

## ON THE TONGUE OF A HUMMINGBIRD: ITS ROLE IN THE RATE AND ENERGETICS OF FEEDING

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**Abstract**—1. Rate of intake of hummingbirds (3.1 and 7.9 g) visiting a feeder was greater for larger hummingbirds but was not dependent on sugar concentration up to 1.0 molar sucrose.

2. Most flowers produce nectar with concentrations (0.24–1.48 molar sucrose) that should not influence rate of nectar intake.

3. Rate of tongue licking was independent of body size (2.6–3.8 licks/sec), but the larger hummingbird obtained more nectar per tongue lick.

4. Morphological studies indicated that the grooves on the tongues of hummingbirds may play a minor role in determining rate of nectar intake at a feeder with large nectar volumes, but they could be important in emptying small nectar volumes from flowers.

5. Adding a "corolla" to the feeder resulted in a linear decrease in rate of intake with increasing "corolla" length. However, corolla curvature, position and the volume of nectar in flowers are also important for determining rate of nectar extraction from flowers.

### INTRODUCTION

RECENT studies of hummingbird foraging have provided estimates of the rate and energetic efficiency (energy expended relative to energy intake) with which hummingbirds can extract nectar from flowers (Wolf *et al.*, 1972; Hainsworth & Wolf, 1972c). This energetic efficiency should determine the extent of the energy reserves of a hummingbird and should govern which flowers it visits for food. Also, the flowers visited by a hummingbird will have an impact on cross-fertilization of those flowers which utilize hummingbirds as pollinators.

One factor that influences the energetic efficiency of foraging is the time a hummingbird must expend energy while it is hovering and extracting nectar from flowers. Another factor is the size of the hummingbird, since this will influence the cost of hovering (Hainsworth & Wolf, 1972b). We wished to systematically analyze variables which could influence the rate of nectar extraction of hummingbirds of different sizes. We have done this by filming hummingbirds visiting a feeder. Hummingbirds of two sizes visited the feeder, and we could control the concentration of the "nectar" and the length of the artificial "corolla". The results demonstrate the role of the length and structure of a hummingbird's tongue, the amount of nectar the tongue can hold, as well as the rate of licking for determining the rate and efficiency of nectar uptake.

## MATERIALS AND METHODS

*Feeding experiments*

The experiments were performed at the Southwestern Research Station, Portal, Arizona, in June 1972. The most common hummingbirds visiting feeders at this time were male, female and juvenile Black-chin Hummingbirds (*Archilochus alexandri*) and male Blue-throat Hummingbirds (*Lampornis clemenciae*). Female and juvenile *Archilochus* could not be distinguished, and, therefore, they had to be classed together. There were no obvious differences between individuals visiting the feeders that would suggest a difference in feeding habits between females and juveniles. The two species differed more than twofold in body weight. On the average male *Archilochus* weigh 3.1 g and females and juveniles weigh 3.3 g (Stiles, 1970), while male *Lampornis* weigh 7.9 g (Lasiewski & Lasiewski, 1967).

The birds were offered sucrose solutions of either 0.25, 0.5, 1.0, or 2.0 molar concentration from a hanging feeder with a tubular glass spout. The feeder was weighed ( $\pm 0.1$  mg) before and after a visit and the intake in grams was converted to a volume intake from the specific gravities of the sugar solutions. The birds visited the feeder with sufficient rapidity that controls for evaporation were judged to be unnecessary. The birds were timed at the feeder either with a stopwatch or by analyzing movie film records of visits to the feeder. Films were taken at either 18 or 24 frames/sec, and this allowed resolution of time intervals of 0.05 or 0.04 sec through a frame by frame analysis.\*

Hummingbirds consume nectar by licking with their tongues. The tongue is forked at the tip and contains a groove on each side into which the nectar flows (Scharnke, 1931; Weymouth *et al.*, 1964). On many of our film records we could distinguish individual tongue movements. Therefore, we were able to count the total number of tongue licks during a visit and divide this into the volume of fluid taken to obtain the average volume of "nectar" consumed per tongue lick. The total number of tongue licks divided by the time feeding gave the average rate of licking.

