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A new dimension to hummingbird – flower relationships

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Abstract The close correspondence between the bills of hummingbirds and the lengths of the flowers they feed from has been interpreted as an example of coadaptation. Observations of birds feeding at flowers longer and shorter than their bills, however, and the lack of experimental evidence for any feeding advantage to short bills, seem to contradict this interpretation. I address this problem by considering a little-studied dimension of floral morphology: corolla diameter. In laboratory experiments on female ruby-throated hummingbirds (*Archilochus colubris*), probing abilities (maximum extraction depths) increased with increasing corolla diameter. Handling times increased with decreasing corolla diameter, resulting in “handling time equivalents”, i.e., flowers having the same handling times but different lengths and diameters. Longer-billed birds had greater maximum extraction depths and shorter handling times than shorter-billed birds at all corolla diameters greater than the width of the bill. In contrast, shorter-billed birds made fewer errors inserting their bills into narrow flowers. Hence, differences in bill lengths apparently are associated with trade-offs in foraging abilities, whereby longer-billed birds are able to feed at long flowers and may do so more quickly, whereas shorter-billed birds are able to feed more successfully at narrow flowers.

Key words Plant-pollinator interactions · Foraging behavior · Hummingbirds · Feeding adaptation · Trochilidae

Introduction

The coevolutionary relationships between flowers and their pollinators have fascinated scientists since the earliest years of evolutionary biology. This fascination is due

in large part to the remarkable diversity of flower shapes and sizes, and the tendency for some flowers to correspond to the morphology of their pollinators. Darwin (1862) was among the first to document both the variation in floral structures and the match between flower and pollinator morphology. From his studies, he concluded that the great diversity of floral structures in nature generally has evolved through the diverse array of interactions with different pollinators (Darwin 1862).

One of the most striking examples of this diversity is provided by hummingbirds and their flowers. Species of hummingbirds exhibit extraordinary variation in the relative dimensions of their bills, with bill lengths ranging from as little as 5 mm in the purple-backed thornbill, *Ramphomicron microrhynchum*, to well over 100 mm in the swordbill, *Ensifera ensifera* (Snow and Snow 1980; Feinsinger 1983; Johnsgard 1983). This great variation in bill lengths is matched by the relative dimensions of the flowers visited by the birds (Snow and Snow 1980; Feinsinger 1983; Johnsgard 1983). The close correspondence between bill lengths of hummingbirds and the lengths of the flowers they commonly use led Darwin (1876) to declare that the “beaks of humming-birds are specially adapted to the various kinds of flowers they visit”, and the bill length – flower length relationship is often used as an example of coevolution and feeding adaptation (e.g., Johnsgard 1983).

Two lines of evidence, however, seem to weaken the case for coadaptation between hummingbirds and flowers. First, although some studies have reported correlations between bill and flower lengths, the correlations resulted from the authors’ use of mean corolla lengths of the flowers visited by each bird species (e.g. Snow and Snow 1980; Arizmendi and Ornelas 1990). In fact, most hummingbirds visit flowers with floral tubes substantially longer and shorter than their bills (e.g., Feinsinger 1976; Snow and Snow 1980; Arizmendi and Ornelas 1990). At first glance, the range of flower lengths visited by each hummingbird species seems to contradict Darwin’s view (1876) that the great diversity of hummingbird bills is the result of each species’ interaction with flowers of a different size.

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Second, the hummingbird-flower coevolution example assumes that differences in bill lengths are associated with differences in the abilities to feed at flowers of different sizes; i.e., longer bills are better for feeding from long flowers, and shorter bills are better for feeding from short flowers (Darwin 1876; Temeles and Roberts 1993). Experimental studies of hummingbirds feeding at artificial flowers, however, fail to support this assumption. Whether the studies involved different species (Hainsworth 1973; Montgomerie 1984), sexes within the same species (Temeles and Roberts 1993), or individuals within the same sex of the same species (Temeles and Roberts 1993), longer-billed birds were able to use longer flowers and feed from them more quickly than shorter-billed birds. In contrast, shorter-billed birds were not able to use shorter flowers and feed from them more quickly than longer-billed birds (Hainsworth 1973; Montgomerie 1984; Temeles and Roberts 1993). Thus, longer bills were always better, which raises the question of why some hummingbirds have short bills (Montgomerie 1984).

