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# PHYLOGENETIC CONSTRAINTS UPON MORPHOLOGICAL AND ECOLOGICAL ADAPTATION IN HUMMINGBIRDS (TROCHILIDAE): WHY ARE THERE NO HERMITS IN THE PARAMO?

**F. Gary Stiles**

Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá D.C., Colombia.
*E-mail:* fgstilesh@unal.edu.co

**Resumen. – Limitaciones filogenéticas en la adaptación morfológica y ecológica en colibríes (Trochilidae): ¿por qué no hay ermitaños en el páramo? –** Los ermitaños (subfamilia Phaethorninae), aunque posiblemente eran capaces de ocupar todo el rango altitudinal disponible cuando se separaron de los no ermitaños (subfamilia Trochilinae), no pudieron aumentar sus distribuciones altitudinales y diversificarse en las elevaciones altas durante el levantamiento de los Andes, mientras que los no ermitaños si lo lograron. Aquí examino la morfología externa de 21 especies de ermitaños y 115 de no ermitaños (1265 individuos en total) para explorar las posibles causas de esta diferencia. Once medidas morfológicas, incluyendo varias medidas de las alas y patas imposibles de tomar de pieles de estudio, la masa corporal y cuatro parámetros aerodinámicos fueron usados en los análisis. El análisis discriminante logró separar las dos subfamilias casi completamente con base en sus morfologías. El análisis de regresión reveló que los no ermitaños han variado de manera significativa con respecto a la elevación en casi todas las medidas, al contrario de los ermitaños en que ningún parámetro mostró algún cambio significativo con respecto a la elevación. Esta aparente in1flexibilidad morfológica de los ermitaños pudo haber limitado su habilidad para ocupar montañas altas. Se discuten las razones que podrían explicar este fenómeno.

**Abstract. –** The hermits (subfamily Phaethorninae), despite presumably being able to occupy the full range of elevations present at the time of their divergence from the Trochilinae (nonhermits), have failed to expand and speciate into higher elevations as the Andes rose, while the nonhermits succeeded. Here I use a detailed examination of external morphology of 21 hermit and 115 nonhermit species (1265 individuals in all) to explore the reasons for this diference. Eleven morphological measurements, including several of wings and feet impossible to obtain from study skins, body mass and four calculated aerodynamic parameters for each bird were used in a discriminant analysis that demonstrated that the two subfamilies are quite distinct morphologically. Regression analysis revealed significant variation with elevation in nearly all parameters in the nonhermits, whereas variation in the morphology of the hermits was independent of elevation in every parameter. This apparent inflexibility of hermit morphology might have limited their ability to occupy high mountains, and possible reasons for this are discussed. *Accepted 15 January 2004.*

**Key words:** Adaptation, Andes, evolution, high elevations, hummingbirds, morphology.

## INTRODUCTION

The hummingbirds (family Trochilidae) are the most specialized and successful nectar-feeding birds, with over twice as many species as any other anthophilous group (Stiles 1981). For some 150 years, the hummingbirds have been divided into two subfamilies, the hermits (Phaethorninae) and nonhermits or "typical" hummingbirds (Trochilinae). Hermits are relatively dull-colored, with little or none of the brilliant iridescence and extreme sexual dimorphism characteristic of many groups of nonhermits. Their bills are mostly long and/or curved, whereas nonhermits exhibit a much wider range of bill types. Most hermits are specialized for visiting the flowers of large monocots (e.g*., Heliconia, Costus*), while different groups of nonhermits show varying degrees of specialization for visiting a wide variety of flower groups. Comprising only c. 11% of extant hummingbird species, the hermits are mostly limited to wet tropical lowland forests; only a few species occur up to c. 2000 m on tropical mountains or in drier forests. By contrast, the nonhermits have speciated prolifically in the highlands of South and Central America, occupied desert habitats wherever flowers occur, and have extended far beyond the tropics into the cool temperate zones of both northern and southern hemispheres.

