The Role of Flower Width in Hummingbird Bill Length–Flower Length Relationships[1]

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ABSTRACT

Observations of hummingbirds feeding at flowers longer or shorter than their bills seem to contradict the view that bill lengths of hummingbirds evolved in concert with the lengths of their flowers. Recent experiments, however, indicate that a hummingbird's ability to feed at artificial flowers of different lengths depends on the widths of the flowers. We examined if the broad range of flower lengths visited by many hummingbird species can be explained by the widths of the flowers. We predicted that both short- and long-billed hummingbirds would include long, wide flower species in their diets, but that short-billed hummingbirds would not include long, narrow flower species because nectar in these species might be beyond the reach of their bills. If so, the slope of the regression for flower width versus flower length should be smaller for flower species visited by longer-billed hummingbirds relative to those visited by shorter-billed hummingbirds. Analyses of data sets for some North American and Monteverde hummingbirds and their food plants were consistent with this prediction, and bill lengths were significantly correlated with the slopes of the regressions of flower width versus length for seven hummingbird species. Comparisons of observed flower use by some Monteverde hummingbird species to flower assemblages generated at random suggest that these significant regressions were not simply a result of allometric relationships between flower lengths and widths, but in some cases reflected active choice by the birds. The two hummingbird–flower data sets also differed significantly in the scaling of corolla width relative to corolla length. In particular, the Monteverde data set contained a large number of long, narrow flower species, which we suggest is a consequence of a different floral evolutionary history and association with long-billed hummingbird species. The evolutionary effects of hummingbirds and their flowers upon one another are more complex than has generally been realized, and a consideration of corolla length jointly with other floral characters may improve our understanding of hummingbird–flower relationships.

Key words: flower morphology; foraging behavior; hummingbirds; pollination; specialization; Trochilidae; Monteverde; North America.

A MAJOR GOAL OF EVOLUTIONARY ECOLOGY has been to understand the processes that structure communities (Strong *et al.* 1984). Plants and their pollinators have been central to this goal because the morphology of a pollinator often matches the morphology of the flower species it pollinates. Darwin and others have interpreted such matches between flowers and pollinators as examples of coevolution and specialization (Darwin 1862, Faegri & van der Pijl 1966, Stiles 1985, Stebbins 1989). Although many studies of plant–pollinator relationships support the hypothesis of coevolution and specialization (Nilsson 1988, Temeles *et al.* 2000), some do not (Waser *et al.* 1996).

One plant–pollinator relationship that has re-ceived mixed support from empirical studies is the relationship between bill lengths of hummingbirds and the lengths of the flower species they visit. The close correspondence between bill lengths of hummingbirds and the lengths of the flowers they visit has been used as an example of feeding specialization and coevolution ever since Darwin commented on the relationship more than a century ago (Darwin 1876). Many species of hummingbirds, however, feed from flower species with floral tubes substantially longer or shorter than their bills (Feinsinger 1976, Snow & Snow 1980, Arizmendi & Ornelas 1990, Cotton 1998). Such visits by some hummingbird species to a broad range of flower lengths seem to weaken the case for coadaptation, and most present-day interactions between hummingbirds and their flowers are thought to have arisen through diffuse coevolution at best (Feinsinger 1983, Cotton 1998; *cf.* Stiles 1985).

Here we advance the view that the lack of correspondence between bill lengths and flower lengths observed in some studies (Feinsinger 1983, Cotton 1998) may be due to a failure to consider additional morphological features of flowers that define hummingbird–flower relationships. For our study, the additional feature is flower width. Recent laboratory experiments have indicated that the foraging behavior of hummingbirds at artificial flowers of different lengths varies as a function of the diameters of the flowers (Grant & Temeles 1992, Temeles 1996). A hummingbird's ability to probe into flowers increased with increasing flower diameter: the wider the flower, the farther a bird of a given bill length could probe (= its maximum extraction depth; Grant & Temeles 1992, Temeles 1996). Handling times of hummingbirds decreased with increasing corolla diameter (Temeles 1996). The latter result follows directly from the first: because maximum extraction depths increase with increasing flower diameter, for a given flower length, a bird's bill tip will be closer to the nectar source at wider (as opposed to narrower) flowers. Consequently, the bird does not have to extend its tongue as far on each lick, thereby shortening the licking cycle and resulting in faster handling times at wider flowers (Temeles & Roberts 1993, Temeles 1996). At corolla diameters greater than the width of the birds' bills (*ca* 1.6 mm; Temeles 1996), longer-billed hummingbirds had greater maximum extraction depths than shorter-billed hummingbirds (Grant & Temeles 1992, Temeles 1996). Similarly, handling times of longer-billed birds were shorter than those of shorter-billed birds, but only at the longest flowers studied (Temeles & Roberts 1993, Temeles 1996). The greater maximum extraction depths and shorter handling times of longer-billed hummingbirds imply that they have the potential to use longer flowers than shorter-billed birds, and to do so more efficiently.

These experiments suggest that the broad range of flower lengths visited by many hummingbird species does not necessarily reflect a lack of correspondence between bill and flower; rather, bill length may correspond closely to flower length when flower diameter also is taken into consideration. Specifically, both long- and short-billed hummingbirds may be able to access nectar in a long flower having a wide opening, whereas short-billed hummingbirds may be unable to access nectar in a long flower having a narrow opening because the combination of a long floral tube and a narrow opening may make the flower's nectar beyond the reach of a short bill. If this argument is correct, then we predict that the slope of the regression for flower width versus flower length will be less steep for flower species visited by longer-billed hummingbirds relative to those visited by shorter-billed hummingbirds.