In this paper, I address these problems by examining hummingbird-flower relationships from a different perspective: in addition to looking at the lengths of flowers, I also look at their diameters. Although studies of hummingbirds have analyzed a number of floral characteristics (e.g., corolla length and angle, nectar volume and concentration: Hainsworth 1973; Montgomerie 1984; Roberts 1992; Temeles and Roberts 1993), the effect of corolla diameter on hummingbird foraging behavior and flower use has for the most part been overlooked.

Here, I examine the effect of corolla diameter on two parameters of hummingbird foraging behavior known to be associated with differences in bill lengths: maximum extraction depth of nectar from a flower (i.e., how deeply a bird can successfully feed from a flower; Montgomerie 1984), and handling time at artificial flowers of varying corolla lengths (i.e., the time it takes a hummingbird to insert its bill, extract nectar, and withdraw its bill from a flower: Hainsworth 1973; Hainsworth and Wolf 1976; Montgomerie 1984).

In an earlier study (Grant and Temeles 1992), I found that a hummingbird's maximum extraction depth decreases as flowers become smaller in diameter. Because a bird's handling time depends on the difference between its maximum extraction depth and the length of a given flower [(maximum extraction depth – corolla length) is a measure of how much the bird extends its tongue; Ewald and Williams 1982; Montgomerie 1984], and because maximum extraction depth decreases with decreasing corolla diameter, I predicted that a hummingbird's handling time at flowers of a given length should increase with decreasing corolla diameters.

Materials and methods

The hummingbirds

Fourteen ruby-throated hummingbirds (*Archilochus colubris*) were captured at Amherst, Massachusetts during August and September

1992. On 15 September 1992, I transported seven of these birds (all females) to the National Zoological Park in Washington, District of Columbia. When not being used in the experiments, individual birds were housed in either 2.1 m × 1.5 m × 1.9 m or 1.0 m × 0.6 m × 0.8 m (height × width × depth) cages and fed Nektar-Plus commercial food (Nekton USA, Inc.) supplemented with 100% soy protein (Vege Fuel; Twin Laboratories, Inc.) ad libitum.

Hummingbirds were measured shortly after capture, and thereafter periodically throughout the duration of their captivity. Most studies of birds use the length of the exposed culmen, measured from the point where the tips of the forehead feathers impinge upon the culmen to the tip of the culmen, as a measure of bill length (Baldwin et al. 1931). Because bill feathering varies greatly within and between hummingbird species, and species with extensive feathering have been observed to insert their bills as deeply into flower as species with naked bills (P. Feinsinger, personal communication), total culmen, measured from the bird's gape to the tip of the culmen, may reflect more accurately a bird's ability to feed at long flowers, and hence may be a better indicator of bill length. The argument in favor of total culmen, however, may hold only for wide flowers, and at narrow flowers, bill insertion might actually be impeded by the feathering on a bird's bill. Consequently, I used both exposed culmen and total culmen as measures of bill length in this study, and report results for both measurements in my analyses. In addition, I measured bill width at the point where the forehead feathers impinge upon the culmen. All bill measurements were taken using 150-mm calipers accurate to the nearest 0.02 mm. Length of wing chord was measured as described in Baldwin et al. (1931). Weights of hummingbirds were taken on an Ohaus balance accurate to the nearest 0.1 g.

Studies of some birds indicate that bill lengths of individuals may vary seasonally (e.g., Gosler 1987). Such seasonal variation in bill length can have important consequences for studies of feeding adaptation, because if bill lengths of individuals change over time, then observed differences in foraging behavior at one point in time may not reflect differences between individuals over their lifetimes. In an earlier study (Temeles and Roberts 1993), bill lengths of individual rufous hummingbirds (*Selasphorus rufus*) did not change significantly over 9 months in captivity. Similarly, bills of ruby-throated hummingbirds did not change appreciably over the duration of the study: for both exposed and total culmens, regression lines did not differ significantly in slope ($=1$) or intercept ($=0$) from ($Y=X$), the function predicted if first and second measurements were the same ($P>0.5$).

Five adult females were selected from the original seven birds for use in the experiments. Bill measurements of these birds ranged from 16.1 to 18.1 mm ($\bar{x} \pm SE = 17.0 \pm 0.3$ mm) for exposed culmen and from 19.3–21.5 mm ($\bar{x} \pm SE = 20.5 \pm 0.4$ mm) for total culmen, and the two measurements were highly correlated ($P<0.005$, $r^2 = 0.95$). Bill widths ranged from 2.10 to 2.45 mm ($\bar{x} \pm SE = 2.23 \pm 0.07$ mm), and were not significantly correlated with either measure of bill length ($P>0.2$).