Hummingbird flowers are characteristically tubular with the nectar located at the base of the corolla tube. To reproduce this feature of the flowers, we added an artificial "corolla" to our feeder. A piece of clear, plastic tubing (6 mm inside diameter) was fitted to the outside of the tube. Since the sugar water remained within the glass feeder tube, we could vary the distance between the "nectar" and the opening of the "corolla" by varying the length of the plastic tube. The most common flowers that hummingbirds were observed to visit near the research station were *Bouvardia glaberrima* and *Penstemon barbatus*. When mature, these flowers measured 42 and 27 mm in corolla length, respectively, and we used artificial "corollas" between 6.0 and 42.0 mm in length to study the relationship between rate of nectar intake and corolla length. The rate of nectar intake was measured by timing the birds either by stopwatch or by taking movie films. Film records were obtained for hummingbirds visiting the feeder with "corolla" lengths of 6.0, 12.5, 18.0, and 41.0 mm to determine the relationship between rate of "nectar" intake, rate of licking and volume of "nectar" per tongue lick. A sucrose concentration of 1.0 molar was used in all experiments involving variation in "corolla" length.

*Measurement of nectar concentrations*

We also wished to determine the nectar concentrations available to hummingbirds from flowers that they normally visit. The nectar of most angiosperms contains principally sucrose, glucose and fructose in varying relative proportions (Percival, 1961), and measurement of the refractive index of nectar can be used to estimate nectar concentration. The refractive indices of equimolar glucose and fructose are about one-half that of equimolar sucrose such that refractive index can be converted to an equivalent sucrose concentration

\* An edited, 16 mm color film of hummingbirds visiting the feeder and foraging at their flowers is available for loan for educational use. For information, write to the author.

(Hainsworth & Wolf, 1972a; 1972c). The possible error due to differences between refractive index and concentration for these sugars amounts to 3–4% for the range of concentrations reported here.

We sampled nectar from flowers that hummingbirds were known to visit in several localities in Arizona and Colorado. The nectar was removed from the nectar chambers with capillary tubes and the refractive index was measured with a refractometer that was compensated to 20°C. Samples of nectar were also spotted on filter paper for chromatographic analysis of sugar composition according to the methods described by Percival (1961). Rickett (1970) was consulted for identification of the flowers sampled.

#### *Morphology of a hummingbird tongue*

We were not able to obtain tongues from either *Archilochus alexandri* or *Lampornis clemenciae*. However, a tongue was obtained from a 3.0-g female Ruby-throated Hummingbird (*Archilochus colubris*). The tongue was fixed in Bouin's fixative within a few seconds after death. It was then imbedded in paraffin, cross-sectioned at 20- $\mu$ m intervals, stained and the cross-sectional outlines of the grooves were traced at known magnification. A line was then drawn across the top of the groove at what should represent the maximum fluid volume a groove could hold. The cross-sectional area ( $\pm 0.002$  mm<sup>2</sup>) was then determined through the use of a planimeter. This procedure was followed for the best sections obtained, as judged by the absence of obvious tissue damage, and the cross-sectional areas of the groove were plotted as a function of distance along the groove in order to determine the volume of nectar a groove could hold.

### RESULTS

#### *Rate of "nectar" intake as a function of concentration*

The rate of "nectar" intake from a feeder with no "corolla" is shown in Fig. 1 as a function of sucrose concentration. Male *Archilochus* had the lowest rate of intake; female and juvenile *Archilochus* had a higher rate of intake, and the larger male *Lampornis* had the highest rate of intake at all sucrose concentrations. There was a significant decrease in rate of intake for female and juvenile *Archilochus* between 0.25 and 0.5 molar ( $P < 0.05$ ) and for male *Archilochus* between 0.5 and 1.0 molar ( $P < 0.05$ ). Both male *Lampornis* and female and juvenile *Archilochus* showed a significant decrease in rate of intake between 1.0 and 2.0 molar sucrose ( $0.01 < P$ 's  $< 0.02$ ).

The feeding habits of the birds are important in interpreting these results. Male *Archilochus* consistently "held back" from the opening of the feeder. On the other hand, female and juvenile *Archilochus* and male *Lampornis* consistently positioned themselves closer to the feeder. Thus, less of the tongue may have come in contact with the "nectar" for male *Archilochus*. The difference between the rate of intake for female and juvenile *Archilochus* and male *Lampornis*, which showed similar feeding habits, indicated that the larger hummingbird had an average rate of intake 1.7–2.4 times that of the smaller species.

