887, 32888, 32889, 32900, 32903, 3655, 3698, 3700, 3785, 40727, 40728, 40731, 41534, 41927, 4194, 4195, 43242, 45343, 5249, 77338, 80946.

NMNH: 233774, 101885, 101886, 103295, 108743, 117267, 127670, 127671, 128173, 130564, 131574, 132865, 134348, 134353, 140265, 140275, 140281, 140316, 140331, 142249, 149468, 149470, 149482, 149486, 149489, 149490, 149492, 149495, 149497, 150791, 152545, 154785, 154787, 154791, 154792, 154793, 154820, 162635, 170608, 170656, 174575, 174579, 174583, 174585, 174586, 174587, 174589, 174590, 174592, 174594, 174596, 174597, 174599, 174600, 174603, 174604, 174605, 174619, 174627, 184077, 189789, 190522, 190524, 190525, 190526, 190527, 190972, 200318, 200319, 200322, 200324, 201116, 201118, 201122, 201123, 201125, 201126, 204617, 208257, 220663, 233773, 233775, 233776, 236667, 24624, 24625, 24626, 24627, 253389, 253390, 253723, 263880, 263881, 263882, 263883, 264509, 264759, 273932, 274230, 274236, 277269, 287983, 2896, 30274, 309063, 309718, 309720, 309722, 309723, 309777, 309879, 317261, 32048, 327689, 333521, 349574, 35175, 352823, 352824, 375720, 375722, 386974, 386975, 386976, 386977, 386978, 386979, 386980, 389269, 392260, 392262, 392264, 392265, 392270, 392271, 392271, 401554, 401554, 401556, 401557, 41473, 41475, 44741, 453719, 453720, 453723, 453725, 453726, 453727, 453735, 453736, 453739, 453740, 456067, 456069, 456475, 45863, 462930, 462937, 47183, 50278, 52295, 52297, 52298, 54321, 543863, 55964, 573638, 60088,

6054, 6058, 627430, 74023, 74659, 74662, 74665, 74665, 74666, 74668, 84137, 84221, 86348, 90369, 92045, 99368, 99513, 108369, 117258, 117269, 129247, 129249, 129250, 129252, 129257, 134343, 140254, 140255, 140256, 140257, 140258, 140259, 140266, 168422, 203268, 234334, 235077, 235074, 258387, 467031, 589963, 91738, 91740, 94957, 91959.

SDNHM: 12411, 12423, 12436, 15648, 15794, 15828, 15860, 15860, 15924, 17485, 17488, 17842, 19265, 22427, 22428, 22429, 22430, 22431, 22432, 22433, 22434, 31503, 31504, 3196, 3197, 36032, 36033, 43552, 469, 50045, 50616, 51785, 9286, 9492, 9753, 17251, 22386, 22387, 22389, 22463, 30108, 30417, 449, 450.

UMMZ: 126341, 126344, 126345, 126347, 126348, 126350, 126373, 126374, 126376, 126377, 126378, 126382, 126383, 126425, 126432, 126434, 132424, 132425, 132426, 132428, 150182, 164649, 164662, 164664, 164667, 164668, 164669, 215480, 27469, 60462, 62719, 62721, 65094, 98235, 100160, 111051, 111052, 111054, 119549, 126351, 126424, 126428, 126429, 134979, 27465, 49777, 92163, 111820, 113646, 113649, 126291, 126292, 126294, 126295, 126296, 126297, 126299, 126300, 126301, 126301, 126302, 126303, 126304, 126306, 126307, 126310, 126314, 134697, 136434, 156250, 164455, 164461, 164463, 164468, 164470, 164471, 164472, 164473, 164474, 164490, 164491, 164492, 164492, 164496, 164498, 164500, 164501, 164502, 164504, 164505, 164506, 164507, 164508, 164509, 164510, 164514, 164515, 164517, 164518, 164519, 164525, 164526, 164527, 164528, 164529, 164530, 199030, 199031, 213109, 213110, 221599, 221794, 224043, 231028, 231029, 236468, 238200, 239425, 239499, 239601, 239604, 239631, 240778, 240967, 241265, 241283, 31639, 52980, 55809, 62710, 62711, 62713, 62714, 67020, 71337, 74542, 90352.