Experiments were conducted from 27 April 1993, by which time all five birds had completed their wing molts (wing chords of the birds ranged from 45 to 47 mm), to 10 June 1993. Birds were tested in the morning from approximately 0900 to 1300 hours (or earlier) on one corolla diameter per day. To reduce the possibility that birds would become satiated during the experiments, I fasted birds by removing their food for 30 min on the evening before and 30 min on the morning of the experiments. Birds were tested individually in a 2.1 m high × 1.5 m wide × 1.9 m deep cage having an opaque lining to prevent birds from seeing the observer.

Experiment 1: maximum extraction depth

The maximum depth from which a bird could extract nectar was determined following procedures outlined in Montgomerie (1984) and Temeles and Roberts (1993). An acrylic tube, or "corolla", was attached to a wooden dowel at a height of 1.25 m above the ground and positioned horizontally to resemble a flower on a stalk. Maximum extraction depths were measured for four corollas having internal diameters of 1.6, 3.0, 5.0, and 6.5 mm, and lengths

of 90 mm. For each diameter, the corolla was filled to its opening with 20% sucrose solution by weight, and then each bird was allowed to feed freely from the corolla. Maximum extraction depth was determined by measuring the distance from the lip of the corolla to the meniscus of nectar in the tube at 15-min intervals until the distance no longer increased. Three measurements of maximum extraction depth were taken for each bird, and the average was used in the data analyses.

Experiment 2: handling time

As used here, handling time is the total time that a hummingbird spent on a single visit to a flower, and includes the time it takes a bird to insert its bill, lick up nectar, and withdraw its bill from a flower (Montgomery 1984; Temeles and Roberts 1993). To measure handling times, I filmed birds using a video camera with a built-in stopwatch (Panasonic model WV 3250/12× camera and model AG 2400 recorder). Films were then analyzed on a VHS video recorder with a jog/shuttle feature that permitted analysis at 60 frames/s (Panasonic model PV 4264). Times were measured from the moment that the tip of the bird's bill entered the corolla until the moment it was withdrawn to the same position. Handling time thus includes both the time for bill insertion and retraction, and the time it takes a bird to lick up nectar. To increase the visibility of nectar for video analysis, two drops of red food coloring (FD&C red 40) were added to every 100 ml of sucrose solution.

The major objective of this experiment was to examine the effect of corolla diameter on hummingbirds' handling times at corollas of different lengths. Accordingly, I measured handling times at 15 different artificial corollas having internal diameters of 1.6, 3.0, 5.0, and 6.5 mm, and lengths which increased in 10-mm increments from 5 to 35 mm, except at the narrowest diameter, where the maximum length examined was 25 mm (this lower maximum was used because 35 mm exceeded the maximum extraction depths of birds at this diameter; see Results). These corolla diameters and lengths corresponded closely to the range for flowers of 31 species of North American plants visited by short-billed hummingbirds in the field (Grant and Grant 1968; E.J. Temeles, unpublished work). Corollas were presented to birds in order of decreasing diameter and increasing length, and each bird was tested until at least 30 measurements of handling time were recorded at each of the 15 diameter × length combinations.

Handling times of the five birds were measured at the 15 different corolla diameter and length combinations while keeping nectar volume and concentration constant at 8 µl of 20% sucrose solution (weight:weight). Nectar volume and concentration were held constant because previous studies emphasized the effect of corolla length on both foraging behavior and resource partitioning of hummingbirds (e.g., Snow and Snow 1980; Montgomery 1984; also see Temeles and Roberts 1993). To ensure that handling times were measured precisely for a known volume of nectar, only those visits in which a bird completely consumed all 8 µl of nectar in a single probing of the corolla were used in the analyses; visits in which a bird probed the feeder two or more times or failed to consume the total nectar reward were discarded. Finally, to avoid problems of unequal sample sizes and pseudoreplication, I used the means of all measurements of handling times for each bird at each of the 15 corolla diameter × length combinations in the data analyses.

