TABLE 1.   Nest types selected by experimental and control populations of House Sparrows.

	Nestlings		Nest-building by surviving ♂♂ and ♀♀		Nest-building by surviving ♂♂ only		Nest-building by surviving ♀♀ only	
	Number marked	Number fledged	Natal Nest type	Other Nest type	Natal Nest type	Other Nest type	Natal Nest type	Other Nest type
Experimentals (transferred)								
Hole type nests	100	73	14	9	8	7	3	5
Box	50	37	6	5	5	4	1	1
Crevice	50	36	8	4	3	3	2	4
Tree nests	50	33	5	9	3	5	2	4
Controls								
Hole type nests	100	79	19	10	8	6	11	4
Box	50	40	10	4	5	2	5	2
Crevice	50	39	9	6	3	4	6	2
Tree nests	50	36	7	10	4	4	3	6

in the control population ($\chi^2 = 2.837$, df = 2). Experimental and control populations were not significantly different in the number of sparrows choosing natal nest types over other nest types ($\chi^2 = 0.066$, df = 1).

It is possible that one sex might influence the selection of the nest site more than the other. A male selects the nest site, from which he advertises his presence to females; a female selects not only her mate but also the site associated with him.

Considering males alone, I still found no significant differences between the three types of nest sites selected in either the experimental population (Fisher's exact test, $P = 0.888$, 0.769, and 0.529) or the control population ($P = 0.881$, 0.897, and 0.785). Females also show no significant differences ($P = 0.411$, 0.121, and 0.464 in the experimentals; $P = 0.157$, 0.769, and 0.109 in the controls).

Although the three nest types appear distinctly different, sparrows may discriminate only between tree nests and hole type nests (either box or crevice). Pooling the data for box and crevice nests, I still found no significant preference for hole nests over tree nests in either the experimental population (Fisher $P = 0.156$) or the control population ($\chi^2 = 3.56$, $P > 0.05$), although a slight preference was shown for hole type nests and it approached significance. No difference was evident between the two populations ($\chi^2 = 0.023$).

Considering males alone, there were still no significant preferences for one nest type over the other ($\chi^2 = 0.348$ for experimentals, 0.825 for controls). Females, however, did show a significant preference for

hole nests (Fisher $P = 0.054$) in the experimental population and the preference approached significance in the control population ($\chi^2 = 3.425$, $P > 0.05$). Differences between populations for males alone and females alone were not significant ($P > 0.05$).

Although my data are limited, two conclusions can be drawn from this experiment. First, in answer to the original hypothesis, there seems to be no early learning or imprinting involved in nest site selection in the House Sparrow. Second, females clearly seem to choose hole type nests over tree nests. Such nonrandom nest choice regardless of natal nest type indicates that females possess a possible innate preference for hole type nests. If so, then males advertising from tree nests would seem to be at a distinct selective disadvantage in terms of securing a mate, unless the number of holes is limited. Other data suggest that the number of tree nests is influenced not only by the availability of holes, but also by the density of sparrows in a given area, the food supply, and the percentage of first-year breeding birds in the population.

ON THE TONGUES OF SUNBIRDS

ROBERT SCHLAMOWITZ

F. REED HAINSWORTH

AND

LARRY L. WOLF

The successful existence of any animal depends to a large extent on its ability to satisfy the energetic demands of everyday life. Although an animal can live temporarily on a negative energy budget, eventually

it must account for its energy expenditures in order to carry on its activities and to reproduce. The efficiency with which an animal can exploit food resources will influence its ability to survive and reproduce. This foraging efficiency (caloric value of food relative to the caloric costs for obtaining food) should be optimized through natural selection (Emlen 1968, Royama 1970, Tullock 1971, Wolf et al., unpubl. data). This optimization should reflect characteristics of the food resource, such as availability and quality, as well as the mechanisms for ingesting food.
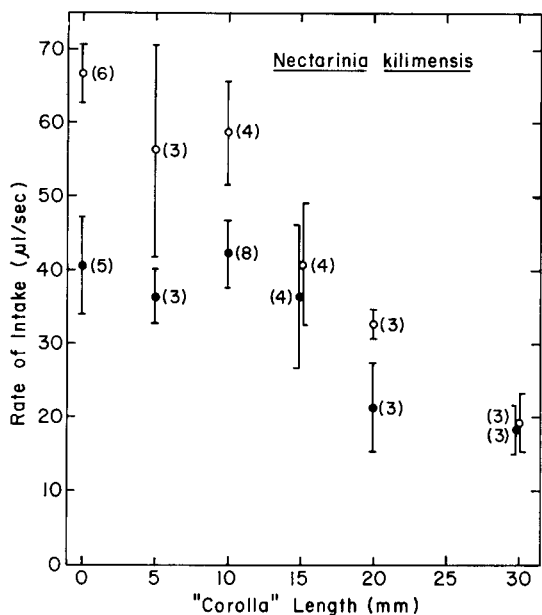
FIGURE 1. Rate of intake as a function of "corolla" length for male (closed circles) and female (open circles) *Nectarinia kilimensis*. Means ±95% confidence intervals. Numbers in parentheses are numbers of measurements.

