

## SHORT COMMUNICATIONS

### Function of the Bill and Tongue in Nectar Uptake by Hummingbirds

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Hummingbirds extract nectar from flowers by licking with their tongues. According to the current explanation, nectar flows into the lateral grooves of the tongue by capillary action and is then transported into the bill by retraction of the tongue (Scharke 1931, Weymouth et al. 1964, Hainsworth 1973). The next step of the process is uncertain: How do hummingbirds remove nectar from their tongues? One hypothesis is that the tips of the mandibles close tightly around the tongue when it is being extended. Such compression could simultaneously squeeze nectar out of the grooves and wipe nectar off the outside surface of the tongue. In the present study, measurements were made to determine whether the tongue is compressed dorsoventrally and/or laterally as the tongue is extended from the bill. A second goal of this study was to determine whether or not rates of licking depend on the distance between the bill tip and the food supply. Investigating such relationships should aid our understanding of the co-evolution of flowers and hummingbirds, because, for a given bill length, an increased corolla length will often lead to an increased distance between the bill tip and the nectar supply. If this increased distance results in a lower licking rate, then long bills may have evolved as an adaptation to reduce the distance between bill tips and nectar in long corollas.

Measurements of food uptake by Black-chinned Hummingbirds (*Archilochus alexandri*) at feeders suggest that, as corolla length increases, rates of nectar extraction decrease but rates of licking do not decrease (Hainsworth 1973). For birds feeding at

feeders that provided unrestricted amounts of sucrose solution and had no corollas, the load of solution per lick calculated from these measurements was more than an order of magnitude greater than the volume of the tongue grooves (Hainsworth 1973). Hainsworth therefore concluded that the grooves were of minor importance in transporting nectar. This conclusion leads to a perplexing question: How do hummingbirds transport such large quantities of nectar per lick? They do not suck nectar through the tongue (Weymouth et al. 1964), and the remaining surface of the tongue seems inadequate for transporting such large quantities of nectar. Resolution of this question was the third goal of the present study.

We investigated the preceding questions by analyzing movie film of foraging hummingbirds. Our study subjects were noncaptive, male Anna's Hummingbirds (*Calypte anna*). Movies were filmed in Laguna Hills, Orange County, California. Rates at which sucrose solution was extracted from feeders were measured at a different site, approximately 20 km to the east in the Santa Ana Mountains.

Bill and tongue movements were filmed at 70 frames/s using a Beaulieu super 8 movie camera attached to either a 230 mm lens and an extension tube or a Schneider 6 to 66 zoom lens. Birds were filmed while they fed at feeders providing unobstructed access to unlimited food (see Ewald and Rohwer 1980) or feeders designed to provide a clearer view of the bill tips and tongue (Fig. 1). The concentration of sucrose solution in the feeders was approximately 0.7 M.

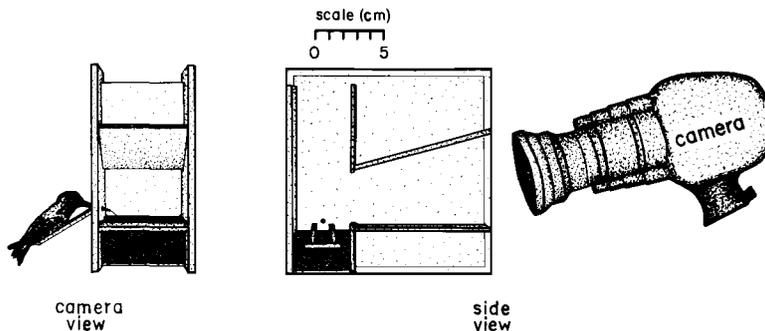


Fig. 1. Plexiglass feeder designed for photography of bill and tongue movements with long extensions of the tongue. Slightly less than 1 cm of the bill tip passed through the access hole during feeding. The tongue traveled the remaining distance between the bill tip and the sucrose solution.