We evaluate this prediction by examining the relationship between the widths and lengths of flower species visited by some North American and Monteverde hummingbird species and by comparing the slopes of these relationships between hummingbird species differing in bill length. We extend our analysis of flower use by hummingbirds to a comparison of the two hummingbird–flower data sets and examine the consequences of adding a long-billed hummingbird to a hummingbird–flower community. We contrast the adaptationist hypothesis that hummingbird bill length–flower length relationships are mediated by flower width against competing hypotheses based only on flower allometry and evolutionary history. Specifically, a hummingbird's use of a given array of flower species may not result from active choice but rather may simply be a consequence of the scaling of flower width and flower length, such that longer flowers are always wider flowers (*i.e.,* allometric relationships). Alternatively, differences in the lengths and widths of flower species used by hummingbirds may result from differences in the evolutionary histories of communities rather than from active choice on the part of hummingbirds. We conclude with a discussion of the difficulties in interpreting patterns of plant–pollinator associations based on a consideration of only a few morphological features of the plants and their pollinators.

MATERIALS AND METHODS

THE DATA SETS.—Only data pertaining to tubular flowers were examined in the analyses; *i.e.,* brush and cup flowers (*sensu* Faegri & van der Pijl 1966, Stiles 1981) were excluded. We classified flowers as "tubular" if their inside diameters measured less than 50 percent of their lengths. The measure of flower diameter used here was the width of the flower at its inside distal opening (Grant & Temeles 1992) and not at its base (Snow & Snow 1972). We restricted our analyses to tubular flower species because they correspond to the dimensions of artificial flowers used in laboratory experiments of hummingbird bill length–flower length relationships (Temeles 1996). Tubular flower species thus permitted an analysis of how a hummingbird's ability to use a broad range of flower lengths varies with the widths of the flowers, and also allowed an

examination of how changes in flower length and width affect flower use by birds of different bill lengths.

The North American data set (Appendix 1) was compiled from a review of reference works on hummingbirds and the flowers they visit (Jepson 1951, Grant & Grant 1968, Munz 1974, Johnsgard 1983) and original articles (Schemske 1978, Bertin 1982), supplemented by Temeles' observations. Although Johnsgard (1983) listed over one hundred species of North American flowers as "hummingbird flowers," the number of flower species for which the identity of the hummingbird visitor was recorded is considerably less. Moreover, although researchers often list lengths of flower species visited by hummingbirds (Brown & Kodric-Brown 1979), few list widths (Grant & Grant 1968). Consequently, we were able to obtain lengths and widths for only a small sample of flower species ($N = 31$) visited by five species of North American hummingbirds: *Archilochus colubris*, *Calypte anna*, *Selasphorus rufus*, *S. sassin*, and *Stellula calliope* (see Appendix 1 for flower measurements and hummingbird visitors). Our North American data set thus excludes three short-billed hummingbird species with broad geographic distributions (*Archilochus alexandri*, *Calypte costae*, and *Selasphorus platycercus*) as well as hummingbird and flower species restricted to the southwestern United States (including the long-billed *Lampornis clemenciae* and *Eugenes fulgens*, and the curve-billed *Calothorax lucifer*). As a result, hummingbird and flower species from eastern North America and the West Coast are fairly well represented, whereas hummingbird and flower species from the Rocky Mountains and southwestern United States are under represented. Despite these limitations, our data set allows us to examine flower length–width relationships for a sample of short-billed hummingbird species.

The Monteverde data set (Appendix 2) was compiled from Feinsinger's and Linhart's year-round studies of hummingbird species and their food plants at Monteverde Cloud Forest Reserve, Provincia de Puntarenas, Costa Rica (*cf.* Feinsinger *et al.* 1986, 1987, 1988; Linhart *et al.* 1987; Murray *et al.* 1987) and includes previously unpublished measurements of corolla widths. The Monteverde site is a 5100 ha tract comprised chiefly of pristine lowland rain forest (= lower mountain rain forest life zone of Young *et al.* 1998). The Monteverde site thus encompasses a much smaller geographic area than our North American data set, but nonetheless allowed us to examine flower length–width relationships for hummingbird species having longer bills than the short-billed species in the North American data set. Although Feinsinger *et al.* (1986, 1987, 1988) observed 11 hummingbird species at Monteverde, we focused on 2 hummingbird species, *Phaethornis guy* and *Lampornis calolaema*, because they are the most frequent in the forest, perform the bulk of pollinations of understory bird-pollinated plants (96.9% of visits to short flowers and 68.2% of visits to long flowers; Feinsinger *et al.* 1986), have broad diets, and have relationships with understory food plants that are best understood (Feinsinger *et al.* 1986, 1987, 1988). Moreover, these two species permitted a comparison of a short- versus a long-billed hummingbird species within the Monteverde assemblage. Because *L. calolaema* exhibits sexual differences in flower use (females visited the flowers of 11 plant species that were not visited by males; Feinsinger *et al.* 1988), we analyzed data for each sex separately. Measurements of flower lengths and widths and visitor information were recorded by Feinsinger, Linhart, and their coworkers.