Recent biochemical data have confirmed the hermit-nonhermit split as the deepest divergence among extant hummingbirds and have resolved the subfamilial allocation of problematical genera (Bleiweiss *et al.* 1994, 1997; McGuire & Altshuler unpubl.). The DNA-DNA hybridization data of Bleiweiss (1998) place the divergence of the two subfamilies in the early Miocene, c. 17 mya. At this time the southern and central Andes had been uplifted to elevations probably not exceeding 1000–1500 m, whereas the uplifting of the northern Andes did not commence until c. 12–13 mya (Taylor 1995, Burnham & Graham 1999). Thus, based upon their current altitudinal distribution, the hermits could have occupied the entire range of available elevations of the early to mid-Miocene. The late Miocene and Pliocene saw the Andes rise to much higher elevations and become divided into several different cordilleras. At the same time, took place the uplift of high mountains in Central and North America and the closure of the seaway between North and South America by the Panamá landbridge. The resulting wealth of opportunities for range expansion and speciation was exploited to a far greater extent by the nonhermits than by the hermits. Given that both groups have presumably been "*in situ*" since their divergence, the absence of hermits from the high Andes is particularly intriguing: why are there no hermits in the páramo (or puna)?

One possible approach toward answering this question is to examine in more detail the morphologies of the two groups. Heretofore, hummingbird morphology has been treated only rather superficially, in the context of flower visitation. Only bill length and (sometimes) curvature, body mass and a measure related to wing span (wing disc loading) have been incorporated into most studies of hummingbird community ecology, mainly to explain or predict patterns of partitioning of nectar resources (e.g., Snow & Snow 1972, Feinsinger 1976, Feinsinger & Colwell 1978, Brown & Bowers 1985, Stiles 1985, and many others); only Feinsinger *et al.* (1979) specifically addressed the effects of elevation, but their analysis was weakened by use of inadequate aerodynamic parameters (Altshuler *et al.* 2004). Therefore, in this paper I take a much wider range of morphological measurements and calculate several pertinent aerodynamic parameters to characterize hummingbird morphology in more detail. These data permit me to answer the following specific questions: do hermits and nonhermits differ in overall morphology? How does morphology change with elevation in the two groups? And, do these patterns suggest a reason for the apparent inability of the hermits to occupy high-elevation habitats?

## METHODS

The basic method was to take a wide range of measurements on each individual hummingbird. Since several key measurements cannot be taken on study skins, I mostly measured hummingbirds captured in the field, or in some cases, frozen and thawed carcasses. Body mass, measured in the field or as soon as possible after death, was the most essential datum as it provided a scaling factor for other measurements. Most carcasses and a selection of wild-caught birds were dissected to check sex and age determination, and prepared as study skins that were deposited as vouchers in various museums.

The measurements taken were: length of exposed culmen and total culmen, width of the commissure or "mouth", height of the bill at the midpoint of the nasal opercula, length (chord) of the closed (folded) wing, tail length, tarsus length and length of the hallux claw (for details see Baldwin *et al.* 1931). I also measured the maximum extension of the toes for an estimation of foot size (see Marín & Stiles 1992). I extended the wing in a standard position to take a tracing of its silhouette or planform, measured its length *R* and maximum width (at the level of the tips of primaries 1–2), then cut out the planform and measured its area using a leaf area meter or image analysis software (Stiles 1995, Stiles & Altshuler 2004). The following aerodynamic parameters were then calculated: shape ratio $R_S$ (the ratio of the length *R* to the maximum width of the planform), aspect ratio $R_A$ (the ratio of 2*R* divided by the area of the wing – equivalent to dividing by the mean width of the wing averaged over its entire length), wing loading $P_W$ (body mass divided by the area of both wings), and wing taper $((R_A / 2\ Rs) - 1)$ which quantifies the relative pointedness or bluntness of the wingtip. All linear measurements were taken to 0.1 mm with a dial calliper, and body mass was taken to 0.1 g with a Pesola spring balance. For linear measurements, relative values were obtained by dividing each measurement by the cube root of the body mass of the hummingbird, permitting comparisons of shape independent of absolute size.