#### *Rate of licking and volume per lick as a function of concentration*

Table 1 summarizes the analysis of rate of intake into the average licks/sec and the average  $\mu$ l/lick for hummingbirds visiting a feeder with no "corolla". The average rate of licking was quite uniform for all three hummingbird types at

TABLE 1—AVERAGE RATE OF LICKING AND AVERAGE VOLUME PER TONGUE LICK AT DIFFERENT "NECTAR" CONCENTRATIONS

Concentration (molar sucrose)	<i>Archilochus</i> (female—juvenile)		<i>Archilochus</i> (male)		<i>Lampornis</i> (male)	
	Licks/sec	$\mu\text{l}/\text{lick}$	Licks/sec	$\mu\text{l}/\text{lick}$	Licks/sec	$\mu\text{l}/\text{lick}$
0.25	$2.7 \pm 0.3$ (5)	$13.4 \pm 3.2$ (5)	3.8 (2)	4.1 (2)	3.1 (2)	25.4 (2)
0.50	$3.3 \pm 0.5$ (4)	$8.6 \pm 2.0$ (4)			3.1 (2)	16.5 (2)
1.0	$2.6 \pm 0.7$ (8)	$12.9 \pm 3.8$ (8)	$3.8 \pm 1.6$ (4)	$5.1 \pm 3.4$ (4)	$3.7 \pm 0.7$ (5)	$16.1 \pm 4.4$ (5)
2.0	$3.9 \pm 0.7$ (4)	$5.2 \pm 1.2$ (4)	3.8 (2)	3.0 (2)	4.7 (3)	10.0 (3)

Values are means  $\pm$  1 S.D.; ( ) indicate number of observations.

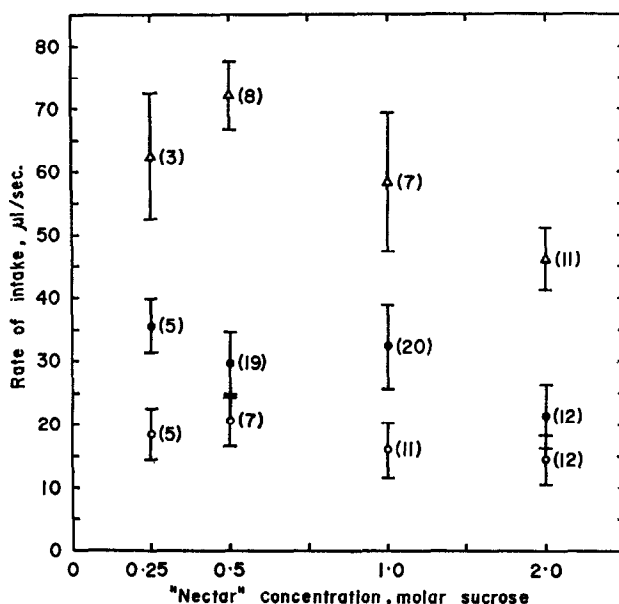


FIG. 1. Rate of "nectar" intake as a function of concentration for male *Archilochus* (○), female and juvenile *Archilochus* (●), and male *Lampornis* (△). Values are means  $\pm$  one standard deviation. Numbers in parenthesis are numbers of measurements.

concentrations of 0.25–1.0 molar, with mean rates of licking between 2.6 and 3.8 licks/sec. At a concentration of 2.0 molar the rate of licking increased for female and juvenile *Archilochus* and male *Lampornis*. The increase for female and juvenile *Archilochus* could be compared statistically and was significant ( $0.01 < P < 0.02$ ).

Differences in rate of "nectar" intake appear to be primarily the result of differences in volume of "nectar" obtained per tongue lick. Male *Archilochus* had the lowest volume per lick with female and juvenile *Archilochus* intermediate and male *Lampornis* the highest. Generally, the volume per lick for male *Lampornis* was about twice that for female and juvenile *Archilochus*. The lower volume per lick for male *Archilochus* may have resulted from their different feeding habits. At a concentration of 2.0 molar sucrose the volume per tongue lick decreased for all hummingbirds. The decrease for female and juvenile *Archilochus* could be tested statistically and was significant ( $P < 0.01$ ).