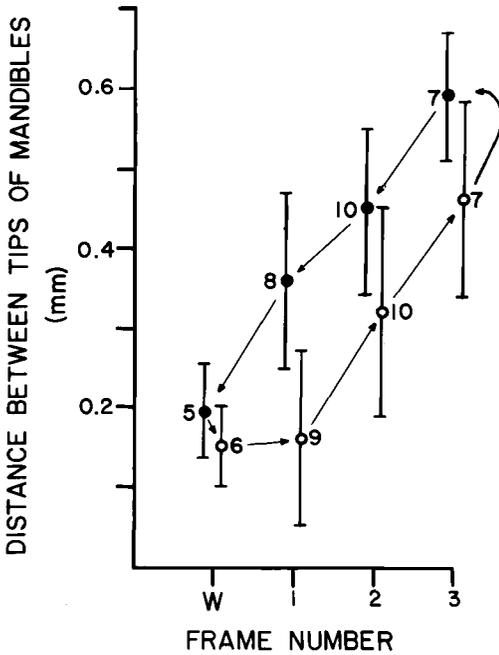


Fig. 2. Distance between the tips of the upper and lower mandibles during extension and retraction of the tongue. For frame numbers one, two, and three, open circles represent the first, second, and third frame of tongue extension; closed circles represent the first, second, and third frames before complete retraction of the tongue. The "W" category consists of frames taken when the tongue was completely withdrawn into the bill. The difference between the solid and open circles in the "W" category was not statistically significant (one-tailed  $P < 0.2$ ). For each frame category, the open and closed circles were staggered slightly to illustrate the standard deviations clearly. Arrows represent the sequential progression during the lick cycle. The number next to each data point represents the number of frames in the sample. (Sample sizes varied, because poor photographic quality made some frames unusable and because the number of frames per cycle varied slightly.)

To evaluate the importance of the tongue grooves in nectar extraction, we estimated extraction rates and groove volumes. To derive extraction rates, we measured rates of weight gain with perch-weighting scales (see Ewald and Rohwer 1980) while hummingbirds fed from feeders that provided sucrose solution in unrestricted amounts. Rates of weight gain were converted into rates of nectar extraction using the specific gravity of the sucrose solution. Measurements of tongue morphology were made with calipers under a dissecting microscope on a

tongue from a bird that was frozen promptly after death.

If the tongue is compressed dorsoventrally during extension, the distance between the tips of the upper and lower mandibles should be smaller during extension than during retraction. To test this prediction, we measured for each frame both the distance between the bill tips and the length of tongue extension beyond the bill tips. We then calculated the mean of these distances for each stage of the cycle, from bill closure before extension until bill closure after retraction. To convert measurements from the film to actual measurements, we used as a conversion factor the quotient of actual bill depth and the depth measured from the film.

The bill tips closed more completely around the tongue in the first frame showing tongue extension than in the first frame before complete retraction (one-tailed  $P < 0.01$ ;  $t$ -test comparing the two means for frame #1 in Fig. 2). The mean distance of tongue extension did not differ between these two groups (both means were 4 mm; two-tailed  $P \geq 0.1$ ;  $t$ -test). The bill also opened less during the second frame of extension than during the second frame before complete retraction (frame #2 in Fig. 2). Similarly, the bill opened less during the third frame of tongue extension than during the third frame before complete retraction (frame #3 in Fig. 2; one-tailed  $P < 0.05$  for each comparison). The length of tongue extension could not be accurately measured for either of these two comparisons because in most of the frames the tongue had already penetrated the sucrose solution.

To determine whether or not the restricted opening during tongue extension was sufficient to compress the grooves of the tongue, we measured the depth of a tongue that was obtained from a bird frozen promptly after death. When the troughs of the tongue were filled with water, the depth of the tongue, 4 mm from the tip, was 0.31 mm. The depth of the loaded tongue is therefore approximately twice as great as the distance between the bill tips during the first frame of extension (0.16 mm; see Fig. 2). In contrast, the mean distance between the bill tips in the first frame before complete retraction (0.36 mm; see Fig. 2) was slightly greater than the depth of the loaded tongue. (Accuracy of these measurements was approximately 0.02 mm.) These results indicate that the tongue is compressed dorsoventrally when it is being extended but not when it is being retracted. When compressed dorsoventrally with micrometers, the tongue depth was between 0.1 and 0.2 mm. Our accuracy was limited in this case, because we could not determine when maximal compression of the grooves first occurred in this dimension. The range we obtained is consistent with the idea that the tongue is entirely or almost entirely compressed dorsoventrally during extensions.