Statistical analyses

On the basis of previous studies (see Introduction and Montgomery 1984; Grant and Temeles 1992; Temeles and Roberts 1993), I predicted that maximum extraction depth should decrease, whereas handling time should increase, with decreasing corolla diameter. Consequently, I used Page's test for ordered alternatives in combination with one-tailed nonparametric multiple comparison procedures (Siegel and Castellan 1988) to analyze maximum extraction depths and handling times at the different corolla diameters, with individual birds as blocks. Page's test evaluates the null

hypothesis of equality among populations against an alternative in which order is specified. I preferred it for my analyses, because I was primarily interested in whether maximum extraction depth decreased with decreasing corolla diameter (i.e., 6.5 mm > 5.0 mm > 3.0 mm > 1.6 mm) and handling time increased with decreasing corolla diameter (i.e., 6.5 mm < 5.0 mm < 3.0 mm < 1.6 mm). Minitab statistical packages (Minitab 1989) were used to perform regression analyses, and methods in Siegel and Castellan (1988) were followed for Cochran's Q -test and Friedman's two-way ANOVA.

Results

Maximum extraction depths

Corolla diameter significantly affected the maximum depth a hummingbird could probe into flowers ($P < 0.001$, Page's test). Maximum extraction depths decreased as tubes became narrower, and dropped off sharply from 3.0 to 1.6 mm wide tubes. Maximum extraction depths of the five birds were significantly shorter at 1.6 mm diameter corollas than at either 5.0 or 6.5 mm diameter corollas ($P < 0.05$, nonparametric multiple comparisons). Similarly, maximum extraction depths were significantly shorter at 3.0 as opposed to 6.5 mm diameter corollas ($P < 0.05$). No other multiple comparison was significant.

Moreover, at corolla diameters of 3.0, 5.0, and 6.5 mm, maximum extraction depth was correlated with both measures of bill length, exposed culmen and total culmen; i.e., longer-billed birds had greater maximum extraction depths than shorter-billed birds ($P < 0.02$ for all correlations; Fig. 1). In contrast, at corollas having diameters of 1.6 mm, maximum extraction depth was not significantly correlated with bill length, and there was no difference between long- and short-billed birds in the maximum depth they could probe into these narrow flow-ers ($P > 0.8$ for both exposed and total culmen; Fig. 1).

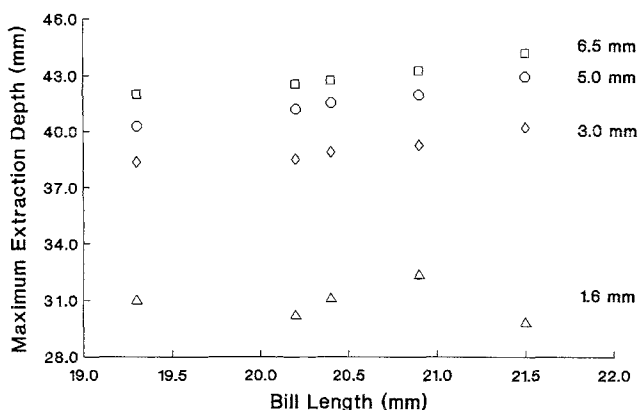


Fig. 1 Relationships between total culmen lengths (bill length) and maximum extraction depths (maxdepth) for five female *Archilochus colubris* at corolla diameters of 1.6, 3.0, 5.0, and 6.5 mm. The statistics for these correlations are: 1.6 mm: maxdepth = 33.9 - 0.15 (bill length), $r^2 = 0.016$, $P = 0.842$; 3.0 mm: maxdepth = 21.7 + 0.85 (bill length), $r^2 = 0.871$, $P = 0.02$; 5.0 mm: maxdepth = 17.2 + 1.19 (bill length), $r^2 = 0.988$, $P = 0.001$; 6.5 mm: maxdepth = 22.8 + 0.98 (bill length), $r^2 = 0.949$, $P = 0.005$

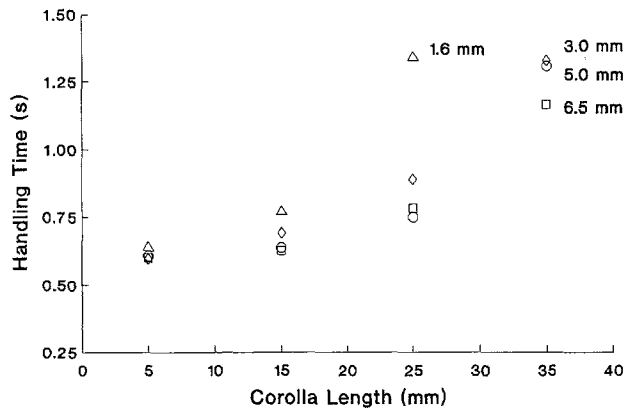


Fig. 2 Handling times of *A. colubris* at artificial flowers of various corolla lengths and 1.6, 3.0, 5.0, and 6.5 mm diameters. Each point represents the mean handling time for each corolla computed from the means of five individuals

The reason for lack of significant correlations was that bills of the birds were too wide to completely enter these narrow floral tubes, and differences between birds in how far they could insert their bills and extend their tongues were not correlated with bill length.