#### *Rate of "nectar" intake as a function of "corolla" length*

Adding an artificial "corolla" to the feeder resulted in a decrease in rate of "nectar" intake for both female and juvenile *Archilochus* and male *Lampornis* (Fig. 2). The decrease appeared linear with increasing "corolla" length for both species. The least-squares regression equation for female and juvenile *Archilochus* was

$$\mu\text{l/sec} = 24.4 - 0.51 (\text{mm}); \quad S_{y_x} = \pm 2.21; \quad n = 38.$$

The least-squares regression equation for male *Lampornis* was

$$\mu\text{l/sec} = 66.8 - 1.21 (\text{mm}); \quad S_{yx} = \pm 4.76; \quad n = 10.$$

The slopes of these two equations are significantly different ( $P < 0.01$ ). The intercept for zero intake was at a "corolla" length of 48 mm for female and juvenile *Archilochus* and 55.2 mm for male *Lampornis*.

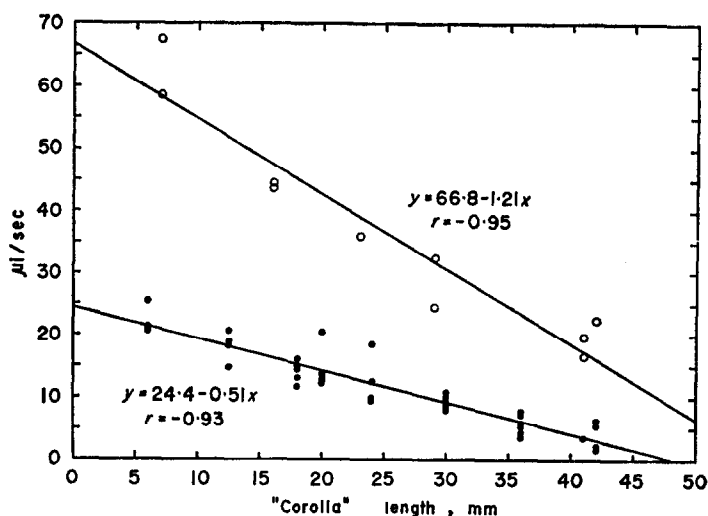


FIG. 2. Rate of "nectar" intake as a function of "corolla" length for female-juvenile *Archilochus* (●) and male *Lampornis* (○). Regression lines are by least squares, and each point represents one measurement.

#### *Rate of licking and volume of "nectar" per lick as a function of "corolla" length*

The analysis of rate of "nectar" intake into licks/sec and  $\mu\text{l}/\text{lick}$  as a function of "corolla" length is presented in Table 2. Sufficient film data were obtained only for female and juvenile *Archilochus*. The addition of a 6.0 mm "corolla" resulted in a significant increase in the rate of licking ( $0.02 < P < 0.05$ ), but further increases in "corolla" length had no effect on rate of licking ( $0.2 < P < 0.3$ ). There was a significant decrease in volume/lick from no "corolla" to a "corolla" length of 6.0 mm ( $P < 0.001$ ). There was no significant change in volume/lick between "corolla" lengths of 6.0 and 12.5 mm ( $0.1 < P < 0.2$ ) and between 12.5 and 18.0 mm ( $0.2 < P < 0.3$ ); however, the volume/lick was significantly less between "corolla" lengths of 6.0 and 18.0 mm ( $P < 0.01$ ).

#### *Nectar concentration from flowers*

All of the nectars analyzed for sugar composition contained only sucrose, glucose and fructose. The concentration of nectar from flowers sampled in the

TABLE 2—AVERAGE RATE OF LICKING AND AVERAGE VOLUME PER TONGUE LICK AT DIFFERENT "COROLLA" LENGTHS

Corolla length (mm)	<i>Archilochus</i> (female-juvenile)	
	Licks/sec	μl/lick
0	2.6 ± 0.7 (8)	12.9 ± 3.8 (8)
6.0	3.3 ± 0.4 (5)	6.3 ± 1.6 (5)
12.5	4.4 ± 1.9 (4)	4.6 ± 1.8 (4)
18.0	4.8 ± 1.7 (5)	3.3 ± 1.2 (5)
41.0	5.1 (1)	0.1 (1)

