**THE EVOLUTION OF TAIL SHAPE IN HUMMINGBIRDS**

**Christopher J. Clark**

*Museum of Vertebrate Zoology, 3101 VLSB, University of California, Berkeley, California 94720, USA*

**ABSTRACT.**—The tail morphology of many birds is shaped by both natural and sexual selection. Models of tail aerodynamics predict that functions related to flight naturally select for moderately forked tail shapes, constraining the tendency of sexual selection to generate interspecific morphological diversity. Moreover, models predict that small birds will have low variation in tail morphology. Although hummingbirds (family Trochilidae) depend exclusively on flight for locomotion, the diversity of their tail morphology is among the greatest in all bird families. Hummingbird tail length exhibits positive allometry, scaling as approximately mass^{0.5}, which causes tail surface area to scale as mass^{1.0}. Forked tail morphology arises at least 26 times in the clade, and forked taxa tend to be sexually dimorphic, whereas species with graduated tails tend to be monomorphic. Small hummingbird species exhibit higher variation in tail morphology than large species. These results suggest that moderately forked tail morphology tends to arise via sexual selection in hummingbirds and that large species are more constrained in tail morphology than small species. Both patterns are inconsistent with current models of how bird tails function. This suggests that, in terms of aerodynamics, hummingbird tails function differently from the tails of other birds. Received 26 January 2009, accepted 31 July 2009.

Key words: allometry, dimorphism, hummingbird, ornament, tail length, tail shape.

Closely related animal taxa often differ in the morphology of sexually selected ornaments, for example the ornamental eye stalks of stalk-eyed flies (Baker and Wilkinson 2001), bird plumage color (Burns 1998), horns and spines in agamid lizards (Ord and Stuart-Fox 2006), and bird tail morphology (Winquist and Lemon 1994). Morphological diversity is also present in sexually selected weapons, such as the horns of beetles (Emlen 2001, Emlen et al. 2005). Research on sexually selected morphologies has primarily focused on explaining the benefits of such traits to show why these traits have evolved (Andersson 1994), but they are hypothesized to incur costs as well (Emlen 2001, Emlen et al. 2005, Ouher and Garland 2007), for example by interfering with locomotion (Basolo and Alcaraz 2003, Clark and Dudley 2009). Consequently, both the benefits and costs act in concert to shape interspecific morphological diversity. By mapping the evolution of these characters on a phylogeny, it is possible to test...
preexisting hypotheses of functional optima and constraint. Here, I use patterns of hummingbird tail morphologies to test preexisting hypotheses of functional optima and constraints on sexually selected tail ornaments.

The diverse tail morphologies of many kinds of birds are a classic example of a sexually selected ornament. Many birds, such as swallows (Hirundinidae), pheasants (Phasianidae), tropical birds (Phaethontidae), birds of paradise (Paradisaeidae), and some hummingbirds (Trochilidae), have long or elaborate tail morphologies. Most of these species are sexually dimorphic, and this ornamental diversity tends to be concentrated in polygynous birds in which the males provide no care (e.g., hummingbirds; Schuchmann 1999), which indicates that it is generated by sexual selection (Darwin 1871, Winquist and Lemon 1994). Experiments have generally suggested that long tails can increase mating success via female choice (Andersson 1982; Barnard 1990; Andersson 1992; Pryke and Andersson 2002, 2005). However, this ornamental diversity is expected to be constrained by natural selection for flight performance.

The tail plays an aerodynamic role in flight, by streamlining the body (Maybury and Rayner 2001, Clark and Dudley 2009) and producing the aerodynamic forces of lift and drag (Maybury and Rayner 2001, Maybury et al. 2001, Usherwood et al. 2005). Experimentally manipulating tail morphology alters flight performance (Evans et al. 1994; Evans 1998; Matyjasiak et al. 1999, 2000, 2004; Balmford et al. 2000; Buchanan and Evans 2000; Park et al. 2000; Rowe et al. 2001). The delta-wing hypothesis, proposed as an aerodynamic model of how the tail functions, makes quantitative predictions about the optimal shape of bird tails. It assumes that the avian tail produces lift in a fashion similar to aircraft with low-aspect-ratio wings and that lift is dominated by attached vortices that form on the lateral, leading edges of the tail, whereas drag is proportional to the exposed surface area. It also assumes that tail–body and tail–wing aerodynamic interactions are negligible (Thomas 1993, Maybury et al. 2001). According to this aerodynamic model, lift is generated in proportion to the maximum continuous span (MCS) of the spread tail (Fig. 1). Wind-tunnel tests have shown that these assumptions break down at high angles of attack (Maybury and Rayner 2001, Evans 2003) and that significant tail–body aerodynamic interactions can affect both lift and drag production of the tail (Maybury and Rayner 2001, Maybury et al. 2001). However, it is unclear to what degree these demonstrated violations of the model’s assumptions limit its utility for understanding patterns of bird tail shape.