Only data for adult females are included here, to avoid complications deriving from sexual selection and resultant extreme morphologies of males of many species; sexual dimorphism will be treated elsewhere. A female was considered "adult" if its remiges and rectrices were full-grown and it showed no corrugations on the maxillary ramphotheca (Ortiz-Crespo 1972). Birds molting the remiges were included if it was possible to estimate fairly precisely the "missing" wing area (usually possible except when the outer 2–3 remiges were growing), and birds with heavy deposits of migratory fat or excessively desiccated in the freezer were excluded.

To determine to what extent hermits and nonhermits could be distinguished by the above suite of morphological and aerodynamic variables, I performed a discriminant analysis using the species means for each variable. I used regression analysis to determine whether any intraspecific variation in any variable existed with respect to elevation, for those species in which ten or more captures had been made over an elevation range of at least 1000 m. Then I used the regressions of species means of morphological and aerodynamic parameters on mean capture elevation for hermits and nonhermits, separately, to determine how the members of each subfamily responded to differing elevations.

## RESULTS

In all, measurements of a total of 1265 hummingbirds (322 hermits, 943 nonhermits) representing 136 species (21 hermits, 115 nonhermits) are included in this study. Most individuals and species were from Colombia and Costa Rica, but I also include measurements of several species from the USA and Brazil. For 7 species of hermits and 15 nonhermits, 2 or 3 morphologically distinct popu-

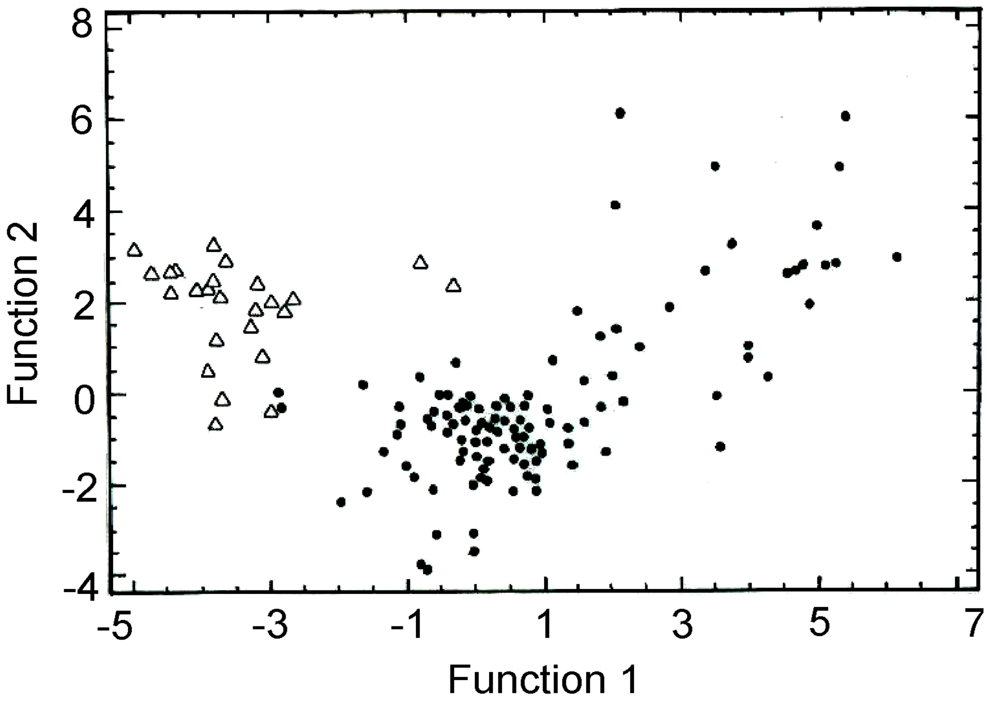

FIG. 1. Results of the discriminant analysis of morphological and aerodynamic variables for hermits (open triangles) vs nonhermits (solid circles): scores of discriminant functions 1 and 2. Note the almost complete separation of hermits vs nonhermits, with only two nonhermits misclassified (see text).

lations (usually different subspecies) from different geographic areas are included as distinct samples, for a total of 158 taxa. I found no statistically significant variation of any morphological or aerodynamic parameter within any species or subspecies with respect to capture elevation, hence used species or subspecies means for all further analyses.