Handling times

Handling time increased with decreasing corolla diameter, and for a given corolla length, birds had longer handling times at narrower diameters (Fig. 2). At 1.6 mm diameter flowers, handling times of hummingbirds were significantly longer than at 6.5 mm diameter flowers for each corolla length, and were longer than at 5.0 mm diameter flowers for 15 and 25 mm corolla lengths ($P < 0.05$, nonparametric multiple comparisons). Differences in handling times at wider flowers were less pronounced, and occurred at longer flowers owing to the more gradual non-linear increase in handling times (Fig. 2). Accordingly, at 3.0 mm diameter flowers, handling times were longer than at 6.5 mm diameter flowers for 35 mm corolla lengths ($P < 0.05$). No other multiple comparisons were significant.

In addition, regardless of the diameter of the flower, longer-billed birds had shorter handling times than shorter-billed birds, but only at long flowers. At the longest flower studied for each of the four corolla diameters, handling time was significantly negatively correlated

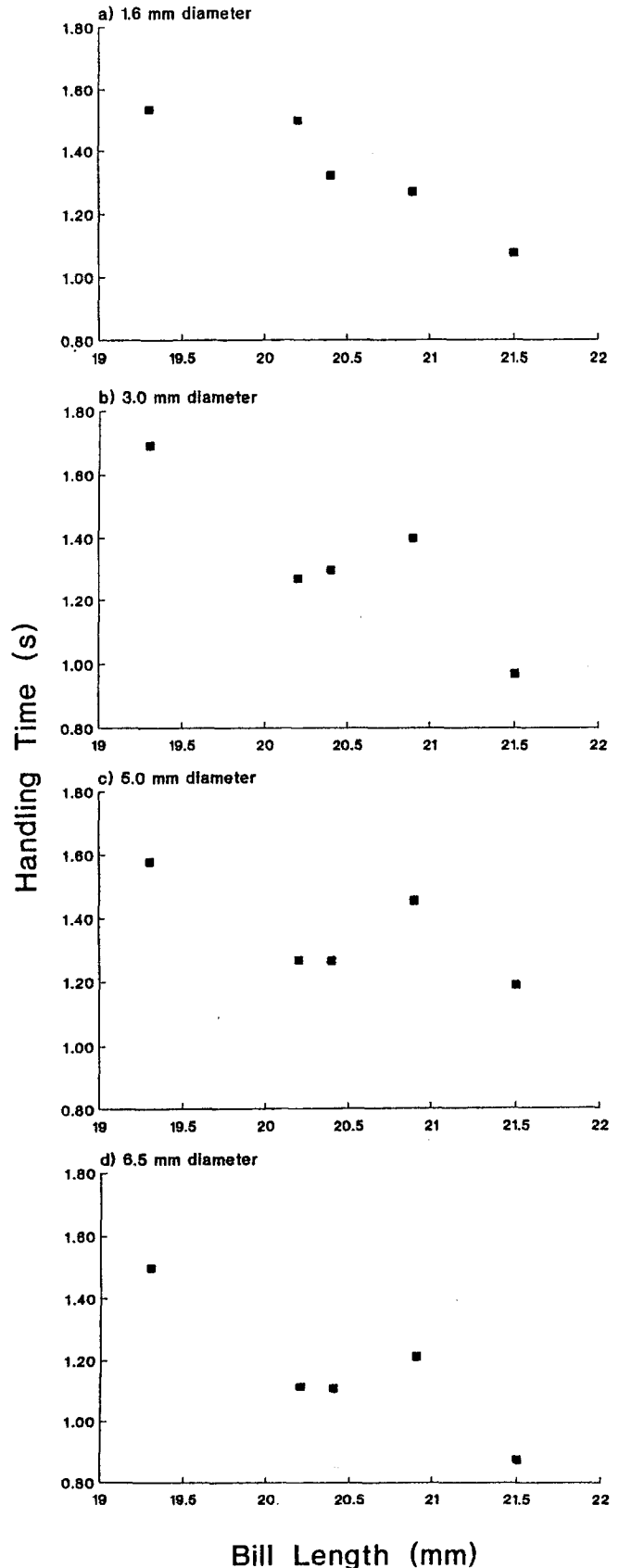


Fig. 3a-d Relationships between total culmen lengths (bill length, BL) and handling times (HT) for five female *A. colubris* at the longest flowers studied at **a** 1.6, **b** 3.0, **c** 5.0, and **d** 6.5 mm corolla diameters. Flower lengths measured 25 mm for the 1.6 mm diameter corollas, and 35 mm for the 3.0, 5.0 and 6.5 mm diameter corollas. A shorter flower was used for the 1.6 mm diameter corollas because 35 mm exceeded the maximum extraction depths of birds at this diameter. The statistics for these relationships are: **a** 1.6 mm: $HT = 5.66 - 0.21 BL$, $r^2 = 0.88$, $P = 0.018$; **b** 3.0 mm: $HT = 6.99 - 0.28 BL$, $r^2 = 0.77$, $P = 0.05$; **c** 5.0 mm: $HT = 4.79 - 0.17 BL$, $r^2 = 0.811$, $P = 0.037$; **d** 6.5 mm: $HT = 6.11 - 0.24 BL$, $r^2 = 0.78$, $P = 0.048$

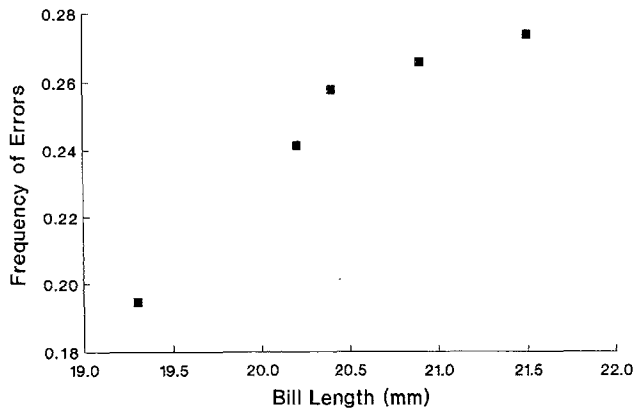


Fig. 4 Relationship between the frequency of feeding errors (errors) and total culmen length (bill length) for five female *A. colubris* at artificial flowers of 1.6 mm diameters. Errors = $-49.4 + 3.62$ bill length, $r^2 = 0.89$, $P = 0.015$, error frequencies arcsine-transformed