As an alternative approach to laboratory investigation, the delta-wing hypothesis has been used to develop predictions describing the expected evolutionary diversity of bird tail morphologies. Specifically, it predicts that a forked tail is the aerodynamically optimal shape (Balmford et al. 1993, Thomas 1993, Thomas and Balmford 1995) because it maximizes MCS in relation to the tail’s surface area and, therefore, maximizes the tail’s lift:drag ratio (Fig. 1).

According to the delta-wing hypothesis, deviating from a moderately forked morphology, such as by elongating individual pairs of tail feathers, potentially increases the cost of flight and reduces maneuverability by decreasing the lift:drag ratio of the tail (Evans and Thomas 1992, Balmford et al. 1993, Norberg 1995). These modifications may impose high viability costs on birds that...
lies above its lateral neighbor and below its medial neighbor, so asymmetrical in most species. When the tail is folded, each rectrix (Fig. 1). The rectrices are long, stiff, flat, and the outermost are bilateral pairs of rectrices that are individually variable in length and shape of any bird clade (Gould 1861, Ridgway 1892). Because of their small size, they have the highest mass-specific metabolic costs of flight (Bartholomew and Lighton 1986). All species are exclusively dependent on flight for locomotion (Schuchmann 1999) and can fly over a wide range of speeds, from hovering to fast forward flight (Chai et al. 1999). Aspects of their morphological diversity appear to be generated by high levels of sexual selection, given that females alone care for the offspring (Schuchmann 1999), many hummingbirds are highly sexually dimorphic, and they are among the most heavily ornamented and showy of birds (Darwin 1871, Winquist and Lemon 1994).

Here, I examine the apparent incongruity that a large clade of diminutive, flight-reliant birds with energetically flight nonetheless has enormous diversity in tail morphology, by exploring interspecific patterns of hummingbird tail length, shape, dimorphism, and allometry in a phylogenetic context. Tail size is expected to scale with body size, so I estimated the allometry of the length of individual tail-feathers first, as well as the tail’s surface area. Moderately forked tails are hypothesized to be aerodynamically favored in both sexes, which predicts that species with moderately forked tails tend to be monomorphic and that species with other morphologies, such as graduated shapes, are dimorphic. The model of the costs of elongated tails (Evans 2004) hypothesizes that these costs are greater in small birds, which predicts that small hummingbird species show less variation in tail morphology than large ones. The model also predicts that forked elongations are less costly than graduated elongations (Evans 2004), which is tested by comparing the number of times that different tail morphologies have independently evolved. Finally, the analyses presented here assume that hummingbird tail morphologies are sexually selected or selected for aerodynamic functions. Taxa that are possible exceptions to this assumption (i.e., that exhibit possible non-aerodynamic functions of the tail) were identified from natural-history literature.

**Tail morphology and definitions.**—All hummingbirds have 5 bilateral pairs of rectrices that are individually variable in length and shape. They are numbered R1 through R5, from medial to lateral (Fig. 1). The rectrices are long, stiff, flat, and the outermost are asymmetrical in most species. When the tail is folded, each rectrix lies above its lateral neighbor and below its medial neighbor, so that R5 is ventral and R1 is dorsal.

Birds control each side of their tail independently (Baumel 1988), but in most flight contexts they appear to spread (or fan) each side to the same degree. The angle made by the outermost rectrices is the spread angle (β; Fig. 1B). Above a critical value of β, gaps appear between the individual tail feathers, and the tail’s surface area is approximately the sum of the areas of the individual rectrices. By contrast, below this critical angle, the edges of neighboring rectrices overlap (Fig. 1), and the tail’s surface area (SA) can be roughly approximated as the area of a wedge (Fig. 1B) with

\[
SA_{\text{tail}} = \frac{1}{2} (R_5^2 \beta)
\]

where \( R_5 \) is the average rectrix length and \( \beta \) is the spread angle (Fig. 1). Dividing body mass by tail surface area yields tail loading (body mass per unit surface area of the tail). Note that a constant value of \( \beta \) should be used to objectively compare morphologies, whereas live birds actually vary this angle freely. This variable is intended to be analogous to wing disc loading, which is body mass divided by the area swept by the wings during hovering (Epting and Casey 1973, Altshuler et al. 2004). The area swept by the wings is proportional to wing length\(^2\) (Epting and Casey 1973, Altshuler et al. 2004).

The delta-wing hypothesis predicts that forked tail morphologies are optimal because they produce a triangular planform at a particular value of \( \beta \) (Fig. 1B). A triangular planform maximizes the maximum continuous span (Fig. 1), which in turn maximizes the tail’s lift:drag ratio. The “fork ratio” (R5 length / R1 length) that produces a triangular planform depends on \( \beta \), which is itself variable. Thomas (1993) and Thomas and Balmford (1995) used \( \beta = 120^\circ \), which corresponds to an optimal fork ratio of 2.0. But this angle is not universal; during linear flight in Barn Swallows (Hirundo rustica), Rock Pigeons (Columba livia), and Black-billed Magpies (Pica hudsonia), \( \beta < 70^\circ \) (Tobalske and Dial 1996, Park et al. 2001, Evans et al. 2002). At \( \beta = 67^\circ \), a fork ratio of 1.2 is optimal. Hereafter, tail morphologies of 1.2 < R5/R1 < 2.0 are termed “moderately forked” and correspond to the approximate range of morphologies predicted by the delta-wing hypothesis (Thomas 1993). This is in contrast with elongated forks (R5/R1 > 2.0) and tails that are not forked (R5/R1 < 1.2).