The efficiency of foraging has been examined for a number of nectar feeding birds including hummingbirds (Wolf et al. 1972, Hainsworth and Wolf 1972a) and sunbirds (Wolf unpubl. data, Gill and Wolf unpubl. data). Also, the structure and function of the tongues of hummingbirds have been examined and related to their foraging efficiency (Hainsworth 1973). The present report deals with an analysis of the mechanism of nectar intake by sunbirds; the role of tongue structure and function relative to foraging efficiency is examined, and comparisons of factors in feeding mechanisms that influence foraging efficiency are made for hummingbirds and sunbirds.

FEEDING EXPERIMENTS

Bronzy Sunbirds (*Nectarinia kilimensis*, 15–17 g), were filmed at 18 frames/sec or timed with a stopwatch while they consumed sugar water (0.5M sucrose) from a feeder with a tubular glass spout. A perch was provided so the sunbirds could forage in their normal manner. The volume of fluid consumed in a visit was determined from the change in weight of the feeder (±0.2 mg) times the specific gravity of the sugar solution (1.0639 g/ml). Rate of "nectar" intake (μl/sec) was determined from stopwatch times or from frame-by-frame analysis of films (each frame = 0.05 sec). Film analysis also allowed us to count individual tongue licks and the average number of licks/sec was determined for each filmed visit. Rate of intake (μl/sec) together with the average rate of licking (licks/sec) enabled calculation of the average volume of sugar water obtained per tongue lick (μl/lick).

The nectar in flowers visited by sunbirds is normally located at the base of a tubular corolla. To reproduce this feature of the flowers we fitted clear,

TABLE 1. Results of film analysis of *Nectarinia kilimensis* visiting a feeder.

"Corolla" Length (mm)	Average rate of intake (μl/sec)	Average licks/sec	Average μl/lick
0	51.3 (2)	4.3 (2)	12.2 (2)
20	26.7 (4)	5.2 (4)	5.1 (4)
30	18.1 (3)	4.5 (3)	4.0 (3)

( ) represents the number of observations.

plastic tubing to the outside of the feeder spout at lengths of 5, 10, 15, 20, or 30 mm measured from the sugar water to the opening of the plastic tubing. Film records were obtained for seven visits of *N. kilimensis* to the feeder with a "corolla" and two visits to a feeder without a "corolla."

MORPHOLOGY OF SUNBIRD TONGUES

One tongue each from *Nectarinia reichenowi* (15.0 g, female), *N. verticalis* (9.5 g, male), and *N. venusta* (7.0 g, male) were fixed in Bouin's fixative, transferred to 70% ethanol and imbedded in paraffin. The tongues were sectioned at 100 μm, 200 μm, or 1 mm intervals and photographs were taken of the cross sections. The photographs were projected and traced at known magnification. To determine the volume of fluid the grooves on the tongue could hold, a line was drawn across the top of the grooves that simulated the curve of a flattened meniscus, and the cross sectional area was measured with a polar, compensating planimeter. Cross sectional area was plotted as a function of distance along the tongue, and total volume was determined from the area under these curves.

RATE OF NECTAR INTAKE

For both males and females, increasing the length of the "corolla" resulted in a decrease in the rate of "nectar" intake (fig. 1). Females had a higher rate of "nectar" intake at short "corolla" lengths ($P < 0.05$ at "corolla" lengths of 0 and 10 mm). The rate of intake for males appeared to change little until the "corolla" length exceeded 15 mm.

The rate of "nectar" intake can be subdivided into rate of licking and volume per lick from the film analysis data (table 1). Film analysis was limited to two visits to a feeder with no "corolla" and seven visits to a feeder with a "corolla"; the sample size did not permit distinctions between males and females. However, we found no correlation between rate of licking and "corolla" length (r = −0.18; $P > 0.05$). The average rate of licking for all nine visits at all "corolla" lengths was 4.8 ± 0.7 (S.D.) licks/sec. For males, the average was 4.75 (n = 4) and for females the average was 4.80 (n = 5) licks/sec.