Is the tongue also compressed laterally during ex-

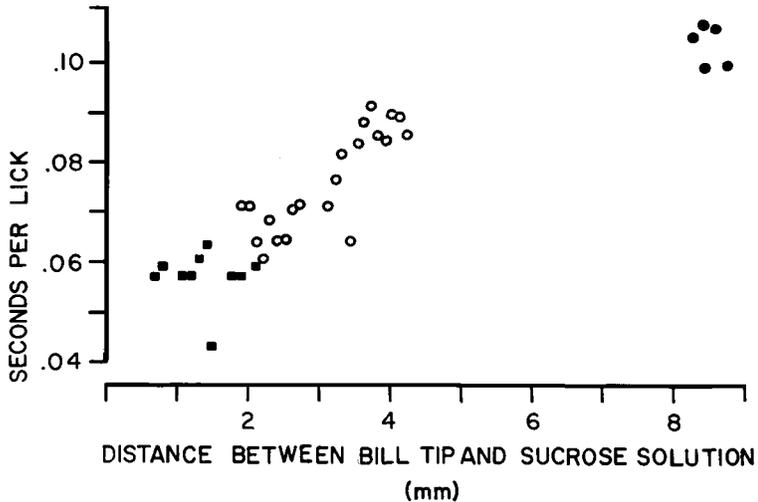


Fig. 3. Mean durations of extrusion-retraction cycles as a function of the distance between the bill tip and the sucrose solution. Squares and open circles represent two different individuals, each feeding at a conventional, unobstructed feeder. Closed circles represent a third individual, which fed at the feeder diagrammed in Fig. 1. The positive correlation was statistically significant for all data points combined ( $P < 0.001$ ; Spearman  $r_s = 0.94$ ) and for the individual represented by open circles ( $P < 0.01$ ;  $r_s = 0.78$ ).  $n = 148$  cycles.

tension? Between 0.2 mm from the tip of the tongue and the proximal end of the grooves, the width of the loaded tongue was between 0.7 and 0.9 mm. Approximately 1 mm from the bill tip the inside of the bill formed a trough, which was 0.2 mm wide in the lower mandible and 0.3 mm wide in the upper mandible. Using calipers, we estimated the width of the tongue under complete lateral compression of the grooves at 2-mm intervals. The measured widths (mean =  $0.4 \pm 0.1$  mm) support the hypothesis that the tongue is compressed laterally by the sides of the bill.

Figure 3 shows that the time spent per lick increased as the distance between the bill tip and the sucrose solution increased. The mean rate of licking at unobstructed feeders was 13.8 licks/s (Fig. 3, open circles and squares). The amount of time that the tongue was out of the bill per lick was also positively correlated with the distance between the bill tips and the sucrose solution ( $r_s = 0.92$ ,  $P < 0.001$ ), but the amount of time spent inside the bill per lick was not ( $r_s = 0.10$ ,  $P > 0.1$ ); thus, the time spent outside the bill yields the strong correlation between time per lick and distance from the sucrose solution (Fig. 3). Unfortunately, the film was not sufficiently clear to determine whether or not time spent in the sucrose solution per lick was positively correlated with distance from the solution.

The maximum rates of licking were above 17/s (Fig. 3, squares), much greater than the  $2.6 \pm 0.7$  licks/s that Hainsworth (1973) measured at unobstructed feeders. This discrepancy probably resulted from

differences in camera speed. Hainsworth used speeds of 18 and 24 frames/s. At such low speeds, many licking cycles could have been missed.