**Methods**

**Measurements.**—I measured body mass, folded wing length, and the length of all 5 rectrices on a sample of 253 live birds caught in the field between 2003 and 2006 and measured as many of these parameters as possible from an additional 2,455 museum skins. All individuals were adults with intact wings and at least 1 of each sex. Each species ranged from 1 to 84 individuals. Males of 331 species, an estimate of mass was taken from the literature, primarily from Schuchmann (1999).

**Allometry.**—For a trait length regressed against body mass, a reasonable null hypothesis is a slope of 0.33, which is the slope expected for geometric similarity (isometry; Greenewalt 1975).
Ordinary least-squares regression (OLS) underestimates slope when there is measurement error in the independent variable (Rayner 1985, Carroll and Ruppert 1996, McArdle 2003). One estimate of this error is the within-species error variance, which is caused by both true variation within a species and measurement error. Body-mass error variance was calculated using an analysis of variance (ANOVA) on all specimens that had an individual measure of body mass; sexes were analyzed separately. I used the method-of-moments (MM) slope correction of

\[ MM(b) = OLS(b)\frac{\sigma^2_{\text{tot}}}{(\sigma^2_{\text{tot}} - \sigma^2_{\text{err}})} \]  

which is equation (7) in Carroll and Ruppert (1996), where \( b \) is the slope, \( \sigma^2_{\text{tot}} \) is the total sample error variance, and \( \sigma^2_{\text{err}} \) is the within-species error variance calculated from the ANOVA. However, use of the raw species data to calculate \( \sigma^2_{\text{err}} \) will cause it to be an underestimate because of an overestimate of the degrees of freedom associated with non-phylogenetically corrected analyses (Felsenstein 1985, Garland et al. 1992). This means that the MM correction will still intrinsically underestimate the true slope, but less than the uncorrected OLS estimate.

Reduced major axis (RMA) regression is often used in allometric studies. This regression model assumes that \( \sigma^2_{\text{err}} \) is proportionally divided between the two variables. This may be the most reasonable assumption when the functional relationship between two similar variables is unknown and neither one could be construed as the independent variable, as in cases in which two similar morphological structures are regressed against each other. But RMA regression inherently overestimates the true slope when one variable functions independently (Rayner 1985, Carroll and Ruppert 1996, McArdle 2003). It seems more reasonable to consider body mass (an index of body size) the independent variable, and other characters (e.g., tail length) the dependent variables, rather than treating both variables as equivalent. If body mass is functionally independent, RMA regression overestimates the true slope. Because the MM-corrected OLS slope is an underestimate and the RMA slope is an overestimate, both were calculated as lower and upper bounds on the true allometric slopes.

**Analyses of shape.**—Because I measured the length of each of 5 rectrices, analyses of tail “shape” consisted of analyses of the co-variation between these 5 lengths, ignoring other components of the tail’s true shape, such as the shape of individual rectrices. Tail shape was assessed using two methods. First, each species and sex was placed into discrete shape categories. “Rounded” tails were those in which lengths of all of the rectrices were within 20% of each other (Fig. 1). Of the remaining, “graduated” tails were those in which R1 was longest, and specifically the length order of the rectrices was R1 ≥ R2 ≥ R3 ≥ R4 ≥ R5. “Forked” tails were those in which the R5 was longest (length order: R5 ≥ R4 ≥ R3 ≥ R2 ≥ R1). Forked shapes were further split into “moderately forked” (R5/R1 < 2.0) and “elongated fork” (R5/R1 > 2.0). “R2” morphologies were those in which R2 was longest (length order: R2 ≥ R3 ≥ R4 ≥ R5 and R2 ≥ R1), “R3” shapes were those in which R3 was longest (R3 ≥ R4 ≥ R5 and R3 ≥ R2 ≥ R1), and “R4” shapes were those in which R4 was longest (R4 ≥ R5 and R4 ≥ R3 ≥ R2 ≥ R1). Rectrices that differed in length by <2 mm were treated as equal in length, to deal with a few species that would otherwise not quite fall into any of these categories. There are many other plausible morphologies than those just described, such a long R1 and R5 but short R3 (i.e., R1 ≥ R3 and R5 ≥ R3), but these numerous potential shape classes were not observed in my sample of hummingbirds. These shape classes were used to identify originations of derived shapes and dimorphism on the hummingbird phylogeny.

Second, because categorical divisions of shape are somewhat arbitrary, tail shape was analyzed by computing principal components (PCs) of body mass, folded wing length, and R1, R2, R3, R4, and R5 length for each sex of each species. To enable comparisons between sexes, both sexes of each species were entered into a single analysis, so that values for male and female tails were computed on common PC axes.

