

ECOMORPHOLOGY AND PHYLOGENY OF HUMMINGBIRDS: DIVERGENCE AND CONVERGENCE IN ADAPTATIONS TO HIGH ELEVATIONS

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Resumen. – Ecomorfología y filogenia de colibríes: divergencia y convergencia en adaptaciones para ocupar elevaciones altas. – En este artículo yo confronto los resultados de un estudio a largo plazo de la ecomorfología de los colibríes que incluye mediciones de varios parámetros de los picos, alas, patas y colas, más otros cálculos de varios parámetros aerodinámicos, con una filogenia recién publicada de la familia Trochilidae para examinar las adaptaciones que han permitido a algunos grupos de colibríes de colonizar las altas montañas del Neotrópico. Sólo dos de los ocho clados principales de colibríes han sido notablemente exitosos en ocupar las elevaciones altas, y éstos muestran adaptaciones morfológicas contrastantes, relacionadas con la ocupación de diferentes hábitats y visitación de diferentes grupos de flores. Miembros de otros clados que ocurren en las elevaciones altas muestran diferentes grados de convergencia con los miembros de estos dos clados.

Abstract. – In this paper I confront the results of a long-term study of hummingbird ecomorphology involving measurements of various parameters of bills, wings, feet and tails, and calculation of several aerodynamic parameters, with a recently published phylogeny of the family Trochilidae to examine the adaptations which have permitted some groups of hummingbirds to inhabit high elevations of the Neotropics. Only two of the eight major clades of hummingbirds have been notably successful in colonizing high elevations, and these show contrasting sets of morphological adaptations related to occupation of different habitats and visitation of different sets of flowers. Members of other clades occurring at high elevations show varying degrees of convergence with the members of these two clades. *Accepted 4 December 2007.*

Key words: Adaptations, ecomorphology, high elevations, hummingbirds, phylogeny.

INTRODUCTION

The family Trochilidae has long been divided into two subfamilies, Phaethornithinae (hermits) and Trochilinae (nonhermits, including c. 90% of all hummingbird species). Recent molecular phylogenetic studies indicate that, within the Trochilinae, there exist seven or eight major clades, one of which might even be basal to the hermit-nonhermit split (Blei-

weiss *et al.* 1997, Altshuler *et al.* 2004, McGuire *et al.* 2007; see Table 1). However, these studies have not considered in any detail how morphology and ecology (including relations with flowers) might reflect phylogeny, perhaps in part because the traditional measurements taken on museum skins give a very incomplete idea of the birds' morphology. For over a decade, I have been taking a wider variety of measurements of the external mor-

TABLA 1. The principal clades of hummingbirds (Trochilidae) with their respective numbers of species represented in the morphological data set, the mean capture elevation of their species and some of their most representative genera (adapted from McGuire *et al.* 2007).

Clade	Number of species	Mean elev. (m)	Some representative genera
0 (“topazes”)	1	480	<i>Florisuga, Topaza</i>
1 (“hermits”)	25	560	<i>Phaethornis, Glaucois, Threnetes, Entoxeres</i>
2 (“mangos”)	15	1234	<i>Anthracothorax, Colibri, Doryfera, Schistes</i>
3 (“coquettes and high Andeans”)	15	2773	<i>Metallura, Chalcostigma, Lesbia, Adelomyia</i>
4 (“brillants”)	32	2198	<i>Coeligena, Eriocnemis, Heliodoxa, Urosticte</i>
5 (“giant”)	0	—	(<i>Patagona</i>)
6 (“Middle American mountaneers”)	6	1717	<i>Lampornis, Eugenes, Panterpe, Heliothraupis</i>
7 (“woodstars and bees”)	9	1117	<i>Selasphorus, Calypte, Calliphlox, Chaetocercus</i>
8 (“emeralds”)	47	743	<i>Amazilia, Hylocharis, Chlorostilbon, Thalassidroma, Chalybura, Campylopterus</i>

phology of live or recently dead hummingbirds (in any case, not museum skins, since once so prepared many measurements, especially of wing and foot, are impossible to take). From these measurements, I have also calculated several aerodynamic parameters for each individual bird (see Stiles 2004, Stiles *et al.* 2005). With this information it is possible to explore in more detail hummingbird ecomorphology in a phylogenetic context.