Values are means ± 1 S.D.; ( ) indicates number of observations.

southwest is given in Table 3. For a given species, the nectar concentration appeared to be dependent on elevation. For example, at an elevation of 1280 m *Penstemon barbatus* had nectar with a mean concentration equivalent to 0.76 molar sucrose, while at 2378 m the mean concentration was significantly less (0.58 molar;  $P < 0.001$ ). A similar trend was found for *Salvia lemmoni*, and the

TABLE 3—NECTAR CONCENTRATION OF FLOWERS FROM THE SOUTHWEST

Species	Elevation (m)	Equivalent sucrose concentration (molar)	S.D.	N
<i>Penstemon barbatus</i> †	1280	0.76	0.05	11
<i>P. barbatus</i>	2378	0.58	0.05	7
<i>P. pinifolius</i> †	2134	1.11	0.10	4
<i>P. pseudospectabilis</i>	2453	0.78		1
<i>Bouvardia glaberrima</i> †	2134	0.52	0.06	6
<i>Ipomopsis aggregata</i> †	2926	0.91	0.10	21
<i>I. laxiflora</i> *†	853	0.77	0.06	5
<i>Salvia lemmoni</i> †	2225	0.88	0.11	6
<i>S. lemmoni</i>	701	1.21	0.04	4
<i>Agave paryii</i> †	1768	0.54	0.09	6
<i>Erythrina flabelliformis</i> †	1250	1.33	0.23	4
<i>Zauschneria latifolia</i> †	701	0.92	0.16	5
<i>Iris missouriensis</i> †	2560	0.24	0.03	5
<i>Delphinium geraniifolium</i> †	2926	1.32		1
<i>Castilleja</i> sp.	2926	0.92		1
<i>Castilleja</i> sp.†	2453	0.84		1
<i>Beleperone californica</i>	701	1.48		1
<i>Jacobinia</i> sp.†	701	0.95		2
<i>Monarda menthaefolia</i> *†	1280	1.10		1

\* Not visited by hummingbirds.

† Analyzed for nectar composition.

lower concentrations at higher elevations may be related to lower average temperatures (Kenoyer, 1917; Oertel, 1946; Shuel, 1951).

Within a given species, there was no indication of a change in nectar concentration during the day. *Penstemon barbatus* was sampled at 2-hr intervals at an elevation of 1280 m between 07:00 and 15:00 hr (Arizona standard time). The range of concentrations was equivalent to 0.70–0.81 molar sucrose with no trend suggesting a change in concentration with time. Similar results were found for *Ipomopsis aggregata* sampled at an elevation of 2926 m.

A striking feature of the measurements of nectar concentrations were the differences between species. Thus, at an elevation of over 2200 m *Salvia lemmoni* had a mean nectar concentration equivalent to 0.88 molar, *Penstemon barbatus*, 0.58 molar and *Iris missouriensis*, 0.24 molar. All of these flowers were sampled in the Chiricahua mountains and the differences probably reflect adaptations for attracting hummingbirds as pollinators (Hainsworth & Wolf, 1972c).

### Tongue structure

Figure 3 presents representative cross-sections at different distances along the grooved portion of the tongue, and the cross-sectional area is plotted as a function

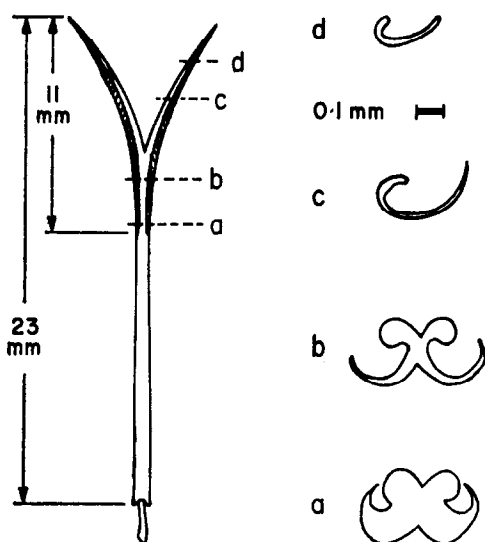


FIG. 3. The morphology of the tongue of *Archilochus colubris*.

of distance along a groove in Fig. 4. The cross-sections were similar to those described for the tongues of other hummingbird species (Scharnke, 1931; Weymouth *et al.*, 1964); however, previous studies have not indicated the morphology of the distal portion of the tongue. The volume of fluid a groove could hold was estimated by determining the area under the curve for Fig. 4. The



results indicated that one groove could hold  $0.4 \mu\text{l}$  or the tongue could hold  $0.8 \mu\text{l}$  if it was fully loaded with nectar.