**Phylogeny.**—I obtained a molecular phylogeny of 151 hummingbirds from McGuire et al. (2007), except that I treated Purple-throated Mountain-gem (*Lampornis calolaemus*) as a subspecies of White-bellied Mountain-gem (*L. hemileucus*), which resulted in a 150-taxon tree. I also obtained a second, unpublished phylogeny of ~290 taxa from J. McGuire and supplemented it with additional taxa based on taxonomic relationships inferred from Schuchmann (1999). All analyses were performed on the 150-taxon phylogeny unless I explicitly state otherwise. For analyses of discrete tail shapes, ancestral character states were inferred by assuming parsimony. In cases in which it was ambiguous whether a novel tail morphology had evolved once and was then lost once or had evolved twice, it was always reconstructed as a gain and a loss, thereby conservatively hypothesizing the fewest possible number of originations of novel tail morphologies.

Using the PDAP module in the program MESQUITE (Midford et al. 2005, Maddison and Maddison 2006), I calculated independent contrasts of mass, folded wing length, and R1, R2, R3, R4, and R5 length for males and females separately. Likewise, independent contrasts of PC2 were computed. Branch lengths were not transformed, because the contrasts of each trait were not correlated with the standard deviation of branch lengths (Garland et al. 1992).

Smaller hummingbird species were hypothesized to exhibit less variation in tail morphology than larger ones. I tested the prediction that absolute body mass (a “state” variable) is correlated with variation in tail length. This cannot be assessed using independent contrasts of body size, because the process of computing independent contrasts of body mass produces a “rate” variable. Garland et al. (1992) recommended regressing the independent contrasts of tail length and dimorphism against nodal values of body mass associated with each contrast. I used the Breusch-Pagan test, which is a regression statistic that tests for heteroskedasticity in Y as a function of X, using the statistical program STATA, version 8.1 (StataCorp, College Station, Texas).

### RESULTS

**Wing and tail allometry.**—Wing and tail length in hummingbirds exhibit positive allometry. Table 1 lists the allometric exponents for folded wing length and rectrix length. All except the OLS estimate of the female R1 were significantly greater than the isometric prediction of 0.33. Male rectrices had OLS scaling exponents between 0.45 and 0.49, and none was significantly different from the others (\( P > 0.05 \)). Females had greater allometric exponents in more lateral feathers, although only R5 was significantly greater
than R1 and R2 after Bonferroni corrections were incorporated (t-test, df = 297, P < 0.005).

On the basis of scaling exponents for all the rectrices of both sexes, a conservative general estimate of average rectrix ($R_n$) scaling is 0.5, which lies between the MM-corrected OLS and RMA estimates of $b$ for most of the individual rectrices (Table 1). Assuming $S_A = R_n^2$ (Equation 1), tail surface area scales as approximately mass$^{1.0}$. Consequently, tail loading (body mass per unit tail surface area) is minimally correlated with interspecific body mass in both males and females (Fig. 2A).

Folded wing length also scales approximately as mass$^{0.5}$ (Table 1). Assuming that measures of folded wing length are highly correlated with the true wing length (which cannot be measured on museum specimens), wing disc loading is not correlated with body size (Fig. 2B), because (folded wing length)$^2$ scales as mass$^{1.0}$. Wing disc loading and tail loading are correlated (Fig. 2C).

Tail-shape evolution.—Phylogenetic reconstruction of tail shape suggested that the ancestral hummingbird had a rounded tail (Figs. 3 and 4), and this reconstruction matches the morphology of a basal fossil hummingbird (Louchart et al. 2007). Males of 169 (of 331) species exhibited the ancestral state of rounded tail shape. Using the unpublished 290-taxon phylogeny, forked tail morphology ($R_5/R_1 > 1.2$) has arisen in at least 26 clades, 12 of which have taxa with extremely forked tails ($R_5/R_1 > 2.0$). Graduated tail morphology is the second most common type of elongation, having evolved a minimum of 10 times (Fig. 4), which is significantly fewer than the number of times that forked morphologies arose (binomial test, $P < 0.01$, $n = 36$), as predicted by the limits model (Evans 2004). The shape $R_2$ evolved twice, in Peruvian Sheartail (*Thaumastura cora*) and Topaza sp. (Fig. 3E); $R_3$ shape evolved once, in the genus *Chaetocercus* (Fig. 3F); and $R_4$ shape arose twice, in the genus *Trochilus* (Fig. 3G) and in Lucifer Hummingbird (*Calothorax lucifer*).

Results from the principal component analysis are presented in Table 2. PC1 represented an index of body size, and PC2 was an index of shape on a forked–graduated continuum (Fig. 5A).

#### Table 1. Phylogenetically corrected allometric exponents for female and male hummingbirds (±SE; OLS = ordinary least-squares regression, RMA = reduced major axis regression).