with the length of the total culmen (Fig. 3a–d). This result was somewhat weaker when exposed culmen was used as the measure of bill length, and a significant correlation was observed for the longest flower studied at the 1.6 mm diameter ($P < 0.01$), but not for wider diameters (although all P -values were < 0.1). In contrast, correlations between handling time and bill length at shorter corolla lengths were not significant whether total or exposed culmen was used as the measure of bill length ($P > 0.1$ for all correlations).

Insertion errors

During the handling time experiments, all five birds were observed to make errors in attempting to feed at artificial corollas: birds would miss the opening of flowers with their bills or tongues, and in some cases, the bill of a bird would probe past the flower as it hovered. "Insertion errors" were associated only with narrow flowers measuring 1.6 mm diameter, and were not recorded at wider diameters ($P < 0.005$, Cochran's Q test). The number of insertion errors at 1.6 mm diameter flowers did not depend on the lengths of the flowers ($P > 0.05$; Friedman's two-way ANOVA using flower lengths as treatments and individual birds as blocks). Durations of insertion errors ranged from 0.02 to 0.36 s ($\bar{x} \pm \text{SE} = 0.14 \pm 0.01$ s; $n = 80$ measurements of error times for five birds). Error times did not depend on the lengths of flowers ($P > 0.4$; Friedman's two-way ANOVA using flower lengths as treatments and individual birds as blocks).

The frequency of insertion errors was significantly correlated with total culmen length (Fig. 4; $P < 0.02$; $P < 0.06$ for exposed culmen; error frequency calculated by combining the number of errors for each bird at 5, 15, and 25 mm corolla lengths divided by 90 flowers per bird; data were then arcsine-transformed). In other words, longer-billed birds made more errors than shorter-billed birds in attempting to feed from narrow flowers.

Error times were not significantly correlated with either measure of bill length (P values > 0.25 for both regressions).