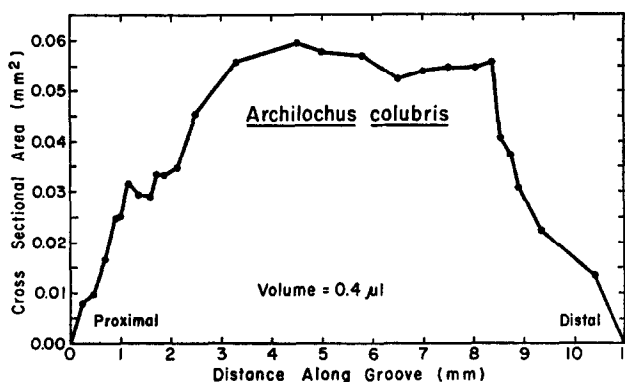


FIG. 4. Cross-sectional area of a tongue groove at various distances along the grooved portion of the tongue.

#### DISCUSSION

Comparison of the volume of fluid that could completely fill the tongue grooves of *Archilochus colubris* and the volume of "nectar" obtained by the similar-sized male and female *Archilochus alexandri* visiting the feeder suggests that the grooves on the tongue played a relatively minor role in determining the volume of nectar obtained per tongue lick at the feeder. This could result if a substantial volume of "nectar" were channelled onto the beak by the tongue along its sides and on its top; however, the mechanism by which this could occur remains to be clarified.

The concentration or viscosity of the nectar might be expected to influence the amount of nectar taken onto the tongue, and this may explain why the tongue held less "nectar" at a concentration of 2.0 molar sucrose for both female and juvenile *Archilochus* and male *Lampornis*. However, at lower concentrations the volume per tongue lick was relatively constant for a given hummingbird type and it is interesting to note that most of the flowers that were sampled secreted nectar that was less than 1.0 molar in concentration (Table 3). This was also found for most of twenty-two species of flowers sampled in Costa Rica (Hainsworth & Wolf, 1972a), and it is unlikely that nectar concentration influences the rate of intake of most hummingbirds visiting flowers.

The rate of licking appeared to be relatively independent of body size for these hummingbirds. Both female-juvenile *Archilochus* and male *Lampornis* had similar rates of licking at the feeder with no "corolla", and both species increased their rate of licking to similar values at a "nectar" concentration of 2.0 molar sucrose. It is interesting that the rate of tongue licking was increased both at the highest "nectar" concentration and when a "corolla" was added to the feeder at a lower "nectar" concentration, since the hummingbirds should be able to maximize their caloric intake by operating the tongue at its maximum speed. The fact

that the hummingbirds did increase their rate of licking under both conditions where the volume of "nectar" per lick decreased suggests that they may be able to measure their rate of "nectar" intake.

Differences in rate of "nectar" intake from the feeder for the two species appear to be primarily the result of differences in the amount of "nectar" obtained per tongue lick. It appears that the volume of "nectar" per tongue lick at zero "corolla" length is such that male *Lampornis*, which weigh more than female and juvenile *Archilochus*, have tongues which obtain more "nectar" per lick. This has some interesting consequences for the energetic efficiency of feeding in hummingbirds of different sizes.