We found a significant relationship between volume/lick and "corolla" length (r = −0.83; $P < 0.05$, n = 9; table 1). This suggests that the decrease in rate of intake with increasing "corolla" length was due primarily to a decrease in the volume obtained per lick. Single visits by a male and a female to a feeder with no "corolla" gave volumes/lick of 8.4 μl and 16.0 μl, respectively. Such differences appear to reflect the higher rates of intake for females at low "corolla" lengths (fig. 1) and could be caused by different methods of feeding (Hainsworth 1973).
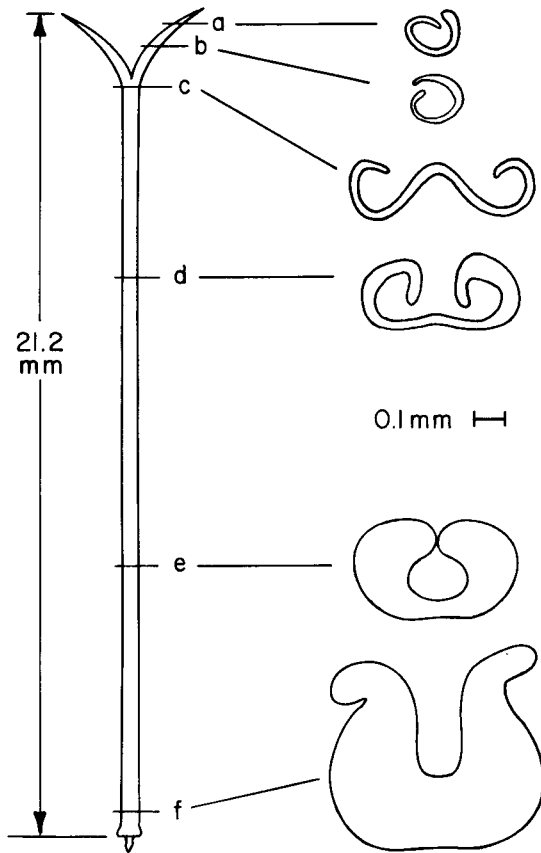
FIGURE 2.   The morphology of the tongue of *Nectarinia verticalis*.

FIGURE 3.   Cross sectional area as a function of distance along the tongue for tongues from three species of sunbirds.

TONGUE MORPHOLOGY AND VOLUME

Tongue lengths were measured from the tips to the attachment on the posterior end of the paraglossal bones. For *N. reichenowi* tongue length was 25.0 mm, for *N. verticalis* 21.2 mm, and for *N. venusta* 21.0 mm.

The tongue morphology of these three species is similar to that of *N. verticalis* (fig. 2; see also, Skead 1967). The distalmost portion is bifurcated and shaped as an open tube (fig. 2a, b). The cross-sectional area increases toward the point of bifurcation (fig. 2c; fig. 3) where the open tubes fuse to a single, open groove. The cross-sectional area of this groove remains relatively constant up to a distance of 15–20 mm from the tips (fig. 3), where it is constricted. Proximal to this, the tongue resembles a trough that continues back to the point where it attaches to the basihyal (fig. 2, f; fig. 3).

Total volumes for the tongues were 2.1 μl for *N. reichenowi*, 1.1 μl for *N. verticalis*, and 0.6 μl for *N. venusta*. For *N. reichenowi* 73% of the tongue groove volume (1.5 μl) was distal to the constriction in the groove, 87% (0.96 μl) for *N. verticalis*, and 76% (0.46 μl) for *N. venusta*.

DISCUSSION

Except at very long "corolla" lengths, the measured volume/lick obtained by the 15g *N. kilimensis* exceeded the total volume of the tongue groove for the similar-sized *N. reichenowi*. This is similar to what
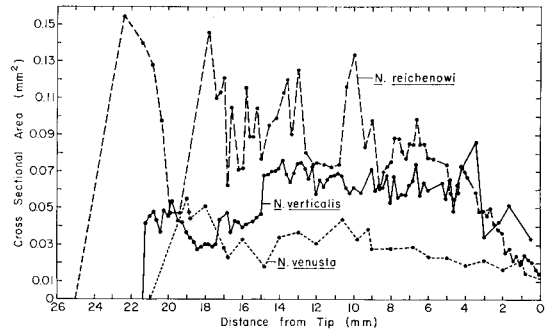
Hainsworth (1973) observed for hummingbirds, although differences in the morphology of the tongues of sunbirds and hummingbirds could yield different mechanisms for consuming an excess quantity of nectar per lick. For both nectarivores the bill could be important at small corolla lengths. For the sunbirds, the extension of the groove over the entire length of the tongue could allow for movement of nectar back into the throat in a continuous stream such that the bulk flow/lick exceeded the total tongue volume. However, sucking nectar would be impossible for both hummingbirds and sunbirds since the grooves on the tongues are open at the top.