The morphological and aerodynamic variables showed different degrees of intercorrelation in the discriminant analysis (relative values of all linear measurements were used). The two measures of bill length were very highly correlated, as were the three tarsus-foot measures, indicating high redundancy in each set. Wing length and length of the closed (folded) wing were nearly as highly correlated, as were shape and aspect ratios indicating moderate redundancies within each pair; body mass and wing area were, somewhat surprisingly, also fairly strongly correlated. Both wing loading and wing taper were highly independent of the other measurements, and the three tarsus-foot measures as a group, as well as tail length, were highly independent of all other measures. The first two discriminant functions explained 76% of the variation between subfamilies, and the third added another 9%.

The variables with greatest weight for separating hermits and nonhermits were relative bill length (longer in hermits), relative tarsus-foot measurements (smaller in hermits), relative bill height and commissure width (greater in hermits) and relative tail length (longer in

TABLE 1. Results of regression analysis for regressions of morphological and aerodynamic variables upon mean capture elevation for nonhermit and hermit species. Nearly all variables show significant changes with elevation in nonhermits; none do so among the hermits. Symbols for p: ns = $P > 0.05$; * = $P < 0.05$; ** = $P < 0.01$: *** = $P < 0.001$.

| Variables | Nonhermits (115 species) | Hermits (21 species) |
|---|---|---|
| Body mass | Increases ($F = 9.28$**) | No change ($F = 3.54$ ns) |
| Relative bill length | No change ($F = 0.04$ ns) | No change ($F = 2.77$ ns) |
| Relative bill depth | Decreases ($F = 21.83$***) | No change ($F = 1.12$ ns) |
| Relative wing length | Increases ($F = 16.91$***) | No change ($F = 2.02$ ns) |
| Shape ratio | Decreases ($F = 66.52$***) | No change ($F = 0.54$ ns) |
| Wing taper | Decreases ($F = 4.81$*) | No change ($F = 0.90$ ns) |
| Wing loading | Decreases ($F = 14.01$***) | No change ($F = 0.02$ ns) |
| Relative tarsus length | Increases ($F = 41.18$***) | No change ($F = 0.51$ ns) |
| Relative length of hallux claw | Increases ($F = 60.08$***) | No change ($F = 2.27$ ns) |

hermits); other variables contributing in lesser degrees were both relative wing lengths (shorter in hermits) and shape and aspect ratios (lower in hermits). The two subfamilies showed no significant differences in wing taper, body masses, wing loading or wing areas.

The discriminant analysis (Fig. 1) produced a nearly complete separation of hermits from nonhermits; no hermit was misclassified as a nonhermit, and only two nonhermits were misclassified as hermits: *Androdon aequatorialis* and *Lesbia victoriae*. The former had often been classified in the Phaethorninae in the past, until Bleiweiss *et al.* (1994, 1997) showed unequivocally that it belongs in a basal clade (the "mangoes") in the Trochilinae. However, its position in this clade is not basal, such that its hermit-like morphology was probably evolved subsequent to the divergence of the two subfamilies rather than representing persistence of a plesiomorphic state. Misclassification of *Lesbia victoriae* was almost entirely due to its very long tail, even in the female, and to a lesser degree to its rather thick bill. Another species approaching the hermits, albeit not misclassified, was *Campylopterus hemileucurus* due to its thick bill, wide mouth and rather long tail. To the first question, whether hermits and nonhermits as groups show characteristic morphologies, the answer is clearly yes.

The regressions of species means of morphological and aerodynamic parameters produced very different results in the hermits and nonhermits (Table 1). All parameters except bill length showed significant regressions on elevation among the nonhermits. Bill length tended to decrease with elevation on average, but the presence of the extremely long-billed *Ensifera ensifera* at elevations of 2500 m or higher tended to nullify this relation. Body mass increased with elevation (expected to decrease surface:volume ratio, and thus rate of heat loss, in cold highlands), bill height and commissure width decreased (smaller bills at higher elevations, adapted to small flowers like those of composites). All measures of relative wing size showed significant variation with elevation: wings become longer, broader (decreases in shape and aspect ratios) and blunter (decrease in taper), and the increase in wing size results in a decrease in wing loading towards higher elevations. This undoubtedly reflects the decrease in air density with elevation. Especially significant are the increases in all foot-tarsus dimensions with elevation. The advantage of larger feet at high elevations is probably twofold: 1) they permit reduction of foraging costs for relatively large hummingbirds by enabling them to perch, rather than hover, while extracting nectar (cf. Wolf *et al.* 1975); 2) and perching to forage likely permits high-elevation hummers to exploit tiny flowers in dense inflorescences, such as composites (cf. Heinrich 1975). Strong feet probably facilitate clinging to perches or inflorescences in the often windy conditions of the open páramo or puna. Thus, a wide range of morphological adaptations have undoubtedly helped the nonhermits to occupy high elevations.