High elevations, with their low temperatures, low air density and oxygen tension, represent a stressful environment for such small, active birds with their energetically demanding flight (Altshuler & Dudley 2002, Altshuler *et al.* 2004). Flower nectar represents a critical energy source for hummingbirds; since the bill-corolla “fit” strongly affects the efficiency

with which the bird extracts nectar, one might expect that, especially in high mountains, the form of the bill would reflect closely the type of flowers to which the bird is adapted. Other aspects of the birds’ morphology should reflect other adaptations for locomotion and feeding at high elevations. Among the Trochilinae, various morphological and aerodynamic parameters showed significant positive or negative relations with increasing elevation; by contrast, no parameter varied significantly with elevation among the hermits, which might help to explain their absence from high-elevation habitats (Stiles 2004).

The objective of this paper is to examine morphological adaptations shown by different clades of the Trochilinae for life at high elevations, in relation to the most recent and

detailed phylogeny of the family (McGuire *et al.* 2007). Specifically, I address the following questions: are some clades more successful than others (in terms of numbers of species, elevations achieved) at inhabiting high mountains? If so, have these clades converged or diverged in morphology? What are the ecological implications of such differences in morphology?

METHODS

I have measured the following parameters of external morphology to 0.1mm with dial calipers: bill length (total and exposed culmen), height of bill at nostril, commissure width, length (chord) of folded wing; length, maximum width and area of a planform of the extended wing; tail and tarsus length, extension of the foot and length (chord) of the hallux claw. I measured body mass with a Pesola spring balance. For comparisons of linear measurements, I divided each measurement by the the cube root of body mass to obtain relative values independent of absolute size of the bird. I calculated wing loading, wing disk loading, aspect and shape ratios and wing pointedness from the above wing measurements (see Stiles 1995, Stiles *et al.* 2005 for details). From museum skins, I made two additional measurements: bill curvature (arc:chord ratio of exposed culmen) and tail shape (ratio of the lengths of the outermost to central rectrices). I then ran a discriminant analysis (using Statgraphics 5.1, Statpoint Inc. 2005) to determine whether the different clades of hummingbirds could be distinguished on the basis of these 16 variables. I used linear regression to identify the variables associated with elevation. In order to identify the clades most associated with high elevations, I pooled the mean capture elevations of all species and, from the resulting distribution, considered the upper 10% to be highly specialized, and the next 11–25% to be weakly

specialized, for life at high elevations. I then determined which clades included the species in the upper 10% and 11–25%. I used a similar procedure for evaluating each morphological and aerodynamic parameter, save that I considered both the upper and lower 10% and 11–25% of each distribution as associations with high elevations could be positive or negative; the middle 50% of the species were considered to be unspecialized for the particular variable in question. This procedure was used because the global distributions of nearly all parameters deviated significantly from normality even when different transformations were applied. I confine my analysis to adult females, to avoid extreme morphologies of males produced by sexual selection. In all, data from 1675 individuals of 146 species and 9 statistically distinctive, allopatric subspecies are included in the analyses.

RESULTS

The discriminant analysis correctly assigned 85% of all taxa to their respective clades on the basis of the morphological and aerodynamic variables. The hermits (clade 1) were completely segregated from the other clades; the members of clade 3 were nearly as cleanly segregated in the opposite direction, the members of clade 4 fell between clade 3 and a dense cluster of points representing the species of the remaining clades, within which the degree of discrimination was less; however, even among these clades, most species were correctly assigned, such that one may, on the whole, speak of characteristic morphologies for each clade (Table 2).

Regression analyses identified the following variables as showing significant positive relations with increasing elevation: body mass; wing length, width and area; tarsus and hallux claw lengths and foot extension. Variables showing significant negative relations with elevation included bill curvature, commissure

TABLA 2. Results of the discriminant analysis among eight clades of hummingbirds, based upon measurements of 14 morphological variables and calculation of four aerodynamic parameters. Numbers along the diagonal represent species correctly assigned to their respective clades according to their morphologies; those off the diagonal showed greater morphological similarity to a different clade than their own. Some 85.7% of the species were classified correctly from morphology.