The mean extraction rate was  $17 \pm 3$  (SE)  $\mu\text{l/s}$  ( $n =$  four birds, total licking time = 549 s). The *C. anna* tongue that we measured was 1.5 times the width and 1.3 times the depth of the *Archilochus colubris* tongue that Hainsworth measured; the *C. anna* groove was 1.8 times as long. Based on these factors, the total volume of the *C. anna* grooves should be approximately 3.5 times that of *A. colubris*. Hainsworth's (1973) measurement of *A. colubris*' groove volume was  $0.8 \mu\text{l}$ ; *C. anna*'s groove volume should therefore be approximately  $2.8 \mu\text{l}$ . Based on our measurements of 13.8 licks/s and  $17 \mu\text{l/s}$ , *C. anna* transports  $1.2 \mu\text{l}$  per lick, well below our rough estimate of the maximum groove volume. The groove volume, therefore, appears to be sufficient for holding the total amount of food gained per lick.

Our photographs also showed that some nectar is carried on the surface of the tongue. When the birds fed from unobstructed feeders, a droplet of food on the tip of the tongue was brought back into the bill during most of the cycles; based on the measurements of droplet diameter from the film, however, the mean volume of the droplets was approximately  $0.08 \mu\text{l}$  ( $n = 51$  droplets), less than 10% of the total sucrose solution transported per lick. The droplets are therefore much less important than the grooves for transport of food.

Our data indicate that nectar is transported to the bill primarily in the grooves and that constriction of

the tongue by the bill removes the nectar from the tongue; it is still not clear, however, how the nectar moves from the anterior portion of the bill into the esophagus. The nectar may adhere to the base of the extruded tongue, being brought to the base of the bill when the tongue is retracted. Suction may help transport nectar into the esophagus: our film shows a bulge in the throat region as the tongue is being extended.

Among hummingbirds, long bills are believed to be beneficial because they facilitate probing of flowers with long corollas (Wolf et al. 1972). Our results provide a mechanism for such a benefit: at flowers with long corollas, long bills may yield greater rates of licking than short bills, because long bills permit maintenance of small distances between nectar and the bill tips, which squeeze loads of nectar off of the tongue. It is therefore not surprising that the bills of hummingbirds tend to be similar in length to the corollas that are visited by the birds (Wolf et al. 1972, 1976). Such matching should result in short transit times by the tongue between the nectar source and the inside of the bill.

Although previously measured negative correlations between extraction rate and corolla length are most pronounced when feeders contain unnaturally large volumes of food, such correlations are still statistically significant when food volumes are similar to those found naturally in flowers (Hainsworth and Wolf 1979). This finding, coupled with our results, suggests that long bills evolved, at least in part, because increased bill length increases rates of licking from flowers with long corollas. Long corollas probably coevolved because of pollination benefits associated with specialization on pollinators (Wolf et al. 1976).

We thank C. E. Bayer, F. R. Hainsworth, B. Hallet, A. Heyneman, and R. D. Montgomerie for comments

on the manuscript, C. E. Bayer, D. Nelson, and L. Shemshedinofski for helping during data reduction, and B. Thomas and R. Munson for providing use of facilities at Tucker Wildlife Sanctuary. Research was supported by grants from the National Science Foundation (DEB 77-15521), the Chapman fund of the American Museum of Natural History, the Orange County chapter of the Audubon Society, and the Harry Frank Guggenheim Foundation.

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Received 28 September 1981, accepted 25 January 1982.

### Tarsometatarsus of *Protostrix* from the mid-Eocene of Wyoming

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Two, probably three (Rich and Bohaska 1976, 1981), families of owls are known from Paleogene sediments of North America and Europe, most taxa being represented by only one or two fragmentary bones. One family, the Protostrigidae, which is endemic to North America, contains two genera, *Eos-trix* and *Protostrix*. Although several specimens (and species) of *Protostrix* are known (Brodkorb 1971), thus far no tarsometatarsus of any species in this genus has been recognized, and it has been difficult to make comparisons with other fossil owls, most

frequently represented by this durable, hind-limb element. It is of some taxonomic interest, then, that a distal fragment of a tarsometatarsus in the Vertebrate Paleontology collections of the American Museum of Natural History appears to represent *Protostrix*.

In 1913 Shufeldt described the distal end of the right tarsometatarsus (AMNH No. 2629, see Fig. 1) among a number of bones that he proposed were from "some medium sized falconine species" (p. 295), which had been collected in 1903 from the lower