The situation in the hermits is completely different: although they occur from sea level to over 2000 m, not a single morphological parameter shows significant variation with elevation. For most variables, the hermits tend to split up into three groups: the very large *Eutoxeres*, the medium-sized *Glaucis, Threnetes* and large *Phaethornis*, and the small *"Pygmornis" Phaethornis*. Within each group, no variation with elevation is evident. Whatever altitudinal tendencies as are shown by the hermits simply reflect the fact that the *Eutoxeres* occur, on average, at higher elevations than the tiny *"Pygmornis"* hermits; the more diverse medium-sized group spans the entire elevation range. In fact, the species reaching the highest elevations (*Phaethornis guy, P. syrmatophorus*) are morphologically indistinguishable from certain congeners of low elevations (e.g., *P. yaruqui* and *P. longirostris*). Thus, the second question also has a clear answer: the nonhermits have occupied upper montane habitats at least in part because they have had the capacity to adapt morphologically to the exigencies of high elevations; the hermits apparently do not have the capacity for such adaptation. It is as though the hermits have an essentially invariant morphological "package" that is resistant to change; they move upslope to the limits established by this "package", and no further.

## DISCUSSION

The reasons for the apparent inability of the hermit clade to produce species with high-elevation morphology are far from clear. Being largely restricted to the understory of wet tropical forest is correlated with sedentariness in hummingbirds and many other birds (e.g., Levey & Stiles 1992), and certainly hermits engage in much less altitudinal migration than nonhermits. On the other hand, hermits often trapline flowers over long distances, and some may move hundreds of meters up- or downslope on a daily basis (Stiles 1985). Also, the clade of nonhermits that includes the most extreme high-elevation specialists also includes a group of lowland species, the "coquettes", which show no evident morphological (pre)adaptations to high elevations, and which mostly do not engage in pronounced altitudinal movements in spite of being species of the upper, outer forest canopy (cf. Stiles & Skutch 1989).

Many hermits are specialized for visiting the nectar-rich flowers of large monocot herbs like *Heliconia*, and may schedule their breeding and molt cycles around the flowering of these plants (e.g., Stiles 1985). The upper altitudinal and latitudinal limits of the hermits and *Heliconia* also coincide quite closely (Stiles 1981). Such large, succulent herbs may be physiologically incapable of surviving cold temperatures and frost, but it is not clear why this should limit hermits (although I am unaware of any studies on physiology and torpor in hermits). At their upper altitudinal limits, hermits are largely dependent upon plants in families like Gesneriaceae, Bromeliaceae and Campanulaceae which occur much higher (Amaya 1998). Moreover, above the limits of hermits such flowers are visited by nonhermits of similar sizes, bill types and habits (e.g., *Lafresanya, Campylopterus, Eugenes*) such that lack of appropriate floral resources at these elevations cannot in itself explain lack of hermits. Competition from nonhermits is also a possibility, as hermits are usually subordinate at flowers (Stiles & Wolf 1979), but hermits can hold their own in exploitative competition when territoriality is not feasible (Gill 1988).

In sum, there are a number of suggestive ecological correlates with the apparent morphological and ecological stagnation of the hermits, but the extent to which these represent causal relationships is not at all obvious. It may be that the ultimate answer to this question will have to await genetic and biochemical studies of the relations between genotype and phenotype, an area where our knowledge is still rudimentary.

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## REFERENCES

Altshuler, D. L., F. G. Stiles, & R. Dudley. 2004. Of hummingbirds and helicopters: hovering cost, competitive ability and foraging strategy. Am. Nat. in press.