Measurements of bill length (exposed culmen) were from Ridgway (1911) and with the exception of *L. calolaema*, were averaged for the two sexes. We did not include an analysis of bill widths in our study because earlier experiments indicated that relative differences in bill lengths had a greater influence on a hummingbird's ability to use flowers of different diameters than bill widths (Grant & Temeles 1992, Temeles 1996). We also did not include other morphological features (*e.g.,* tongue shape, bill shape, and body size). These features almost certainly influence hummingbird–flower relationships, however, and we will address their importance in the Discussion section of the paper.

Data analyses.—Some of the hummingbird species in both the North American and Monteverde assemblages visited flowers traditionally labeled as "insect" flowers (*sensu* Grant & Grant 1965, 1966; Faegri & van der Pijl 1966; Feinsinger *et al.* 1986, 1987, 1988) as well as flowers conforming to the "hummingbird" syndrome (Appendices 1 and 2). Accordingly, we conducted our analyses first on the entire data set ("bird + insect" flowers) and then on a subset of the entire data set consisting only of hummingbird flowers ('bird flowers'). Analysis of variance (ANOVA) and Tukey multiple comparisons were used to contrast flower widths and lengths among hummingbird species, and regression analyses were used to examine the relationship between flower width and length (Minitab 1997).

Comparisons of slopes followed procedures in Zar (1984: 292–295), and Spearman's rank correlations followed procedures in Daniel (1978). We used the nested ANOVA procedure in Minitab (Minitab 1997) to examine the influence of evolutionary history on patterns of flower lengths and widths within the North American and Monteverde communities (Harvey & Pagel 1991).

Null models.—To obtain a more complete picture of whether patterns of flower use of the hummingbird species included in this study were a result of active choice of flower lengths and widths or alternatively were a passive consequence of the positive scaling of flower widths and lengths (allometry), we compared the slopes of the observed regressions of flower width versus flower length to distributions of all possible slopes for samples of the same size drawn from a source pool comprising all the flower species available in the data sets. This analysis was impractical for the North American hummingbirds because the flower species analyzed in Appendix 1 constituted only a small part of the flower species on the North American continent available to the birds; thus, there was no relevant "source" pool of flowers. The analysis was more meaningful for the two species of Monteverde hummingbirds because the flower species listed in Appendix 2 represent most of the flower species available to these birds in the forest understory (Feinsinger *et al.* 1986, 1987, 1988). Because our interest was in determining factors underlying flower preferences by hummingbirds, only plant species visited at moderate to high frequencies (62% ± 6% [$\bar{x}$ ± SE] of hummingbird visits recorded to a subset of 16 plant species listed in Appendix 2; P. Feinsinger, pers. comm.) and available in moderate to abundant numbers (Feinsinger *et al.* 1986, 1987, 1988), rather than raw visit frequencies, were included in these models. We therefore assumed that high visit frequencies relative to flower availability are a measure of flower preference, which may not be the case; both interference and exploitative competition may modify flower use (Paton & Carpenter 1984, Pimm *et al.* 1985). For example, male *L. calolaema* are the territorial dominants in the Monteverde assemblage (Feinsinger *et al.* 1988) and have shorter bills than either female *L. calolaema* or *P. guy*. Assuming that territorial dominance confers priority of access to preferred resources and that flower lengths and widths influence flower preferences, these males would be expected to visit flower species having extremely wide openings relative to their lengths, which would be expressed in terms of very large (steep) slopes. In contrast, *P. guy* has an extremely long bill relative to *L. calolaema*, and might be expected to use flower species having narrower openings relative to their lengths (see Introduction; Temeles 1996). Null models were programmed in Visual Basic. In these models, both slopes and intercepts for observed patterns of flower choice by male and female *L. calolaema* and *P. guy* at Monteverde were compared to the entire distribution of slopes and intercepts for samples of the same size.

RESULTS AND DISCUSSION

Flower use.—We found significant positive relationships between mean flower length and mean bill length across the seven hummingbird species included in this study ($P = 0.023$ for bird + insect flowers; $P = 0.001$ for bird flowers; $N = 8$; note that sexes of *L. calolaema* were treated as separate data points). Nonetheless, all eight hummingbirds visited flowers both longer and shorter than the lengths of their bills, and overlapped considerably in both the lengths and widths of flowers visited (Fig 1a). Differences among the eight hummingbirds in the lengths of flowers visited were not significant, with one exception (*C. anna* versus *P. guy*; $P = 0.05$, Tukey multiple comparisons). When insect flowers were excluded from the analysis, differences among hummingbirds in the lengths of flowers visited were not significant ($P = 0.089$, $F = 1.83$, one-way ANOVA). Likewise, no significant differences were observed among hummingbird species in the widths of flower species visited (Fig.1b; all flowers: $P = 0.481$, $F = 0.94$, one-way ANOVA; hummingbird flowers: $P = 0.851$, $F = 0.47$, one-way ANOVA).

The preceding analyses suggest that bill lengths of hummingbirds are weakly associated with flower lengths and reinforce the view of little specialization between bill and flower lengths. As noted in the Introduction, however, flower width may be important for determining the kinds of hummingbird visitors to a given flower: wider widths may allow both long- and short-billed hummingbirds to visit "long" flower species, whereas narrower widths may exclude short-billed hummingbirds from long flower species. If narrow openings exclude short-billed hummingbirds from long flower species, then slopes of the regression for flower width versus flower length should be smaller for longer-billed hummingbirds relative to shorter-billed hummingbirds.