The efficiency with which a hummingbird can extract nectar is determined by its caloric costs while it is hovering and consuming nectar relative to the caloric value of the nectar consumed. Caloric costs are determined by the costs for hovering ( $\text{cal/g} \times \text{hr}$ ), time to extract nectar and body size. Experimental measurements of oxygen consumption for a variety of flying animals indicate that the cost for hovering is about  $215 \text{ cal/g} \times \text{hr}$  (R.Q. = 1.0) regardless of body size (Lasiewski, 1963; Tucker, 1968; Heinrich, 1971; Wolf & Hainsworth, 1971). Also, theoretical calculations of the output power costs per gram for hovering hummingbirds indicate that the power for hovering per gram may be relatively independent of body size (Hainsworth & Wolf, 1972b). Thus, the costs for hovering ( $\text{cal/hr}$ ) would be scaled proportionally with size. A rate of nectar intake that was scaled to body size would tend to equalize the energetic differences between large and small hummingbirds. Such a comparison, of course, only applies where the rate of intake is not influenced by other factors such as, for example, at a feeder with no "corolla" or where the corolla lengths of different flowers have the same effect on rate of intake for hummingbirds of different sizes.

The linear decrease in rate of "nectar" intake with increasing "corolla" length appears to be primarily the result of less "nectar" obtained per tongue lick. There was an increase in rate of licking at feeders with a "corolla", but this was not related to the length of the "corolla". Thus, this provides information which suggests that the amount of nectar that adheres to the tongue depends on how much of the tongue comes in contact with the "nectar". At long "corolla" lengths the amount of "nectar" obtained per tongue lick appeared to approach the volume for the grooves in the tongue.

Female and juvenile *Archilochus* would have a zero rate of intake at a "corolla" length of 48 mm, while male *Lampornis* would have a zero rate of intake at a "corolla" length of 55.2 mm (Fig. 2). The bill of *Archilochus* measures about 20 mm in length such that this species would have a zero rate of intake when the "nectar" was 28 mm beyond the tip of its bill, or a total of about 2.4 times its bill length. The bill of *Lampornis* measures about 29 mm, and this species would have a zero rate of intake at a distance of 1.9 times its bill length. Although larger hummingbirds appear to be able to probe further, an ability for smaller billed hummingbirds to probe proportionately greater distances than larger billed hummingbirds could be an aid in reaching nectar at the base of long flowers.

How does the rate of intake at the feeder with a "corolla" compare with the rate of nectar intake of hummingbirds visiting flowers? The rates of nectar intake for eight hummingbird species foraging at eight flower species is presented in Table 4. These rates of intake are from regression equations relating seconds of foraging to nectar intake which have been solved for the nectar intake for 1 sec and for 2 sec (Wolf *et al.*, 1972; Hainsworth & Hainsworth, in prep.; Hainsworth & Wolf, 1972c; Wolf & Hainsworth, in prep.). For a number of the bird-flower combinations the first second of foraging is spent in probing the flowers and results in no nectar intake. It can be seen that the relationship between bill length, corolla length and rate of nectar intake is quite variable, and other factors in addition to the length of the corolla must be examined.

Curvature is one aspect of corolla morphology that may influence rate of nectar intake. For example, the *Heliconia* flowers are curved, although the bill of *Phaethornis* is decurved and fits these flowers. Position could also influence rate of nectar intake. The flower of *Heliconia tortuosa* is rotated 180° from the more "normally" oriented *H. rostrata* flower. To probe this flower *Phaethornis* must twist its neck while hovering, and this would disorient the grooves on the tongue relative to the nectar, such that the grooves would be facing down, and this could

TABLE 4—RELATIONSHIP BETWEEN BILL LENGTH, COROLLA LENGTH AND RATE OF NECTAR INTAKE

Bird species	Average bill length (mm)	Flower species	Average corolla length (mm)	Rate of intake ( $\mu$ l/1 sec)	Rate of intake ( $\mu$ l/2 sec)
<i>Selasphorus flammula</i> (2.7 g)*	12	<i>Tropaeolum</i>	17	1.4	2.9
Female <i>Archilochus alexandri</i> (3.3 g)†	20	<i>Penstemon barbatus</i>	27	0.16	1.16
<i>Thalurania furcata</i> (4.5 g)‡	19	<i>Heliconia imbricata</i>	25	0	6.8
<i>Amazilia tzacatl</i> (5.0 g)‡	20	<i>H. imbricata</i>	25	1.3	5.6
<i>Panterpe insignis</i> (5.4 g)§	19	<i>Macleania glabra</i>	24	8.5	33.5
<i>Colibri thalassinus</i> (5.6 g)§	20	<i>Centropogon valerii</i>	33	0	11.7
<i>Phaethornis superciliosus</i> (6.0 g)‡	37	<i>Heliconia rostrata</i>	40	0	2.8
<i>P. superciliosus</i> (6.0 g)‡	37	<i>H. tortuosa</i>	48	0	1.9
<i>Eugenes fulgens</i> (9.0 g)§	33	<i>Centropogon gutierrezii</i>	50	3.5	13.5

\* From Hainsworth & Wolf (1972c).