Correct clide	Clade predicted from morphology							
	0	1	2	3	4	6	7	8
0	2	—	—	—	—	—	—	—
1	—	25	—	—	—	—	—	—
2	1	—	11	—	—	—	—	3
3	—	—	—	14	—	—	—	—
4	—	—	1	—	26	2	—	3
6	—	—	—	1	—	5	—	—
7	—	—	—	—	—	—	8	1
8	—	—	4	—	—	2	1	40

width and bill height, wing loading and wing disk loading and wing aspect and shape ratios; a nearly significant negative relationship ($P = 0.057$) was found between bill length and elevation (see also Stiles 2004).

With respect to elevation, two clades, 3 and 4, stand out as having a high proportion of species occurring at high elevations (Table 3). Indeed, nearly half of the species of clade 3 are among the 10% most specialized, essentially those with mean capture elevations above c. 3000 m, including species of the genera *Oxygogon*, *Chalcostigma*, *Metallura*, *Opisthoprora*, *Heliangelus* and *Ramphomicron*. The species of clade 4 found at high elevations are in the genera *Coeligena*, *Pterophanes*, *Agleactis*, *Eriocnemis*, and *Lafresnaya*. Two species of clade 6 also occur regularly at these elevations, in the genera *Panterpe* and *Eugenes*, as well as one species of *Selasphorus* of clade 7. High-elevation species are notably lacking in the highly speciose clade 8, as well as clades 2 and 1. I now examine in detail representative morphological features of clades 3 and 4 in relation to the overall distributions of these features in the sample of 155 taxa (Table 3).

Body mass. Although there is a general ten-

dency for body mass to increase with elevation, among the two predominant clades at high elevations this tendency is manifest only in clade 4; nearly all members of clade 3 are medium- to rather small-sized. Very large species are found in several other clades as well, including largely species found between 2000 and 3000 m.

Relative bill (total culmen) length. The two clades most notable for containing long-billed species are the hermits (clade 1) and the brilliants (clade 4); the members of clade 3 have mostly moderately to very short, fine bills. Most other clades include a strong preponderance of species with moderate (c. 16–25 mm) bill lengths. Long-billed species also occur in clades 2 (*Doryfera*, *Androdon*) and 6 (*Eugenes*).

Bill curvature. The only clade in which bill curvature is strongly developed is the hermits; only scattered species in other clades have appreciably decurved bills, including especially species of *Lesbia* (clade 3), *Lafresnaya* (clade 4) and *Campylopterus* (clade 8). Of interest here is the other tail of the distribution, which includes species with slightly recurved bills. This feature is most often developed in

clades 4 (*Coeligena*, *Ensifera*) and 2 (*Doryfera*, *Androdon*) and one species of clade 3 (*Opisthoprora*).

Relative (extended) wing length. Clade 4 includes by far the greatest number of long-winged species; of the others, only clade 2 has more than a single species with notably long wings; in clade 3, only *Oxyptogon* is long-winged.

Shape ratio R. High shape ratios denote narrow wings; low ratios, broad wings. Clade 3 has the greatest preponderance of broad-winged species, followed by clade 1 (hermits). Although there is a tendency towards broad wings in clade 4, it is much less pronounced; the tendency in clades 2, 7 and 8 is more towards narrow wings.

Wing loading. Clades 3 and 4, with most high-elevation species, are also those with most species showing notably low wing loading (large wing area in relation to body mass). Aside from these, some species of clade 2 (*Heliothryx*, *Colibri*, *Polytmus*) also have low wing loading. By contrast, most species of clade 7 show very high wing loading.

Relative tarsus length. All measures of hind-limb size are tightly correlated; tarsus length is representative. By far the most striking result is the very long tarsi (and large feet) of the species of clade 3; a much more modest tendency towards large feet/tarsi occurs in clade 4, with only one species in the upper 10% (*Agleactis*). Tarsi are moderate to short in all other clades, but one species of clade 6 (*Pantherpe*) falls just outside the upper 10% in this measure.