We found significant relationships between the

a)

Pg
Lf
Lm
Ca
Sr
Ac
Ss
Stc

5   15   25   35   45   55   65   75
Flower Length (mm)

b)

Pg
Lm
Lf
Ca
Sr
Ac
Ss
Stc

4   9   14   19
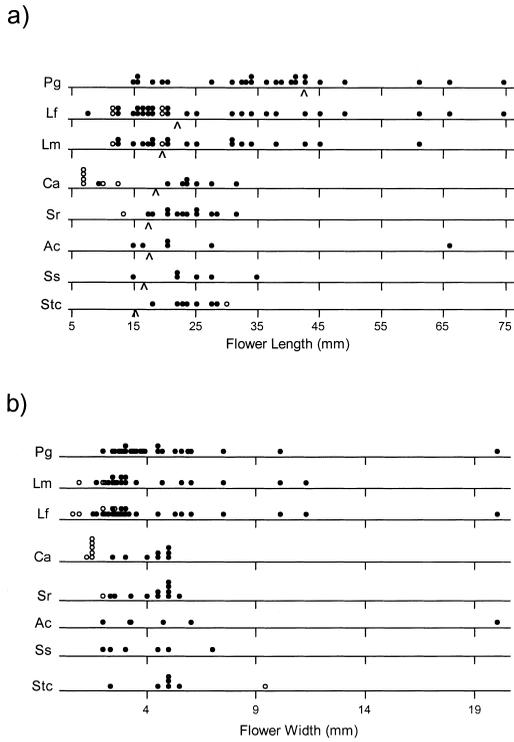Flower Width (mm)

FIGURE 1.   Lengths and widths of flower species visited by seven North American and Monteverde hummingbird species. (a) Flower lengths. Arrow indicates bill lengths relative to lengths of flowers. (b) Flower widths. Abbreviations: Pg = *Phaethornis guy*; Lf = *Lamponis calolaema* (females); Lm = *L. calolaema* (males); Ca = *Calypte anna*; Sr = *Selasphorus rufus*; Ac = *Archilochus colubris*; Ss = *Selasphosus sasin*; and Stc = *Stellula calliope*. Open circle = "insect" flowers and closed circle = "hummingbird" flowers. See Appendices 1 and 2 for flower species and dimensions.

widths and lengths of flower species visited by both the North American and Monteverde hummingbirds (Table 1). For all eight hummingbirds, longer species of flowers tended to be wider, whereas shorter species of flowers tended to be narrower. A similar pattern held when insect flowers were excluded from the analysis for the four hummingbird species that visited both insect and hummingbird flowers (*C. anna*, *S. rufus*, *S. calliope*, and *L. calolaema* males and females; $P < 0.05$ for all regressions).

The slopes of the regressions between flower width and length differed among the hummingbird species (Table 1). The slope of the regression for *A. colubris* was significantly steeper than the slopes for the two longer-billed Monteverde species (*A. colubris* vs. *L. calolaema* [both sexes] and *P. guy*; $P < 0.01$ for all three multiple comparisons at an overall error rate of $P = 0.05$). Similarly, the slope of the regression for *S. calliope* was much steeper than the slopes for the Monteverde species, and these differences bordered on statistical significance (*S. calliope* vs. *L. calolaema* [both sexes] and *P. guy*; $P < 0.1$ for all three multiple comparisons). Differences in slopes among the other species were not significant, although samples sizes of flowers were small for these types of comparisons among hummingbird species. The rank order of slopes for the eight regressions in Table 1 was inversely related to the rank order of bill lengths (all flowers: $P = 0.01$, $r_s = -0.88$; hummingbird flowers: $P = 0.02$, $r_s = -0.86$). This relationship between slope and bill length implies that flower widths increase less rapidly with increases in corolla length for longer-billed hummingbirds relative to shorter-billed hummingbirds.

ACTIVE CHOICE OR PASSIVE CONSEQUENCE?—Although regressions for all the hummingbird species considered in this analysis were significant (*i.e.*,

TABLE 1.   *Relationships between widths and lengths of tubular flowers visited by some North American and Monteverde hummingbird species. Birds are listed in order of increasing bill length. See Appendices 1 and 2 for flower measurements, hummingbird visitors, and sources.*

Species	Slope ± SD	R^2	P	N
Stellula calliope	0.449 ± 0.136	0.645	0.016	8
Selasphorus sasin	0.241 ± 0.075	0.723	0.023	6
Archilochus colubris	0.341 ± 0.034	0.962	0.001	6
Selasphorus rufus	0.190 ± 0.051	0.554	0.004	13
Calypte anna	0.159 ± 0.019	0.850	0.001	14
Lampornis calolaema (males)	0.121 ± 0.041	0.318	0.008	21
L. calolaema (females)	0.142 ± 0.031	0.407	0.001	31
Phaethornis guy	0.134 ± 0.041	0.321	0.003	25

flowers increased in width for a given increase in length), such relationships do not necessarily mean that hummingbirds are actively choosing flower species on the basis of length–width dimensions. The simplest explanation for the significant relationships between flower widths and lengths is allometry; *i.e.,* a longer flower must by necessity be a wider flower. As a consequence, the slopes of the regressions of flower width versus flower length will be both positive and statistically significant for any hummingbird species, provided enough flower species are included in the sample for analysis. Significant positive correlations between flower width and length have been recorded for a number of plant species, some of which are hummingbird-pollinated (*e.g., Ipomopsis aggregata*; Campbell 1996).