<table>
<thead>
<tr>
<th></th>
<th>Female OLS</th>
<th>Female RMA</th>
<th>Male OLS</th>
<th>Male RMA</th>
</tr>
</thead>
<tbody>
<tr>
<td>Wing</td>
<td>0.42 ± 0.02a</td>
<td>0.47 ± 0.02a</td>
<td>0.50 ± 0.02a</td>
<td>0.45 ± 0.02a</td>
</tr>
<tr>
<td>Rectrix 1</td>
<td>0.41 ± 0.05</td>
<td>0.67 ± 0.05</td>
<td>0.70 ± 0.04</td>
<td>0.46 ± 0.04</td>
</tr>
<tr>
<td>Rectrix 2</td>
<td>0.41 ± 0.04a</td>
<td>0.61 ± 0.04a</td>
<td>0.64 ± 0.04</td>
<td>0.46 ± 0.04a</td>
</tr>
<tr>
<td>Rectrix 3</td>
<td>0.48 ± 0.03a</td>
<td>0.60 ± 0.03a</td>
<td>0.55 ± 0.03a</td>
<td>0.45 ± 0.03a</td>
</tr>
<tr>
<td>Rectrix 4</td>
<td>0.52 ± 0.04a</td>
<td>0.65 ± 0.04a</td>
<td>0.59 ± 0.04a</td>
<td>0.49 ± 0.04a</td>
</tr>
<tr>
<td>Rectrix 5</td>
<td>0.58 ± 0.04a</td>
<td>0.76 ± 0.04a</td>
<td>0.89 ± 0.06a</td>
<td>0.49 ± 0.06a</td>
</tr>
</tbody>
</table>

*Exponents significantly differ from 0.33 (P < 0.05, n = 149 contrasts). Method-of-moments correction factors of 1.037 (males) and 1.049 (females) are incorporated into the OLS slopes (Equation 2).*

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**Fig. 2.** Body size explains little of the variation in (A) tail loading and (B) wing disc loading in male and female hummingbirds (tail loading, males: $P = 0.68$, $r^2 = 0.001$; females: $P = 0.04$, $r^2 = 0.01$; wing disc loading, males: $P = 0.95$, $r^2 < 0.001$; females: $P < 0.001$, $r^2 = 0.04$). (C) Wing disc loading and tail loading are positively correlated (males: $P < 0.001$, $r^2 = 0.26$, $n = 316$; females: $P < 0.001$, $r^2 = 0.31$, $n = 311$). Tail loading was calculated using Equation 1, assuming $\beta = \pi/2$ radians for all taxa. Wing disc loading was calculated assuming a stroke amplitude of 150° and that wing length was 1.2× folded wing length for all taxa. Giant Hummingbird (*Patagona gigas*) and White-bellied Woodstar (*Chaetocercus mulsant*) were excluded because they are outliers in mass and wing loading, respectively.
Fig. 3. Evolution of tail shape in male hummingbirds. (E) The shape R2 arises once, (F) R3 arises once, and (G) R4 morphologies, although present in hummingbirds, do not occur in this phylogeny. Origination of possible non-aerodynamic functions are indicated: (i) female Heliothryx sp. may use their tails for crypsis in nest defense; (ii) Oreotrochilus sp. use their tails as mechanical props, as woodpeckers do; and (iii) males in the “bee” hummingbird clade use their tails to produce sound (it is unclear on which branch this character originated; the marked branch conservatively delineates the entire clade). Tail tracings: (A) male Sparkling-tailed Hummingbird (Tilmatura dupontii), (B) male Dusky Hummingbird (Cynanthus sordidus), (C) female Vervain Hummingbird (Mellisuga minima), (D) Pale-bellied Hermit (sex unknown; Phaethornis anthophilus), (E) male Crimson Topaz (Topaza pella), (F) male White-bellied Woodstar (Chaetocercus mulsant), and (G) male Red-bellied Streamertail (Trochilus polytmus). A–D were traced from photographs, whereas E–G are from Ridgway (1892). Tracings are at different scales.
Fig. 4. Evolution of tail shape in male and female hummingbirds (PC2). Tree topology and character states are as in Figure 3. Dimorphic taxa (D) are species in which male and female tail morphology fall into different tail-shape categories, without distinguishing between moderately forked and extremely forked shapes; “M” indicates monomorphic taxa. Originations of forked tail shape are indicated on the male phylogeny (labeled f1 to f18), and originations of graduated tail shape are indicated in the female phylogeny (labeled g1 to g10).
Tail forkedness (PC2) was highly correlated with the R5/R1 ratio (log fit, $r^2 = 0.97$), allowing morphologies predicted by the delta-wing hypothesis to be mapped onto tail forkedness (Fig. 5A). Overall, tail morphology of most hummingbirds did not fall within the band of morphologies predicted by the delta-wing hypothesis (Fig. 5A).