WFVZ: 19187, 19188, 19192, 21786, 21787, 21790, 21796, 21797, 21849, 21850, 25450, 34005, 34006, 39248, 39249, 39250, 39252, 39253, 39254, 48247, 49304, 50642, 8539, 8540, 10119, 1515, 1516, 1517, 21798, 21803, 21804, 21806, 21809, 2714, 32155, 32156, 49304, 49308.

YPM: 6442, 99650.

References

Adams, D. C. (2010). Parallel evolution of character displacement driven by competitive selection in terrestrial salamanders. *BMC Evolutionary Biology, 10*, 1–10.

Adams, D. C., & Collyer, M. L. (2007). The analysis of character divergence along environmental gradients and other covariates. *Evolution, 61*, 510–515.

Adams, D. C., & Collyer, M. L. (2009). A general framework for the analysis of phenotypic trajectories in evolutionary studies. *Evolution, 63*, 1143–1154.

Adams, D. C., & Nistri, A. (2010). Ontogenetic convergence and evolution of foot morphology in European cave salamanders (Family: Plethodontidae). *BMC Evolutionary Biology, 10*, 1–10.

Adams, D. C., Rohlf, F. J., & Slice, D. E. (2004). Geometric morphometrics: Ten years of progress following the 'revolution'. *Italian Journal of Zoology, 71*, 5–16.

Adams, D. C., West, M. E., & Collyer, M. L. (2007). Location-specific sympatric morphological divergence as a possible response to species interactions in West Virginia Plethodon salamander communities. *Journal of Animal Ecology, 76*, 289–295.

Alves, S. M., & Belo, M. (2002). Morphometric variations in the house fly, *Musca domestica* (L.) with latitude. *Genetica, 115*, 243–251.

Anderson, M. J. (2001). A new method for non-parametric multivariate analysis of variance. *Austral Ecology, 26*, 32–46.

Andersson, M. (1994). *Sexual selection*. Princeton, NJ: Princeton University Press.

Berns, C. M., & Adams, D. C. (2010). Bill shape and sexual shape dimorphism between two species of temperate hummingbirds: Black-chinned Hummingbirds (*Archilochus alexandri*) and Ruby-throated Hummingbirds (*Archilochus colubris*). *The Auk, 127*, 626–635.

Bird, D. M. (2004). *The bird almanac: A guide to essential facts and figures of the world's birds*. Firefly Books (U.S.) Inc, Buffalo, NY.

BirdLife International. (2012). *IUCN red list for birds*. Downloaded from http://www.birdlife.org on 29 May 2012.

Bleiweiss, R. (1992). Reversed plumage ontogeny in a female hummingbird- implications for the evolution of iridescent colors and sexual dimorphism. *Biological Journal of the Linnean Society, 47*, 183–195.

Bleiweiss, R. (1997). Covariation of sexual dichromatism and plumage colors in lekking and non-lekking birds: A comparative analysis. *Evolutionary Ecology, 11*, 217–235.

Bleiweiss, R. (1998). Origin of hummingbird faunas. *Biological Journal of the Linnean Society, 65*, 77–97.

Bleiweiss, R. (1999). Joint effects of feeding and breeding behaviour on trophic dimorphism in hummingbirds. *Proceedings of the Royal Society of London. Series B: Biological Sciences, 266*, 2491–2497.

Bookstein, F. L. (1991). *Morphometric tools for landmark data: Geometry and biology*. Cambridge: Cambridge University Press.

Bookstein, F., Schäfer, K., Prossinger, H., Seidler, H., Fieder, M., Stringer, C., et al. (1999). Comparing frontal cranial profiles in archaic and modern *Homo* by morphometric analysis. *The Anatomical Record, 257*, 217–224.

Brown, J. H., & Bowers, M. A. (1985). Community organization in hummingbirds: Relationships between morphology and ecology. *The Auk, 102*, 251–269.

Butler, M. A., Sawyer, M. A., & Losos, J. B. (2007). Sexual dimorphism and adaptive radiation in *Anolis* lizards. *Nature, 447*, 202–205.

Butler, M. A., Schoener, T. W., & Losos, J. B. (2000). The relationship between sexual size dimorphism and habitat use in Greater Antillean *Anolis* lizards. *Evolution, 54*, 259–272.