The relationship between flower width and length, however, was less clear for between-species comparisons. For example, for three of the six North American hummingbird-flower genera for which we have measurements of more than one species (*Aquilegia, Ipomopsis,* and *Penstemon*), the plant species with the shortest flowers also has the widest flowers (Appendix 1). The plant species with the shortest flowers has the widest flowers in three of the seven genera of Monteverde hummingbird plants, as well (*Besleria, Burmeistera,* and *Drymonia,* Appendix 2; insect-pollinated plants were excluded from the comparison). Similarly, North American *Ipomopsis* and *Aquilegia* species pollinated by hawkmoths are both longer and narrower than hummingbird-pollinated species within the same genera (Grant & Temeles 1992). The occurrence of inverse relationships between lengths and widths in at least some hummingbird-pollinated genera indicates that plant species with long flowers do not always have wider flowers, and suggests that the positive slopes for the regressions of flower width versus flower length for the hummingbirds species studied here may not result exclusively from floral allometry but also from flower choice on the part of the birds.

A more direct way to analyze this question of active flower choice versus passive consequence is to compare the slopes of the observed regressions of flower width versus flower length to distributions of all possible slopes for samples of the same size drawn from a source pool comprising all the plant species in the data sets. As noted in the Methods, this analysis was limited to male and female *L. calolaema* and *P. guy.* Observed slopes for the three hummingbirds were consistent with expectations based on bill lengths and dominance relationships (see Methods): the slope for flower species
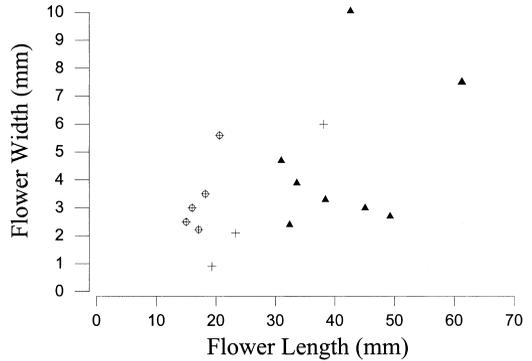

FIGURE 2.   Lengths and widths of flower species "preferred" by *Lampornis calolaema* males, *L. calolaema* females, and *Phaethornis guy*. Open circle = *L. calolaema* (males); cross = *L. calolaema* (females); and solid triangle = *P. guy*. A circle with a cross indicates preference by both sexes of *L. calolaema*. See Appendix 2 for list of preferred flower species.

"preferred" by male *L. calolaema* (0.545) was considerably steeper than similar slopes for female *L. calolaema* (0.147) or *P. guy* (0.097; see Fig. 2 and Appendix 2 for "preferred" flower species). Male *L. calolaema* preferred five flower species, yielding 435,897 possible slopes for samples of five flower species drawn at random from the Monteverde community. The probability of randomly drawing a slope steeper than the slope of 0.545 observed for male *L. calolaema* was 0.002. In contrast, *L. calolaema* females and *P. guy* each preferred eight flower species (although not the same species; Appendix 2), yielding 38,608,020 possible slopes for samples of eight flower species drawn at random from the Monteverde community. The probabilities of randomly drawing slopes steeper than 0.147 (*L. calolaema* females) and 0.097 (*P. guy*) were 0.27 and 0.57, respectively. These results suggest that male *L. calolaema* may have been actively choosing flower species on the basis of width–length dimensions in order to minimize foraging costs. For female *L. calolaema* and *P. guy*, active choice of flower species based on width–length preferences is less clear, but as noted above, their floral preferences may be modified by territorial exclusion from preferred flower species and exploitative competition. These analyses illustrate just how difficult it is, and will be, to predict and measure patterns of floral use by hummingbirds (or other pollinators) only on the basis of bill or tongue dimensions. Laboratory experiments that measure foraging costs and benefits at flower species of varying widths and lengths in combination with field experiments that
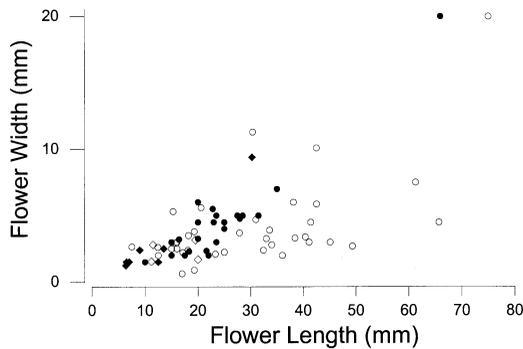
FIGURE 3. Relationship between flower widths (FW) and lengths (FL) for tubular flower species visited by some North American and Monteverde hummingbirds. The statistics for the regressions are: North America: FW = 1.73 + 0.28FL; R^2 = 0.832, $P < 0.001$, $N = 31$; Monteverde: FW = 0.28 + 0.13FL; R^2 = 0.365, $P < 0.001$, $N = 41$. Differences between the slopes of the two regressions are significant ($P < 0.001$). Open circles = Monteverde hummingbird flowers; solid circles = North American hummingbird flowers; open diamonds = Monteverde insect flowers; and solid diamonds = North American insect flowers. See Appendices 1 and 2 for flower dimensions.

exclude territorial dominants may be useful for sorting out patterns of flower use based on feeding preferences from those based on competitive interactions.