Discussion

Effect of corolla diameter

The results of this study demonstrate that a hummingbird's ability to feed from flowers varies as a function of flower diameter. Maximum extraction depth of ruby-throated hummingbirds increased with increasing corolla diameter (Fig. 1). As the diameters of flowers increase, a hummingbird can insert progressively more of its bill and head into the floral tube. At 1.6 mm diameters, a bird can insert its bill only halfway down the floral tube, because the width of the bill at the base is wider than the flower. In contrast, at 6.5 mm diameters, a bird can insert not only its bill but also much of its face into the floral tube, thereby increasing maximum extraction depth.

Handling times of hummingbirds decreased with increasing corolla diameter (Fig. 2). Because a bird can insert more of its bill and/or face into the floral tube as flower diameter increases, the tip of its bill is closer to the nectar source and the tongue does not have to be extended as far, thereby shortening the licking cycle (Ewald and Williams 1982). This may explain why handling times are longer at narrow flower diameters, and in fact, birds were observed to extend their tongues farther at narrow as opposed to wide flowers of the same length.

As shown here, a hummingbird's handling time at a given corolla length is not fixed, but rather varies with corolla diameter (Fig. 2). This result has some important implications for flower use by hummingbirds in the field. For example, the bill (exposed culmen) of the ruby-throated hummingbird averages about 16 mm in length, and for this species, a flower 35 mm in length would be considered a "long" flower relative to a flower 25 mm in length. Inspection of Fig. 2, however, indicates that a ruby-throated hummingbird has roughly the same handling time at a flower 1.6 mm in diameter and 25 mm in length as it has at a flower 3 or 5 mm in diameter and 35 mm in length. For ruby-throated hummingbirds, all of these flowers required the same long handling times, and hence all may be "long" flowers. Other examples of "handling time equivalents" – that is, flowers that have the same handling times, but different lengths and diameters – can be determined from Fig. 2 by drawing a line across the four handling time curves parallel to the x -axis. It is apparent, then, that to understand feeding costs and flower use for a hummingbird of a given bill length, effective flower lengths depend not only on the measured length, but also on the diameters. The robustness of these conclusions can be assessed through experiments in which birds are offered choices between two flowers of different dimensions. When corolla diameter is varied and other variables are held constant, birds should prefer wider flowers to narrower flowers because handling times would be

shorter and insertion errors would be reduced or absent. Similarly, choice experiments could be performed to evaluate handling time equivalents. Based on Fig. 2, birds should prefer flowers whose length and diameters result in the shortest handling times, but should exhibit no preference when flower lengths and diameters result in equivalent handling times. Flower lengths and diameters could then be adjusted through "titration experiments" to determine just how much of a difference in handling time equivalents is important for flower choice.

The relative advantages of long versus short bills

Maximum extraction depths of long-billed hummingbirds were greater than those of short-billed hummingbirds at flower diameters greater than the widths of the birds' bills (Fig. 1). Similarly, handling times of long-billed hummingbirds were shorter than handling times of short-billed hummingbirds at artificial flowers having long corollas, regardless of flower diameter (Fig. 3a–d). These results extend those obtained in earlier studies that compared the foraging abilities of birds having different bill lengths (Hainsworth 1973; Hainsworth and Wolf 1976; Montgomerie 1984; Grant and Temeles 1992; Temeles and Roberts 1993) by demonstrating that the advantages of a longer bill in allowing a bird to use longer flowers and feed from them more quickly occur at all flower diameters greater than the width of the bill.

In contrast, the advantages of a longer bill apparently are partially negated at narrow flowers (Figs. 1, 4). The finding that hummingbirds make insertion errors when feeding at narrow flowers and that these insertion errors are correlated with bill length is the first evidence documenting a feeding advantage for a small bill. One criticism of this result is that the birds were feeding at artificial flowers made from hard plastic, and the hard plastic may have caused the bills of birds to "bounce" off flowers more frequently than would happen had a softer material (or a real flower) been used. However, ruby-throated hummingbirds also make errors with the same or higher frequency when feeding at live flowers (Smith et al. 1996).