Carpenter, F. L., Hixon, M. A., Paton, D. C., Temeles, E. J., & Russell, R. W. (1991). Sexual differences in resource acquisition by migrant hummingbirds. *Acta XX Congressus Internationalis Ornithologici, 2*, 1156–1165.

Collins, B. G., & Paton, D. C. (1989). Consequences of differences in body mass, wing length and leg morphology for nectar-feeding birds. *Austral Ecology, 14*, 269–289.

Collyer, M. L., & Adams, D. C. (2007). Analysis of two-state multivariate phenotypic change in ecological studies. *Ecology, 8*, 683–692.

Colwell, R. K. (2000). Rensch's Rule crosses the line: convergent allometry of sexual size dimorphism in hummingbirds and flower mites. *The American Naturalist, 156*, 495–510.

Darwin, C. R. (1871). *The descent of man and selection in relation to sex*. London: John Murray.

Dryden, I. L., & Mardia, K. V. (1993). Multivariate shape analysis. SankhyÄ: *The Indian Journal of Statistics, Series A (1961–2002), 55*, 460–480.

Dryden, I. L., & Mardia, K. V. (1998). *Statistical analysis of shape*. Chichester: John Wiley and Sons.

Evans, M. R., Martins, T. L. E., & Haley, M. P. (1995). Inter-sexual and intra-sexual patterns of fluctuating asymmetry in the Red-billed Streamertail- should symmetry always increase with ornament size. *Behavioral Ecology and Sociobiology, 37*, 15–23.

Fairbairn, D. J. (1997). Allometry for sexual size dimorphism: Pattern and process in the coevolution of body size in males and females. *Annual Review of Ecology and Systematics, 28*, 659–687.

Feinsinger, P. (1978). Ecological interactions between plants and hummingbirds in a successional tropical community. *Ecological Monographs, 48*, 269–287.

Feinsinger, P., & Colwell, R. K. (1978). Community organization among neotropical nectar-feeding birds. *American Zoologist, 18*, 779–795.

Garland, T., Dickerman, A. W., Janis, C. M., & Jones, J. A. (1993). Phylogenetic analysis of covariance by computer simulation. *Systematic Biology, 42*, 265–292.

Gunz, P., Mitteroecker, P., & Bookstein, F. (2005). Semi-landmarks in three dimensions. In D. E. Slice (Ed.), *Modern morphometrics in physical anthropology* (pp. 73–98). New York: Kluwer.

Hedrick, A. V., & Temeles, E. J. (1989). The evolution of sexual dimorphism in animals: Hypotheses and tests. *Trends in Ecology & Evolution, 4*, 136.

Hendry, A. P., Kelly, M. L., Kinnison, M. T., & Reznick, D. L. (2006). Parallel evolution of the sexes? Effects of predation and habitat features on the size and shape of guppies. *Journal of Evolutionary Biology, 19*, 741–754.

Jones, A. G., & Ratterman, N. L. (2009). Mate choice and sexual selection: What have we learned since Darwin? *Proceedings of the National Academy of Sciences, 106*, 10001–10008.

Kodric-Brown, A., & Brown, J. H. (1978). Influence of economics, interspecific competition, and sexual dimorphism on territoriality of migrant Rufous Hummingbirds. *Ecology, 59*, 285–296.

Lovich, J. E., & Gibbons, J. W. (1992). A review of techniques for quantifying sexual size dimorphism. *Growth, Development, and Aging, 56*, 269–281.

McGuire, J. A., Witt, C. C., Altshuler, D., & Remsen, J. V. (2007). Phylogenetic systematics and biogeography of hummingbirds: Bayesian and maximum likelihood analyses of partitioned data and selection of an appropriate partitioning strategy. *Systematic Biology, 56*, 837–856.

McGuire, J., Witt, C., Remsen, J., Dudley, R., & Altshuler, D. (2009). A higher-level taxonomy for hummingbirds. *Journal of Ornithology, 150*, 155–165.

Potter, K. A., Bose, T., & Yamaguchi, A. (2005). Androgen-induced vocal transformation in adult female African Clawed Frogs. *Journal of Neurophysiology, 94*, 415–428.