COMMUNITY COMPARISON.—A comparison of the lengths and widths of the North American flower species (Appendix 1) to those of the Monteverde flower species (Appendix 2) reveals differences between the two data sets in the scaling of flower dimensions (Fig. 3). The slope of the regression of corolla width versus corolla length for the North American data set was much steeper than the slope for the Monteverde data set, indicating that corolla widths of North American flower species increase more rapidly with increasing corolla length than for Monteverde flower species ($P < 0.001$; Fig. 3). When insect flowers were excluded from the comparisons, the slope of the regression of corolla width versus corolla length of the North American assemblage remained much steeper and significantly different than the slope of the Monteverde assemblage ($P < 0.001$). Thus, hummingbird flowers in the North American data set differed from hummingbird flowers in the Monteverde data set in the scaling of corolla width relative to corolla length.

With the exception of *Campsis radicans*, flowers of plants in the North American data set measured less than 35 mm in length (Fig. 3). In contrast, the Monteverde data set contained 13 plant species having flowers greater than 35 mm in length (Fig. 3). When only flower species less than 35 mm in length were compared, the slope of the regression of corolla width versus corolla length did not differ significantly between the two data sets, although the slope for the Monteverde flower species tended to be less steep than the slope for the North American flower species ($P > 0.05$; slope North American flowers = 0.195; slope Monteverde flowers = 0.091). A similar result occurred when only hummingbird flowers were analyzed ($P > 0.10$; slope North American flowers = 0.193; slope Monteverde flowers = 0.087). Although flower species less than 35 mm in length at Monteverde tended to be narrower for a given length than flower species in North America, this difference by itself cannot explain differences in the scaling of flower dimensions between the two data sets.

More obvious differences become apparent when flower species greater than 35 mm in length are compared between the two data sets. The North American data set contained only one plant with a flower greater than 35 mm in length, *C. radicans*, which averaged 66 mm in length and 20 mm in width (Appendix 1). In contrast, although the Monteverde data set contained one plant species (*Solanophora calycosa*; Appendix 2) with flowers of dimensions comparable to *C. radicans*, the remaining 12 "long" flower species in the Monteverde data set were very narrow relative to their lengths, and the slope of the regression of corolla width versus length for these flower species did not differ significantly from zero ($P > 0.45$; slope = 0.057). In addition, even when *S. calycosa* was included in the sample, flower species greater than 35 mm in length in the Monteverde data set were not significantly wider than flower species less than 35 mm in length in either the North American or Monteverde data sets ($P > 0.1$ for all comparisons; *t*-tests). Differences between the two data sets in the scaling of corolla width relative to corolla length apparently resulted in large part from the occurrence of very long, narrow flower species in the Monteverde data set.

RESOURCE PARTITIONING AND SPECIALIZATION.—The most noticeable difference between hummingbird-visited plant species and between the two hummingbird–plant data sets in this study was the scaling of flower width relative to flower length. Some of the difference in the scaling of flower width relative to flower length between the two data sets may be a consequence of the evolutionary histories

TABLE 2. *Percentage of variation in flower lengths and widths explained at the family and genus levels for North American and Monteverde hummingbird–flower data sets combined. Results were obtained using the nested analysis of variance procedure in Minitab (1997) on the data in Appendices 1 and 2. The analysis was conducted with and without* Campsis radicans *and* Solanophora calycosa, *extremely long and wide outliers in the two data sets (Fig. 3).*

Floral trait	Taxonomic level	Percentage of variation	F	P
Length	Family	0.00	0.63	NS
	Genus	68.64	4.04	0.005
	Error	31.36		
Width	Family	51.05	3.28	0.005
	Genus	27.88	2.84	0.05
	Error	21.08		
Length without *C. radicans* and *S. calycosa*	Family	0.00	0.35	NS
	Genus	68.64	4.04	0.005
	Error	31.36		
Width without *C. radicans* and *S. calycosa*	Family	0.00	0.83	NS
	Genus	56.95	2.84	0.05
	Error	43.05		

of their respective communities. The two hummingbird–plant data sets show little overlap at the family level, with the exception of the Lobeliaceae and Acanthaceae (Appendices 1 and 2). The low degree of phylogenetic overlap could contribute to differences in the scaling of flower width relative to flower length. Nonetheless, the greatest percentage of variation in flower lengths and widths is explained at the genus, rather than at the family, level (Table 2). The greater variation in flower lengths and widths at the genus level is consistent with our finding that flower lengths do not necessarily scale positively with flower widths across species within a genus (see above), and suggests that at least some of this variation may be explained by adaptation and specialization on certain pollinators (Hodges & Arnold 1994).

We suggest that the difference in scaling of flower width relative to flower length is associated with differences between North American and Monteverde in the composition of their hummingbird assemblages. The difference in scaling between the two data sets resulted from the occurrence of several flower species greater than 35 mm in length that are very narrow relative to their lengths in the Monteverde data set (Fig. 3). With few exceptions, these long, narrow flower species are visited by long-billed hummingbird species (*P. guy* and also *Campylopterus hemileucurus, Heliodoxa jacula, Doryfera ludovicae, E. fulgens,* and *Eutoxeres aquila*). Although a variety of factors can modify plant–

pollinator relationships from those predicted on the basis of morphological characters, the narrow openings of these long flower species may play a role in resource partitioning by long- and short-billed hummingbird species. If the long flower species visited by *P. guy* and these other long-billed hummingbird species were any wider, then short-billed hummingbird species may be able to feed from them too, possibly altering plant preferences of long-billed species. Moreover, visits by such short-billed species could possibly decrease a plant's reproductive success through interspecific pollen transfer. These narrow corollas suggest that visits to long flower species at Monteverde may be restricted to long-billed hummingbirds much in the same way as visits to "long" hawkmoth flowers in North America are restricted to long-tongued hawkmoths (Grant & Temeles 1992); a flower that is very long relative to its width allows access to long-billed (or long-tongued) pollinators, while either denying access to shorter-billed or -tongued visitors or at least making such visits unprofitable (Grant & Temeles 1992).