DISCUSSION

The two clades with most species at high elevations are strikingly divergent in most

aspects of their morphology. The members of clade 3 are medium to fairly small in size, with short, straight, rather fine bills, mostly moderately long but notably broad wings giving very low wing loading and very large tarsi and feet. The one species that diverges sharply from this pattern is a *Lophornis* coquette, member of a relatively small, basal subclade of diminutive inhabitants of forest canopy at low elevations. However, unlike the members of clade 7, which it otherwise resembles in morphology, this species does have fairly large feet – perhaps a preadaptation in this clade for invading high elevations?

By contrast, clade 4 species are typically medium-to-large in size, with moderate to long bills that are straight or slightly recurved (except for *Lafresnaya*), low wing loading given by notably long but only moderately broad wings and moderately large tarsi-feet. Of the two clades, those of clade 3 tend to occur higher in the mountains than those of clade 4 (Tables 1 and 3) and are more associated with open páramo and subpáramo habitats, while those of clade 4 occur more in high Andean forest and subpáramo, although clade 3 contains forest species (e.g., *Adelomyia*, *Helianthus*) and some species of clade 4 are mostly páramo inhabitants (*Pterophanes*, *Agleactis*). The very large, broad wings of most clade 3 species represent evident adaptations for flight in the low-density air of high elevations; in clade 4, *Pterophanes* is also notable for its enormous wings; *Agleactis* also has notably low wing loading. The longer, somewhat narrower wings of most members of clade 4 may provide greater maneuverability in their forest habitat, in which members of *Coeligena* and *Ensifera* in particular may make long flights between flowers (cf. Gutiérrez *et al.* 2004).

The difference in bill length between these clades is also very notable. The members of clade 3 at the highest elevations tend to visit flowers of the composite (Asteraceae) family,

TABLE 3. Numbers of species of different clades in different segments of the overall distributions of all species measured in this study with respect to different variables. Species in the two extreme groups (the highest and lowest 10% for each variable) may be considered to be highly specialized with respect to the bulk of the species; those in the next 11-25% on either side of the distribution, weakly specialized, and the middle 50%, unspecialized. Because their members are similar in morphology and ecology, and because they contain only one species and two taxa, I combined clade 0 with clade 2 for this analysis.

Parameters and clades	Segments of the overall distribution				
	10% inferior	11–25% inferior	50% media	11–25% superior	10% superior
Mean capture elevation					
1	5	8	12	0	0
0+2	0	3	11	3	0
3	0	0	2	6	7
4	1	1	12	13	5
6	0	0	4	0	2
7	3	1	4	1	1
8	6	10	32	0	0
Mean body mass					
1	5	0	17	1	2
0+2	0	3	7	4	1
3	1	4	9	1	0
4	1	1	11	12	7
6	0	0	4	0	2
7	2	5	3	0	0
8	6	10	26	3	3
Relative length of total culmen					
1	0	0	7	10	8
0+2	0	5	9	1	2
3	8	7	0	0	0
4	1	1	17	9	4
6	0	0	3	2	1
7	3	1	6	0	0
8	3	9	35	1	0
Bill curvature (arc/chord)					
1					
0+2	4	2	7	4	0
3	1	7	5	2	0
4	10	7	14	1	0
6	0	0	6	0	0
7	0	4	6	0	0
8	0	3	37	7	1
Relative length of extended wing					
1	5	3	16	1	0
0+2	0	0	7	6	1
3	1	2	7	4	1
4	1	1	14	5	11
6	0	1	3	2	0

TABLE 3. Continued.