Both sunbirds and humingbirds should feed in such a way that they maximize their energy intake relative to their energy expenditures for foraging (Wolf et al. 1972, Wolf unpubl. data, Gill and Wolf unpubl. data). An important difference in this context is the hummingbirds' use of the energetically more costly method of hovering to obtain nectar. Certain aspects of tongue morphology appear to reflect these differences. For example, the 3.0 g hummingbird *Archilochus colubris* has a tongue groove volume of 0.8 μl (Hainsworth 1973) which is greater than the volume of 0.6 μl for the 7.0 g *N. venusta*. Both hummingbirds and sunbirds appear to lick at similar rates, but hummingbirds of similar sizes to sunbirds should obtain a greater quantity of nectar/lick despite the fact that a shorter length of the tongue of a hummingbird contains grooves (Hainsworth, 1973). However, the difference in caloric costs for perching and hovering probably still results in a higher efficiency for nectar extraction for sunbirds compared with hummingbirds.

For both hummingbirds and sunbirds the costs for foraging (cal/hr) increase with body size. For hummingbirds the costs for hovering increase linearly with size (Hainsworth and Wolf 1972b), while for perching sunbirds the costs probably increase as some multiple of resting metabolic rate which is proportional to $(weight)^{0.73}$ (Lasiewski and Dawson 1967). Measurements of rates of "nectar" intake for hummingbirds suggest that larger species have higher rates of intake (Hainsworth 1973), and the measurements of tongue volumes for sunbirds indicate an increase in volume with body size (fig. 3). The three tongue volumes for sunbirds suggest an increase in volume with size that may be allometric with respect to metabolic rates rather than isometric. If this were the case, larger sunbirds could have rates of intake that would provide greater foraging efficiencies for their size than smaller sunbirds.

A change in tongue volume with body size could be accomplished in several ways. If larger birds had longer tongues, volume could be increased by lengthening. A change in volume could also result from a change in the dimensions of the grooves in tongues of the same length. This appears to be the case for *N. verticalis* as compared with *N. venusta* (fig. 3), where tongues are the same length but the smaller *venusta* has a smaller tongue volume. For the larger *N. reichenowi*, the greater volume is achieved by a slightly longer tongue with much larger grooves (fig. 3).

Bill length and morphology appear to be well correlated with corolla length and morphology in nectar-feeding birds (Snow and Snow 1972, Wolf et al. unpubl. data). This co-evolutionary relationship presumably provides for ease in reaching and extracting nectar at the base of differently shaped flowers. Bill morphology among hummingbirds and sunbirds is so diverse that birds of similar sizes may have different bill lengths. If tongue morphology reflects such differences, birds of similar sizes could have different tongue volumes. It would be of interest to determine the extent to which this may relate to rates and efficiencies of nectar intake for such species visiting flowers with which they have co-evolved.

SUMMARY

The structure and function of sunbird tongues were compared with those of hummingbirds. In experiments with *Nectarinia kilimensis*, the rate of nectar intake from a feeder decreased with increasing "corolla" length, primarily as a result of less nectar obtained per lick. The grooves on the tongues of sunbirds vary in volume with body size such that the tongues of larger sunbirds could hold more nectar. However, the tongues of sunbirds appear to hold less nectar than those of smaller species of hummingbirds. Thus, hummingbirds, which expend more energy while hovering to consume nectar, may obtain more nectar/lick, but sunbirds' less costly method of perching while feeding should make their nectar extraction more efficient despite proportionally smaller volumes of the tongue grooves.

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CECAL FERMENTATION IN MALLARDS IN RELATION TO DIET

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The digestive system of birds enlarges in response to poor foods (high fiber content, relatively indigestible) and shrinks in response to high quality, easily digested foods (Leopold 1953, Lewin 1963, Gardarsson 1971, Miller 1975, Moss 1972, Pendergast and Boag 1973). Little work has been done on the associated changes in cecal fermentation in relation to diet quality.

The ceca of birds are probably the principal organs where microbial fermentation of cellulose and other constituents of the diet takes place (Suomalainen and Arhimo 1945, Beattie and Shrimpton 1958, Thornburn and Wilcox 1965, Annison et al. 1968, McBee and West 1969, Inman 1973). Ruminants produce volatile fatty acids (VFA's) from a similar fermentation process and the proportion of the different VFA's varies with different diets (McDonald et al. 1969: 117, and many others). More data are required

to understand fermentation processes in birds. It is possible that cecal VFA production increases in birds when the diet contains large amounts of fiber, and this may be a significant energy source (McBee 1970).

The purpose of this paper is to document the effect of three different diets on cecal VFA concentrations and cecal discharge rates in Mallards (*Anas platyrhynchos*).

MATERIALS AND METHODS

Forty-eight Mallards (progeny from a captive flock maintained at the United States Fish and Wildlife Service's Denver Wildlife Research Center, Denver, Colorado), five to six months old, were obtained from a captive flock that had been kept outdoors in a dirt floor enclosure since hatching. Turkey starter (Ralston-Purina turkey startena), whole maize, and limited natural foods in the enclosure were the only foods available to the ducks before the study began in October 1972.

The ducks were housed indoors at 20–22°C under a 12 hr photoperiod and assigned randomly to one of three communal pens with eight males and eight fe-