Our arguments regarding the role of flower width in resource partitioning by hummingbirds are based on a comparison of limited data sets representing two hummingbird–flower communities, and data from additional hummingbird–flower communities are needed (note that the Monteverde data set for the most part excludes canopy flower species, which likely have some role in the evolu-

tion and foraging behavior of the Monteverde hummingbird species). Nonetheless, our results allow us to make the prediction that tropical hummingbird communities containing both long- and short-billed hummingbird species can be distinguished from temperate, short-billed hummingbird communities by the addition of an array of long, narrow flower species, resulting in lower values of slopes for the relationship between flower widths and flower lengths. Whether these long, narrow flowers evolved directly under natural selection exerted by long-billed hummingbirds or entered the hummingbird–flower assemblage from elsewhere, however, requires a more detailed analysis of hummingbird–flower coevolution patterns than attempted here (McDade 1992).

Conclusions.—This study examined a hummingbird's use of flower species in terms of flower dimensions. A hummingbird's use of a flower species also depends on its foraging costs and benefits and the presence or absence of other nectar competitors and other flower species. As suggested here, these factors may complicate or confound relationships predicted from bill and flower dimensions. Even so, a consideration of flower dimensions may be useful for identifying those flower species that offer high benefits, as well as those that offer low costs.

Departures in patterns of flower use from those predicted on the basis of floral and pollinator traits have sometimes been used as an argument for rejecting concepts of pollinator specialization and pollination syndromes altogether (Waser *et al.* 1996, Ollerton 1998) or for at least concluding that coevolution, if it occurs, is diffuse rather than specialized (Feinsinger 1983). Nonetheless, some researchers have found examples of plant–pollinator coevolution that appear to be quite tight (Temeles *et al.* 2000). We suggest that these different conclusions about the prevalence of plant–pollinator coevolution may arise in part from the complexity of the plant-pollinator assemblages examined. The hummingbird–*Heliconia* system studied by Temeles *et al.* (2000) is remarkably simple: the Purple-throated Carib, *Eulampis jugularis*, is the only large hummingbird species in the interior mountain rain forests of St. Lucia and is the sole pollinator of two *Heliconia* species. The depauperate flora and fauna of this island system may facilitate coevolution and specialization between hummingbird and flower along relatively few, and observable, morphological dimensions such as bill and flower size and

shape, body size, and patch size (reward). In contrast, the hummingbird–flower assemblage at Monteverde is anything but simple, and contains over 40 flower species visited by 11 different hummingbird species (and even more when the entire geographic range of the plant community is considered; Feinsinger *et al.* 1987, Young *et al.* 1998). Given the enormity of this assemblage, it is wishful thinking to expect that its hummingbird–flower relationships could be neatly summarized along a single dimension of bill length–flower length relationships. The problem is analogous to a multiple regression, whereby a researcher attempts to explain the greatest amount of variation in the dependent variable using the smallest subset of independent variables. For *E. jugularis*, flower use (the dependent variable) may be completely explained by bill length and curvature, and body size (the independent variables). Explaining flower use by the hummingbirds in the Monteverde assemblage may require a much more complex model with additional variables. We suggest that consideration of additional variables, such as flower width in conjunction with flower length, may provide a more accurate description of patterns of flower use by hummingbirds and the relative advantages of long and short bills. Hence, failure to find plant–pollinator relationships based on predictions from one or two morphological or behavioral characters may not mean that such relationships do not occur, but rather that the set of characters in the analysis is incomplete or inappropriate. Recent findings of flexible pedicels and "mobile" pollination mechanisms, and of tongue pollination of bird flowers (Hurlbert *et al.* 1996, Pauw 1998) suggest that we still have much to learn about bird–flower relationships and that future study will offer exciting and fascinating rewards.

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APPENDIX 1. *Lengths and widths (at orifice) in mm of tubular flowers visited by five species of North American hummingbirds. As used here, "sources" list sight records of hummingbird visits and/or flower dimensions. All measurements are means unless presented as a range of values, in which case the midpoint of the range is used. Width measurements for* P. cordifolius *and* R. malvaceum *were estimated from line drawings in Munz (1974). Key to abbreviations: Ac = Archilochus colubris; Ca = Calypte anna; Sr = Selasphorus rufus; Ss = Selasphorus sasin; and Stc = Stellula calliope. Asterisks (*) denote flowers adapted primarily for insect (bee) pollination.*