The significance of these errors is that they impose a "penalty" for feeding at narrow flowers by increasing feeding time, because a hummingbird must reposition itself in order for its bill to enter the flower so it can feed. For example, error times in this study averaged 0.14 s, whereas handling times at 1.6 mm diameter flowers averaged 0.64 s and 1.34 s for 5 mm and 25 mm long flowers. Insertion errors would thus add a time cost penalty of approximately 10–20% to a hummingbird's feeding time. Because they make more errors, this penalty is greater for longer-billed birds than for shorter-billed birds. In other words, at narrow flowers, longer-billed birds may actually have longer feeding times than short-billed birds when errors are taken into account. Whether or not longer-billed birds have longer feeding times at narrow flowers than shorter-billed birds will depend on the magnitude of time costs associated with insertion er-

rors relative to handling time. Longer-billed birds should have an advantage at long, narrow flowers with large nectar volumes, because under such conditions, the shorter handling times of longer-billed birds at long, narrow flowers (Fig. 3d) compensate for the time-costs of insertion errors. In contrast, shorter-billed birds should have a feeding-time advantage at short, narrow flowers with small nectar volumes, because under these conditions, handling time is not significantly correlated with bill length, and the time-costs associated with insertion errors will likely equal or exceed handling time.

Field observations do suggest, in fact, that long-billed hummingbirds may have difficulties feeding at small flowers. Wagner (1946) noted that the blue-throated hummingbird (*Lampornis clemenciae*), which has a bill approximately 24 mm in length (Johnsgard 1983), seldom visited flowers of *Salvia mexicana*, although smaller-billed species such as white-eared hummingbirds (*Hylocharis leucotis*, bill length about 17 mm; Johnsgard 1983) did. Wagner speculated that bills of *L. clemenciae* were too large for efficient feeding at this small, narrow flower (although differences in body size and energy requirements also may have been a factor). Similarly, Whitten (1981) observed that when ruby-throated hummingbirds fed at *Monarda clinopodia*, the flowers occasionally became stuck on the birds' bills, which caused them to perch and then struggle to remove the corollas. The latter observation indicates that time-costs in addition to feeding errors may occur from visits to narrow flowers. One prediction from my experiments is that in addition to insertion errors, birds with longer bills might have to spend more time "aiming" their bills as they approach a flower. Hence, flowers may have different "lining-up" costs depending upon the sizes of their openings.

Finally, I was able to examine the effect of corolla diameter on foraging behavior for one sex of one hummingbird species, and as a result, the variation in bill lengths and widths was very small relative to the variation in these measurements between hummingbird species. Further studies of hummingbirds (especially long-billed species) feeding at narrow flowers may be useful in understanding the advantages and disadvantages of long and short bills, and also the advantages and disadvantages of differences in bill widths. Hummingbird species exhibit variation in the width of the bill at both the base and the tip (E.J. Temeles, unpublished work). Presumably, such differences between species in bill widths would affect flower choice and foraging behavior.

Conclusions

The results of my 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 corolla length, provided that corolla diameter is taken into account. Similarly, the laboratory experiments indicate that differences in bill lengths

between hummingbirds reflect flower-dependent differences in foraging abilities, and that there are trade-offs in the relative advantages of long versus short bills. Long bills allow birds to use longer flowers and to feed from long flowers more quickly, whereas short bills increase feeding success at short, narrow flowers. Collectively, these results suggest that the evolutionary effect of hummingbirds and flowers upon one another is more complex than has generally been realized, because researchers did not incorporate flower diameter into the trade-off between bill length and flower length.

This conclusion receives some support from recent studies of plants that demonstrate that pollinators can exert directional selection for increases in the corolla widths of flowers (Galen 1989; Campbell 1989; Campbell et al. 1991). In two of these studies (Galen 1989; Campbell et al. 1991), corolla width was correlated with corolla length, which raises the possibility that the long tubes of some hummingbird flowers may have arisen indirectly via pollinator-mediated selection for wider corollas (e.g., Fenster 1991).

Consideration of one additional variable, corolla width, in conjunction with corolla length, offers new insights concerning flower use by hummingbirds and the relative advantages of long versus short bills. Species of hummingbird flowers, however, exhibit an array of shapes, constrictions, and curvatures. Of these other variables, only corolla curvature has received some attention (Wolf et al. 1972; Stiles 1975), and more studies of the effect of flower morphology on pollinator foraging behavior are needed. Studies of foraging behavior in the laboratory should be especially useful, because of the ability to manipulate one component of flower morphology (e.g., flower curvature) at a time. We are beginning to understand why some hummingbird bills are long, whereas others are short, and why some hummingbird flowers are wide, whereas others are narrow. Now, why are bills of some hummingbirds and the tubes of the flowers they visit curved?

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