**Tail-shape dimorphism.**—According to the delta-wing hypothesis, moderately forked morphologies are favored by selection for flight performance, so females (which are presumably under less sexual selection, given that they alone care for the offspring) were predicted to tend to exhibit moderately forked tails (gray band in Fig. 5B), and other tail shapes would be sexually dimorphic, with males deviating farther from the hypothesized aerodynamic optimum. However, the data fit this prediction poorly. In 287 of 310 species, tails were more forked in males than in females (Fig. 5B). When tail shapes were treated as discrete categories, forked tail shapes arose 18 times on the 150-taxon phylogeny (Fig. 4). Fork dimorphism, in which the tail of only one sex is forked, evolved at least 11 times. Rather than being female-biased, as predicted, this dimorphism was significantly male-biased; in all 11 cases, the tail of the male was forked (binomial test, $P < 0.001, n = 11$; Figs. 4 and 5B). Graduated morphology evolved 10 times (Fig. 4). Dimorphism in graduated morphology arose 4 times, and though in all 4 cases the female tail was graduated and the male was not, this was not significantly different from random (binomial test, $P = 0.125$).

**Variation in tail length.**—According to the limits model, small hummingbird species were predicted to exhibit less variation in tail morphology than large ones. Male tail length was heteroskedastic with respect to body size, but opposite to the prediction: small hummingbird species exhibited greater variation in tail length than large ones, in both phylogenetically uncorrected (Fig. 6A) and phylogenetically corrected (Fig. 6B) analyses. Likewise, small species exhibited greater variation in length dimorphism than large species, in both phylogenetically uncorrected (Fig. 6C) and phylogenetically corrected (Fig. 6D) analyses. These two analyses are not independent, because most of the long-tailed species were also highly dimorphic; therefore, panels A–D in Figure 6 essentially depict the same result: small species repeatedly evolved elongated or dimorphic tails (or both) more frequently than large ones, which results in a decrease in variance in tail morphology with increasing body size.

Contrary to a prediction of the limits model (Evans 2004), forkedness (PC2) was not influenced by body size (Fig. 5A). Forkedness and male mass were weakly correlated in the raw species data ($r^2 = 0.02, P = 0.01, n = 315$), but independent contrasts of body mass were uncorrelated with independent contrasts of male forkedness ($P > 0.2, n = 149$), and nodal values of mass were also uncorrelated with independent contrasts of male forkedness ($P > 0.6, n = 149$).

**Other results.**—Males of the tiny, extremely dimorphic Marvelous Spatuletail (*Loddigesia mirabilis*) have minute inner rectrices (Zusi and Gill 2009) that I recorded as having zero length. This species, which has evolved its elongated tail independently of other long-tailed taxa (McGuire et al. 2009), was not included in the multivariate analyses, because log (0) is undefined.

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**Table 2.** Factor loadings from a principal component analysis of morphology of 623 species–sex classes of hummingbird, and percentage of variation attributable to the first and second principal components.

<table>
<thead>
<tr>
<th>PC1</th>
<th>PC2</th>
<th>%</th>
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<tbody>
<tr>
<td>Mass</td>
<td>0.389</td>
<td>0.044</td>
</tr>
<tr>
<td>Wing</td>
<td>0.413</td>
<td>0.058</td>
</tr>
<tr>
<td>R1</td>
<td>0.313</td>
<td>0.622</td>
</tr>
<tr>
<td>R2</td>
<td>0.385</td>
<td>0.346</td>
</tr>
<tr>
<td>R3</td>
<td>0.418</td>
<td>−0.055</td>
</tr>
<tr>
<td>R4</td>
<td>0.376</td>
<td>−0.415</td>
</tr>
<tr>
<td>R5</td>
<td>0.340</td>
<td>−0.559</td>
</tr>
<tr>
<td>%</td>
<td>77.0</td>
<td>15.5</td>
</tr>
</tbody>
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Fig. 5. Male tail shape plotted against (A) male body size and (B) female tail shape for 330 and 310 hummingbird species, respectively. Gray bands indicate moderately forked tail shape as predicted by the delta-wing hypothesis. Dashed lines delineate three morphological categories: f = forked (R5/R1 > 1.2), r = rounded (0.83 < R5/R1 < 1.2), and g = graduated (R5/R1 < 0.83). Square symbols in A indicate related hummingbirds in the genus *Phaethornis*. In B, monomorphism is indicated by the solid diagonal line (arrow). The 23 points below the line represent species in which tails of females are more forked than those of males.
Three possible originations of derived, non-aerodynamic tail functions are shown in Figure 3: (i) the genus *Heliothryx* exhibits the greatest reverse sexual dimorphism of any hummingbird (females have longer tails than males), and females spread their tails while mimicking falling leaves as they leave the nest (Cintra 1990, Schuchmann 1990); (ii) the genus *Oreotrochilus* has stiffened, slightly elongated tail-feathers, which the birds use as a prop while clinging to cave walls, as woodpeckers do (Picidae; Pearson 1953, Carpenter 1976); and (iii) in the bee hummingbird clade, many males have tapered or narrowed rectrices (Fig. 3F) and use their tails to produce sound (Clark and Feo 2008). The branch on which this function originates is unclear. Dropping these 3 clades from the analyses does not affect the statistical significance of the morphological patterns.