Flower species	Length	Width	Visitor	Source
Aquilegia canadensis	27.95	4.76	Ac	this study
A. formosa	27.50	5.00	Ca, Sr, Ss, Stc	Grant & Grant 1966, 1968
*Arctostaphylos manzanita**	9.00	2.40	Ca	Jepson 1951, Stiles 1972
*A. pringlei**	6.40	1.24	Ca	this study
Beloperone californica	17.50	2.00	Sr	S. Vetault, pers. comm.
Campsis radicans	66.00	20.00	Ac	Bertin 1982
Castilleja miniata	18.30	2.30	Sr, Stc	Grant & Grant 1966; this study
Delphinium cardinale	22.00	2.00	Ss	Grant & Grant 1968
*Eriastrum densifolium**	12.50	1.50	Ca	Grant & Grant 1965
Fourquieria splendens	20.00	4.50	Ca, Sr	Grant & Grant 1968; this study
Impatiens capensis	16.40	3.20	Ac	Schemske 1978, Hurlbert *et al.* 1996
Ipomoea coccinea	15.00	2.00	Ac	Grant & Grant 1968, Austin 1975
Ipomopsis aggregata	21.62	2.34	Sr, Ss, Stc	Grant & Grant 1968; this study
I. rubra	20.00	6.00	Ac	Grant & Grant 1965, Oberholser 1974
Keckia ternata	25.00	4.00	Ca, Sr	Grant & Grant 1968
Lobelia cardinalis	20.00	3.25	Ac, Sr	Grant & Grant 1966
Lonicera involucrata	15.00	3.00	Ss	Grant & Grant 1968
Mimulus cardinalis	31.50	5.00	Ca, Sr	Grant & Grant 1968, Vickery 1990
*M. lewisii**	30.30	9.40	Stc	this study
Penstemon barbatus	22.80	5.50	Sr, Stc	this study
P. bridgesii	28.50	5.00	Sr, Stc	Grant & Grant 1966, Munz 1974
P. centranthifolius	23.50	3.00	Ca	Straw 1956, Grant & Grant 1968
P. cordifolius	23.00	4.50	Ca	Stiles 1972, Munz 1974
P. newberryi	25.00	4.50	Sr, Ss, Stc	Grant & Grant 1968
*Ribes malvaceum**	6.50	1.50	Ca	Stiles 1972, Munz 1974
*R. sanguineum**	13.50	2.50	Sr	Jepson 1951, Grant & Grant 1966
*Salvia apiana**	7.00	1.50	Ca	Jepson 1951, Grant & Grant 1964
*S. mellifera**	6.50	1.50	Ca	Jepson 1951, Grant & Grant 1964
S. spathacea	35.00	7.00	Ss	Grant & Grant 1968
Trichostema lanatum	10.00	1.50	Ca	Grant & Grant 1966, 1968
Zauschneria californica	23.50	5.00	Ca, Sr, Stc	Grant & Grant 1968

APPENDIX 2. *Lengths and widths (at orifice) in mm of some tubular flowers visited by two hummingbird species at Monteverde, Costa Rica. All measurements are means. Key: Lf = Lampornis calolaema (females); Lm = Lampornis calolaema (males); Pg = Phaethornis guy; 1 = "preferred" flowers used for comparison to null models of flower use drawn from the entire Appendix; and * = flowers adapted primarily for insect pollination.*

Flower species	Length	Width	Visitor
Alloplectus tetragonus	36.0	2.00	Lf, Pg
Aphelandra tridentata	40.4	3.39	Pg
Besleria formosa	17.1	2.22	Lf[1], Lm[1]
B. notabilis	12.4	2.61	Lf, Lm
*B. princeps**	19.5	3.16	Lf
B. triflora	15.0	2.50	Lf[1], Lm[1], Pg
Bomarea caldasii	30.4	11.30	Lf, Lm
Burmeistera cyclostigmata	15.8	2.94	Lf, Pg
*B. microphylla**	20.0	1.70	Lf, Lm
B. parviflora	7.5	2.65	Lf
B. tenuiflora	19.3	0.90	Lf[1], Lm
Centropogon costaricae	18.1	2.40	Lf, Lm
C. solanifolius	41.1	3.00	Pg
Cephalis elata	18.2	3.50	Lf[1], Lm[1], Pg
Columnea anisophylla	42.5	5.87	Pg
C. lepidocaula	33.0	3.27	Pg
C. magnifica	27.9	3.69	Pg
C. microcalyx	19.3	3.80	Pg
Costus barbatus	32.4	2.40	Lf, Lm, Pg[1]
Dicliptura trifurca	23.3	2.10	Lf[1], Lm
Drymonia conchocalyx	61.3	7.50	Lf, Lm, Pg[1]
D. rubra	42.5	10.10	Lf, Lm, Pg[1]
Gasteranthus wendlandianus	17.0	0.62	Lf
*Gonzalgunia rosea**	11.2	1.53	Lf
Guzmania nicaraguensis	38.1	6.00	Lf[1], Lm, Pg
C. plicatifolia	25.0	2.25	Lf, Lm
Hansteinia blepharorachis	20.6	5.60	Lf[1], Lm[1], Pg
Heliconia montaverdensis	12.5	2.00	Lf, Lm
H. tortuosa	31.0	4.70	Lm, Pg[1]
Justicia aurea	33.6	3.90	Pg[1]
Malvaviscus palmanus	38.4	3.30	Pg[1]
Palicourea lasiorrachis	16.0	3.00	Lf[1], Lm[1]
*P. macrocalyx**	11.5	2.80	Lf, Lm
Pitcairnia brittoniana	45.1	3.00	Lf, Lm, Pg[1]
Poikilacanthus macranthus	41.4	4.50	Pg
Psammisia ramiflora	34.0	2.80	Lf, Lm, Pg
Ravnia triflora	65.7	4.50	Lf, Pg
Razisea spicata	49.3	2.70	Lf, Pg[1]
Renealmia thrysoides	15.3	5.30	Lf, Pg
Solanophora calycosa	75.0	20.00	Lf, Pg
Tillandsia insignis	16.0	2.50	Lf