† From Hainsworth & Hainsworth (in preparation).

‡ From Wolf *et al.* (1972).

§ From Wolf & Hainsworth (in preparation).

result in the tongue holding less nectar/lick. Other morphological features that could influence the rate of nectar intake include "plates" in the corollas of *Centropogon* flowers. These are located just above the nectar chamber and contain holes which must be probed to obtain nectar. The holes vary in diameter with the size of the flower species and probably influence the rate of nectar intake.

Finally, the volume of nectar available from a flower may influence the rate of nectar intake. To illustrate this, we can compare female *Archilochus alexandri* visiting the feeder with a "corolla" length of 27 mm and visiting *Penstemon barbatus* with a corolla length of 27 mm. Figure 5 shows a longitudinal section

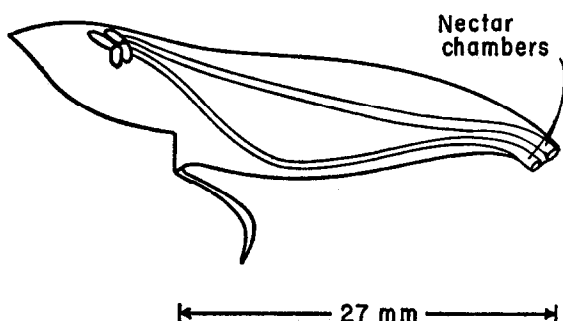


FIG. 5. Longitudinal section of a flower of *Penstemon barbatus*.

of a *P. barbatus* flower. Several morphological features could influence the rate of nectar intake. There is a curvature in the corolla just prior to the nectar chambers which are located at the outer bases of the stamens, the stamens partially block the corolla tube, and the hummingbirds must approach the flowers from below since the opening points downward. When visiting a feeder with a "corolla" length of 27 mm, female *Archilochus* would have a rate of intake of  $10.6 \mu\text{l}/\text{sec}$  (Fig. 2), but while visiting *P. barbatus* their rate of intake would be  $0.16 \mu\text{l}/\text{sec}$  (Table 4). When they visit *Penstemon* flowers, the hummingbirds *empty* the flowers, but when they visit the feeder they are probing a continuously large reservoir of "nectar". Small flowers tend to contain smaller quantities of nectar than larger flowers (Wolf & Hainsworth, in preparation), and in emptying a small quantity of nectar the tongue is probably protruded several times without carrying a maximum volume of nectar. In emptying a flower the grooves on the tongue would serve an important role in removing these small quantities of nectar. At the feeder and at flowers with large nectar volumes, however, the tongue licks should return much larger volumes of nectar. This difference may partially explain the low rates of nectar intake for hummingbirds visiting *Tropaeolum* and *Penstemon* flowers which offer relatively small quantities of nectar to hummingbirds of those flowers we have studied (Hainsworth & Hainsworth, in preparation; Hainsworth & Wolf, 1972c).

In summary, the rate of intake of hummingbirds visiting flowers appears to be influenced by a variety of morphological and functional characteristics of both the

birds and flowers. To the extent that rate of nectar intake influences the efficiency of foraging, these characteristics will influence the energy budgets of the hummingbirds and should have an impact on their foraging strategies. A given hummingbird species should forage in such a way that its energy uptake is maximized relative to its energy expenditure (Wolf & Hainsworth, 1971; Hainsworth & Wolf, 1972b; Wolf *et al.*, 1972). The matching between tongue structure and function and flower structure and function should influence which flowers are visited. This, in turn, will have an impact on the movement of pollen between the flowers visited by the hummingbirds.

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*Key Word Index*—*Archilochus alexandri*; body size; foraging; feeding strategies; flower nectar; *Lampornis clemenciae*; pollination; rate of nectar intake; tongue structure and function.