**Discussion**

I mapped the evolution of hummingbird tail morphologies on a phylogeny to test preexisting hypotheses of how ornamental (elongated, dimorphic) morphologies may be constrained. Below, I elaborate upon the following two points. First, aerodynamic models of how bird tails function failed to predict hummingbird tail shape, especially of females. Yet females are likely to experience low levels of sexual selection, which indicates either that assumptions of the models are inappropriate for hummingbirds or that the assumption that hummingbird tail morphology is selected for flight performance is incorrect. Second, the overall allometry of tail morphologies in hummingbirds may place constraints on large hummingbirds, limiting (although not entirely preventing) the evolution of dimorphic tail ornaments in large species. This may explain the negative correlation between variation in tail morphology and body size. That is, it may explain why, in this clade, the smallest animals have tended to evolve the longest ornamental tails.

**Wing and tail allometry.**—Both wing and tail length exhibit positive allometry (hyperallometry): large hummingbird species have disproportionately longer wings and tails than small ones (Table 1). This pattern differs from birds in general, in which wing length scales isometrically (Greenewalt 1975). The same holds true for tail length: Fitzpatrick (1999) presented an OLS regression of tail length on tarsus length for 742 diverse species that did not include any hummingbirds. The RMA slopes recalculated from her figure 1 are \( \sim 1.0 \), which suggests that tail length scales isometrically with tarsus. Hovering flight could be the cause of this unusual wing allometry in hummingbirds: hovering flight is one of the most demanding forms of flight (Altshuler and Dudley...
2003), and, because its costs are a function of wing disc loading
(Altshuler et al. 2004), wing length may evolve in response to se-
lection for the ability to hover.

It is unclear why the rectrices have the same allometric ex-
ponent as the wings. Possibly the tail’s size complements that of
the wings. The tail produces force in concert with the wings during
flight (Usherwood et al. 2005). Assuming that aerodynamic forces
are produced in proportion to surface area, tail force production
may scale the same, matching the concomitant increase in size and
force production of the wings. This is also suggested by the cor-
relation between wing disc loading and tail loading (Fig. 2C),
which implies that, independent of body size (as seen in Fig. 2A,
B), the tail’s optimal size is influenced by wing size. However, how
forces produced by the wings interact with forces produced by the
tail is potentially complex, presumably varies with mode of flight,
and has not been adequately studied.

**Tail shape and aerodynamic function.**—The morphological
patterns within hummingbirds are not consistent with predic-
tions of the delta-wing hypothesis. Hummingbird tail shape is
highly variable, with most of the variation (after accounting for
body size) lying on a forked–graduated continuum (Table 2 and
Figs. 1 and 5). Most hummingbirds do not have moderately forked
tails (Figs. 3 and 5), and most of the moderately forked tails that
have evolved are sexually dimorphic, which implies that sexual
selection is involved in their origination. I therefore conclude that
natural selection for flight performance does not generally result
in moderately forked tail morphology in hummingbirds.

Hummingbirds have unique wing kinematics (Tobalske et al.
2007), and the tail’s unique positive allometry (Table 1) suggests
that hummingbird tail morphologies are under different selective
pressures than those of other birds, so hummingbirds may be an
exception to more general patterns. However, it is not clear which
assumptions of the delta-wing hypothesis may be invalid in hum-
mingbirds. One possibility is the importance of aerodynamic in-
teractions between the wings and tail. Given that hummingbirds
have high wingbeat frequencies, shed vortices from the wings may
interact with the tail to a greater degree than in other birds. This
possibility deserves further attention; during flight, the wings of
other kinds of birds also create an induced airflow that could in-
teract with the tail. Therefore, wing–tail aerodynamic interactions
are plausible in other birds as well. It is also possible that the delta-
wing hypothesis applies only to high-speed flight (Balmford et al.
2000), whereas hovering flight plays an important role in hum-
mingbird ecology. However, if the delta-wing hypothesis primar-
ily applies to high-speed flight, it would be important to account
for body–tail aerodynamic interactions, which increase with, and
are significant at, higher flight speeds (Maybury and Rayner 2001,

**Moderately forked morphology is sexually selected in
hummingbirds.**—In hummingbirds, moderately forked tails are
primarily observed in two evolutionary scenarios. Either male
hummingbirds have them, whereas females have rounded or grad-
uated tail morphology, or males have extremely forked tails and
females have moderately forked tails (Figs. 4 and 5B). The latter
pattern may be caused by genetic correlation between the sexes,
but I will elaborate on this possibility in future publications. This
dimorphism suggests that moderately forked tail morphology
arises via sexual selection.