Amaya M., M. 1998. Hummingbird pollination, phylogeny and conservation of *Columnea* (Gesneriaceae) in the Reserva Natural La Planada, Western Andes of Colombia. M. Sc. thesis, Univ. Nacional, Bogotá, Colombia.

Baldwin, S. P., H. C. Oberholser, & L. G. Worley. 1931. Measurements of birds. Sci. Pub. Clevel. Mus. Nat. Hist. 2: 1–165.

Bleiweiss, R. 1998. Tempo and mode of hummingbird evolution. Biol. J. Linn. Soc. 65: 63–76.

Bleiweiss, R., J. A. W. Kirsch, & J. C. Matheus. 1994. DNA-DNA hybridization evidence for subfamily structure among hummingbirds. Auk 111: 8–19.

Bleiweiss, R., J. A. W. Kirsch, & J. C. Matheus. 1997. DNA hybridization evidence for the principal lineages of hummingbirds (Aves: Trochilidae). Mol. Biol. Evol. 14: 325–343.

Brown, J. H., & M. A. Bowers. 1985. Community organization in hummingbirds: the relationship between morphology and ecology. Auk 102: 251–269.

Burnham, R. J., & A. Graham. 1999. The history of Neotropical vegetation: new developments and status. Ann. Mo. Bot. Gard. 86: 546–589.

Feinsinger, P. 1976. Organization of a tropical guild of nectarivorous birds. Ecol. Monogr. 46: 257–291.

Feinsinger, P., & R. K.Colwell. 1978. Community organization among Neotropical nectar-feeding birds. Am. Zool. 18: 779–795.

Feinsinger, P., R. K. Colwell, J. Terborgh, & S. B. Chaplin. 1979. Elevation and the morphology, flight energetics and foraging ecology of tropical hummingbirds. Am. Nat. 113: 481–497.

Gill, F. B. 1988. Trapline foraging of hermit hummingbirds: competition for an undefended, renewable resource. Ecology 96: 1933–1942.

Heinrich, B. 1975. Energetics of pollination. Ann. Rev. Ecol. Syst. 6: 139–170.

Levey, D. J., & F. G. Stiles 1992. Evolutionary precursors of long-distance migration: resource availability and movement patterns in Neotropical landbirds. Am. Nat. 140: 447–476.

Marín A., M., & F. G. Stiles. 1992. On the biology of five species of swifts (Apodidae, Cypseloidinae) in Costa Rica. Proc. West. Found. Vertebr.

Zool. 4: 287–351.

Ortiz-Crespo, F. I. 1972. A new method to separate adult and immature hummingbirds. Auk 89: 851–857.

Snow, B. K., & D. W. Snow. 1972. Feeding niches of hummingbirds in a Trinidad valley. J. Anim. Ecol.41: 471–485.

Stiles, F. G. 1981. Geographical aspects of bird-flower coevolution, with particular reference to Central America. Ann. Mo. Bot. Gard. 68: 323–351.

Stiles, F. G. 1985. Seasonal pattern and coevolution in the hummingbird-flower community of a Costa Rican subtropical forest. Ornithol. Monogr. 36: 757–787.

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

Stiles, F. G., & D. L. Altshuler. 2004. Conflict in wing terminology between ornithology and aerodynamics. Auk in press.

Stiles, F. G., & A. F. Skutch. 1989. A guide to the birds of Costa Rica. Cornell Univ. Press, Ithaca, New York.

Stiles, F. G., & L. L. Wolf. 1979. Ecology and evolution of a lek mating system in the Long-tailed Hermit hummingbird. Ornithol. Monogr. 27: 1–78.

Taylor, D. W. 1995. Cretaceous to Tertiary geologic and angiosperm paleogeographic history of the Andes. Pp. 3–19 *in* Churchill, S. P. (ed.). Biodiversity and conservation of Neotropical montane forests. New York Botanical Garden, New York, New York.

Wolf, L. L., F. R. Hainsworth, & F. B. Gill. 1975. Foraging efficiency and time budgets in nectar-feeding birds. Ecology 56: 117–128.