Parameters and clades	Segments of the overall distribution				
	10% inferior	11–25% inferior	50% media	11–25% superior	10% superior
7	6	4	0	0	0
8	2	12	30	4	0
Shape ratio of wing (length/maximum width)					
1	5	7	12	1	0
0+2	1	3	5	4	4
3	7	2	5	0	1
4	2	8	19	2	1
6	0	1	2	3	0
7	0	0	6	1	3
8	0	2	28	12	6
Wing loading (Mass/wing area)					
1	0	3	11	7	4
0+2	3	2	11	1	0
3	4	6	4	1	0
4	7	7	13	2	3
6	0	1	2	2	1
7	0	0	4	0	6
8	1	4	32	10	1
Relative tarsus length					
1	10	9	4	2	0
0+2	3	2	11	1	0
3	0	0	0	1	14
4	0	2	16	13	1
6	0	0	2	3	1
7	2	2	6	0	0
8	0	6	37	5	0

the predominant family of shrubby dicots at these elevations; the genus *Espeletia* may be a particularly important floral resource (Gutiérrez *et al.* 2004, Gutiérrez 2005; Stiles, unpublished data). The short, fine bills of these species appear well adapted for extracting nectar from the numerous tiny florets of the flower heads of these plants. By contrast, the moderate to long, straight to slightly recurved bills of most upper-elevation clade 4 species (*Eriocnemis*, *Coeligena*, *Ensifera*) appear best adapted for extracting nectar from the long, pendulous flowers of the family Ericaceae, which includes many shrubs and epiphytes of

high Andean forest and subpáramo (Gutiérrez *et al.* 2004, Gutiérrez 2005, Stiles unpublished data), as well as other flowers of similar morphology (e.g., *Fuchsia*, *Passiflora*, *Aetanthus*, *Bomarea*, etc.). A similar bill is possessed by *Pterophanes*, which visits especially flowers of *Puya* (Bromeliaceae); its huge wings may aid in its often very long flights between the widely scattered inflorescences, and I have seen it set its wings and soar as it descends to feed. The only species of clade 3 with a recurved bill, *Opisthoprora*, forages very differently: perched on an inflorescence of Ericaceae and bracing itself with its huge feet, it

pierces the tough corollas of the flowers to reach the nectar.

Tarsus and foot size is the final difference between the members of these two clades. Relative foot size is closely and directly related to the proportion of flower visits in which the hummingbird perches to feed, rather than hovering (Stiles 2004). Very long tarsi and large feet are the rule among clade 3, and may represent an adaptation for perching while feeding at the inflorescences of composites. Heinrich (1975) showed that the most efficient way for bumblebees to feed at inflorescences with many tiny flowers was to alight and walk between them, only taking flight to reach the next inflorescence; the hummingbirds appear to use a similar strategy and their very large feet might well help to cling to the inflorescences in the often windy conditions of the páramo. Among clade 4, the species of *Eriocnemis* and *Agleactis* tend to have the largest feet and perch most frequently, often at inflorescences of Ericaceae; *Coeligena* species and *Ensifera* have relatively smaller feet and nearly always feed while hovering.

Species in other clades that occur at high elevations show some striking convergences with members of these two clades. Most notably, *Panterpe insignis* of the high mountains of southern Middle America is morphologically very similar to members of clade 3 in its broad wings with low wing loading and very large feet; its bill is straight, slender and of moderate length, very like those of *Eriocnemis* or *Helianthus*; it visits a wide variety of flowers, including many Ericaceae, usually perching to do so (Wolf *et al.* 1976). Sympatric with it in these mountains is *Eugenes fulgens*, which in its large size, large but relatively longer and narrower wings, long bill and moderately large feet, is much more like a *Coeligena* of clade 4 save that its bill is not recurved and it visits relatively fewer pendulous flowers, but it also usually hovers to feed (Wolf *et al.* 1976).

Convergent with *Coeligena* in possessing long, recurved bills are the species of *Doryfera* in clade 2, which also show specialization for visiting pendant flowers of Ericaceae, albeit at mostly lower elevations (Stiles 1985). The species of clade 2 occurring at highest elevations, members of the genus *Colibri*, have converged with members of clade 4 in size and wing morphology but not so noticeably in other features.

In sum, the two clades to invade the high Andes have done so with quite different morphological adaptations; they are largely segregated in different habitats and mostly use different flowers which they visit in different ways, at least in part; they are most similar in having large wings, but even here there are pronounced differences in wing shape. Species of other clades that occupy high elevations show convergence in varying degrees to the members of these two clades.

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