Although forked tail shape appears to arise via sexual selec-
tion, it could nevertheless have aerodynamic functions, provided
that it is the aerodynamic functions that are subject to sexual se-
lection. For example, maneuverability apparently plays a role in
high-speed chases, fights, and displays, behaviors that may be
sexually selected by either male–male competition for courtes-
tory or female choice (Clark 2009). Males could therefore be
sexually selected for morphology more optimized for maneuver-
ability. By contrast, females tend to be less aggressive and ter-
ritorial than males (Altshuler et al. 2004) and may be selected
for more efficient flight. This suggests that forked tails may arise
through selection for maneuvering flight, at the expense of some
other aspect of flight, such as energetic efficiency, as was suggested
by Park et al. (2000), who showed that forked tail morphologies in-
crease maneuverability at the expense of linear flight capabilities
in House Martins (*Delichon urbica*).

Data on how males compete for reproductive territories are
not yet available for most hummingbird species. But one example
shows that moderately forked tail morphologies can be sexually
selected for reasons other than aerodynamic functions. Males of
the sexually dimorphic Anna’s Hummingbird (*Calypte anna*) have
recently evolved a moderately forked tail (Fig. 3, and f1.5 in Fig. 4),
but this shape has arisen in conjunction with the production of
loud sounds with outer tail-feathers (Clark and Feo 2008). Females
of this species have rounded tails and do not produce sound with
their tails.

**Body-size limits on the evolution of ornamental tail
morphology.**—Hummingbird tail morphology is inconsistent with
nearly all the hypothesized size-related limits on tail shape (Ev-
ans 2004). Small hummingbird species exhibited far greater varia-
tion in tail morphology and degree of dimorphism than large ones
(Fig. 6A–D), which suggests that the latter are more constrained
in their morphology. These unsupported predictions may result
from the model’s failure to consider allometry. The model esti-
mates the cost of tails ≤1 m long attached to birds of different sizes
(Evans 2004), without considering the relative magnitude of this
morphology. A 1-m rectrix is a 5-fold increase in tail length to a
pigeon, the largest species that Evans (2004) considered, but 1 m
is nearly a 30-fold increase in rectrix length to a small bird, such
as the average hummingbird. Some hummingbirds bear the costs
of a 5-fold rectrix elongation, as shown by species that have tails
nearly 0.2 m long (Fig. 6A). By contrast, elongation of the tail by
30× does not appear to occur naturally in birds of any size. The
only bird with a tail close to 30× longer than normal is the Onaga-
Dori, a Japanese breed of Domestic Chicken (*Gallus gallus*; Sasaki
and Yamaguchi 1970, Takahashi et al. 1998). It does not fly with
such a tail; in fact, the tail can only reach this length when a cock
is prevented from molting through confinement in a small cage for
several years (Sasaki and Yamaguchi 1970).

The greater diversity of tail length in small hummingbirds
(Fig. 6) may be caused by the general pattern of positive tail al-
lometry (Table 1). Sexually selected traits that also serve viability-
related functions may impose body-size-dependent costs (Bon-
duriansky and Day 2003, Bonduriansky 2007). In hummingbirds,
tail length appears to be naturally selected to scale as mass$^{0.5}$,
which means that all large species have disproportionately large
tails. I hypothesize that, owing to the tail’s allometrically greater
size in larger species, stabilizing selection is greater in these
taxa, which constrains diversification. The less plausible alternative explanation would be that the strength of sexual selection scales hypoallometrically, for example if females have a tendency to evolve preferences for long tails of a particular absolute length. Because large species already have proportionally larger tails, further elongation via sexual selection could be reduced, compared with the elongation favored in small taxa.

**Tail length, costs, and diversification.—**Previous studies of bird tail function have primarily focused on swallows (Norberg 1994; Matyjasik et al. 1999, 2000, 2004; Buchanan and Evans 2000; Rowe et al. 2001), which as a clade seem to exhibit low interspecific variation in tail morphology. This low variation may be attributable to higher flight costs and concomitant constraints on their tail morphology, as caused by the high flight speeds they maintain for long periods throughout the day. By contrast, wind-tunnel experiments using the Red-billed Streamertail’s (*Trochilus polytmus*) tail (Fig. 3G), which has essentially the longest tail of any hummingbird, suggest that although a long tail increases the energetic cost of flight, it does so by a modest amount and only at high flight speeds (Clark and Dudley 2009). Because hummingbirds appear to differ from other birds in that their tail length exhibits positive allometry (Table 1), it is unclear whether other patterns shown here (e.g., greater variation in tail morphology exhibited by small hummingbirds; Fig. 6) will generalize to other birds.

Forked tail morphologies seem to be aerodynamically advantageous in some circumstances (Balmford et al. 1993, Thomas and Balmford 1995, Buchanan and Evans 2000, Park et al. 2000, Rowe et al. 2001), but it would appear that this is not the only optimal morphology and that tail morphology tends to lie along a forked-graduated continuum. A better understanding of the aerodynamic function(s) of all these morphologies will require further empirical studies that explore and clarify the relationship between tail shape and the aerodynamic forces produced by the tail (including wing–tail and body–tail interactions), as well as the actual function of these forces in various modes of flight, such as forward flight at various speeds or maneuvers.

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**Literature Cited**


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