R Development Core Team. (2010). *R: A language and environment for statistical computing, version 2.11.1 R Foundation for Statistical Computing*, Vienna.

Rodríguez-Flores, C. I., & Stiles, G. (2005). Ecomorphological analysis of a community of hermit hummingbirds (Trochilidae, Phaethorninae) and their flowers in Colombian Amazonia. *Ornitología Colombiana, 3*, 7–27.

Rohlf, F. J. (1999). Shape statistics: Procrustes superimpositions and tangent spaces. *Journal of Classification, 16*, 197–223.

Rohlf, F. J. (2004). *TPSSplin, version 1.20*. Department of Ecology and Evolution, State University of New York, Stony Brook.

Rohlf, F. J. (2005). *TPSRelW, version 1.42*. Department of Ecology and Evolution, State University of New York, Stony Brook.

Rohlf, F. J. (2010). *TPSDig2, version 2.16*. Department of Ecology and Evolution, State University of New York, Stony Brook.

Rohlf, F. J., & Marcus, L. F. (1993). A revolution in morphometrics. *Trends in Ecology & Evolution, 8*, 129–132.

Rohlf, F. J., & Slice, D. E. (1990). Extentions of the procrustes method for the optimal superimposition of landmarks. *Systematic Zoology, 39*, 40–59.

Selander, R. K. (1972). Sexual selection and dimorphism in birds. In B. G. Campbell (Ed.), *Sexual Selection and the descent of man (1871–1971)* (pp. 180–230). Chicago, IL: Aldine.

Serb, J. M., Alejandrino, A., Otárola-Castillo, E., & Adams, D. C. (2011). Morphological convergence of shell shape in distantly related scallop species (Mollusca: Pectinidae). *Zoological Journal of the Linnean Society, 163*, 571–584.

Slatkin, M. (1984). Ecological causes of sexual dimorphism. *Evolution, 38*, 622–630.

Stephens, P. R., & Wiens, J. J. (2009). Evolution of sexual size dimorphism in emydid turtles: Ecological dimorphism, Rensch's Rule, and sympatric divergence. *Evolution, 63*, 910–925.

Stiles, F. G. (1983). Systematics of the southern forms of *Selasphorus* (Trochilidae). *The Auk, 100*, 311–325.

Stiles, F. G. (1995). Behavioral, ecological and morphological correlates of foraging for arthropods by the hummingbirds of a tropical wet forest. *The Condor, 97*, 853–878.

Stuart-Fox, D. M., & Ord, T. J. (2004). Sexual selection, natural selection and the evolution of dimorphic coloration and ornamentation in agamid lizards. *Proceedings of the Royal Society of London. Series B: Biological Sciences, 271*, 2249–2255.

Temeles, E. J., Goldman, R. S., Kudla, A. U., & Stouffer, P. C. (2005). Foraging and territory economics of sexually dimorphic Purple-throated Caribs (*Eulampis jugularis*) on three *Heliconia* morphs. *The Auk, 122*, 187–204.

Temeles, E. J., & Kress, W. J. (2003). Adaptation in a plant-hummingbird association. *Science, 300*, 630–633.

Temeles, E. J., Miller, J. S., & Rifkin, J. L. (2010). Evolution of sexual dimorphism in bill size and shape of hermit hummingbirds (*Phaethornithinae*): A role for ecological causation. *Philosophical Transactions of the Royal Society B: Biological Sciences, 365*, 1053–1063.

Temeles, E. J., & Roberts, W. M. (1993). Effect of sexual dimorphism in bill length on foraging behavior: An experimental analysis of hummingbirds. *Oecologia, 94*, 87–94.

Wood, G. L. (Ed.). (1983). *Guinness book of animal facts and feats*. New York: Sterling Publishing Co Inc.

Worthington, A. M., Berns, C. M., & Swallow, J. G. (2012). Size matters, but so does shape: Quantifying complex shape changes in a sexually selected trait in stalk-eyed flies (Diptera: Diopsidae). *Biological Journal of the Linnaean Society, 106*, 104–113.

Zusi, R. L., & Gill, F. B. (2009). The marvelous tail of *Loddigesia mirabilis* (Trochilidae). *The Auk, 126*, 590–603.