

COMPARATIVE FORAGING EFFICIENCIES OF SOME MONTANE SUNBIRDS IN KENYA

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An animal's ability to obtain food depends strongly on its feeding apparatus, while the efficiency with which it forages depends also on the costs associated with obtaining the food. It is the interaction between the benefits and costs of foraging that determines which foraging tactics will be employed and which food items will be chosen (Schoener 1971, Pulliam 1974). This interaction will affect the animal's entire time and energy budget because time not used for feeding is available for other activities. Maintaining energy and nutrient balance usually takes precedence over other activities although exceptions are made for predator escape and short-term sacrifices during breeding (King 1974). Thus foraging behavior and efficiency influence an animal's division of its time and energy budget, which in turn may affect survivorship and reproductive success. Ultimately such partitioning may affect coexistence and patterns of competition among species that exploit the same food resources.

The foraging success of nectar-feeding birds seems to be dictated by morphological details of the bill and the flower (Hainsworth and Wolf 1972, Snow and Snow 1972, Wolf et al. 1972, 1976). These features are subject to coevolutionary modifications and increased specializations. In this paper we compare the foraging efficiencies of four species of sunbirds (Nectariniidae) feeding at one species of bird-pollinated flower in central Kenya. We examine first the relative abilities of these birds to extract nectar as revealed by details of the bill and corolla. Next we calculate rates of nectar intake based on average rates of flower visitation and success at nectar removal. Finally we determine the degree to which estimated differences in size-dependent costs of foraging compensate for differences in ability to extract nectar.

BACKGROUND

STUDY AREAS

Our study areas were located near Lake Naivasha in the Rift Valley in central Kenya, 100 km south of the equator at an altitude of 1800 m. They consisted of large fields of *Leonotis nepetifolia* R. Br., a common species of mint (Labiatae). These were the same

areas used in our previous studies of this system (Gill and Wolf 1975a, 1977).

THE FLOWER

Leonotis nepetifolia is found along roadsides and in fallow fields at 1600–2500 m in central Kenya (Agnew 1974). It is a tall, annual herb which bears flowers in dense globular inflorescences at the upper nodes (Agnew 1974, Gill and Wolf 1975a). These plants were abundant in our study areas, normally 10–30 inflorescences per square meter. We called these inflorescences "paws" in reference to the local vernacular name for the plant, "Lion's Paw." Each paw produces a single ring of tubular flowers. The number of flowers per paw varies from 1–20, depending on the age of the paw and its position on the stalk.

The bright orange corolla of the flower averages 37.3 mm in total length. The closed tube averages 19.9 mm in length; it is deepest (4.2 mm) at the lower lip, where a sunbird inserts its bill, and narrows to 2.5 mm near the proximal end, where the nectar is produced (Fig. 1). The corolla is strongly decurved, which both insures that the anthers and stigma press against the sunbird's forehead, and increases the difficulty of access to the nectar for straight-billed species. The length and curvature of corollas vary slightly, though significantly, in relation to the age of a paw.

Inside the proximal third of the corolla are three or four partitions. The proximal partition is the most substantial, being a hard, annular lip that supports a dense mat of short stiff hairs. Access to the basal chamber, through a central narrow gap, is permitted by the flexible nature of the hairs, which bend inward when pushed by a bill. The two or three outer partitions are thinner and more flexible. They assume an oval or even circular shape when a bill is inserted.

Our research to date indicates that nectar is produced only by the hairs of the basal partition, although more study may reveal minor production distally as well. Nectar is present first near the basal partition and then accumulates in the basal chamber; once this chamber is full, the nectar flows into the more distal chambers. Apparently the outer diaphragms serve primarily to restrict the outward flow of nectar.

THE BIRDS

The sunbirds attracted to *Leonotis* flowers near Lake Naivasha in 1971–78 were mostly species typical of montane nonforest habitats (Moreau 1966). We studied three large species—*Nectarinia kilimensis*, *N. reichenowi*, and *N. famosa*, and a small one—*N. venusta*. These species differ in the length, curvature and thickness of their bills (Fig. 1, Table 1).

These sunbirds usually perch on the stalks of *Leonotis* below a paw and probe upwards consecutively into adjacent flowers. They spin quickly around the ring of flowers and rarely skip flowers or visit the

same one twice. Occasionally they reject a paw after probing 1–4 flowers (Gill and Wolf 1977). They fly or jump quickly between inflorescences, which usually are less than 1 m apart.

FIELD MEASUREMENTS

We measured the average duration of a flower visit for males of each species by timing with a stopwatch the total duration of a series of counted flower visits. We then computed linear regressions using least squares, where X is the number of flowers probed and Y the total time. The slope of the regression is a measure of the average duration of one flower visit. Statistical comparison of slopes required logarithmic transformation to equalize the variances about the regression.

The total time measured included (1) the time the sunbird spent probing flowers and removing nectar, (2) the time between flowers within an inflorescence excluding major pauses or other interruptions of continuous feeding, and (3) some brief transits between inflorescences. The first of these was the major component of the measurement. The other two were subjectively standardized, minor components. Movement between flowers on a paw was normally a short, inseparable part of the feeding action. Movements between inflorescences normally comprised less than 5% of total foraging time and an even smaller fraction of these closely controlled measurements. Time between paws did not seem to differ among species, and decreased in relative importance as time within paws increased. Thus we feel our measurement of the average duration of a flower visit reflects the minimum time for one flower visit during continuous active foraging at high density *Leonotis* flowers.

To estimate the amount of nectar a sunbird removed from a flower we chased it from a paw with 10 or more flowers after it had probed 5 flowers. We then measured the volume in visited and unvisited flowers on that paw. We grouped paws by average volume in unvisited flowers, i.e., less than $1 \mu\text{l}$, $1\text{--}1.9 \mu\text{l}$, etc., and then calculated (A) the mean nectar volume for all unvisited flowers in each group and (B) the mean volume for all visited flowers in each group. We divided the difference (A-B) by A and multiplied by 100 to give the percent removed. This procedure assumes nonselective feeding within a paw.

RESULTS

DURATION OF FLOWER VISITS

In all four species, foraging time increased linearly with the number of flowers visited (Fig. 2). The slopes of the regressions averaged 0.99 s/fl for *kilimensis*, 1.24 for *reichenowi*, 1.71 for *famosa* and 2.65 for *venusta*. With one exception the slopes differed significantly among species (Table 2). The slope of the regression for *kilimensis* was not significantly different from that for *reichenowi*. Both feed rapidly and more data are needed for *kilimensis* to eliminate a possible problem in sample size. The coefficient of determination (r^2) ranged from 0.75 to 0.87.

Differences between species in the average duration of a flower visit correspond princi-

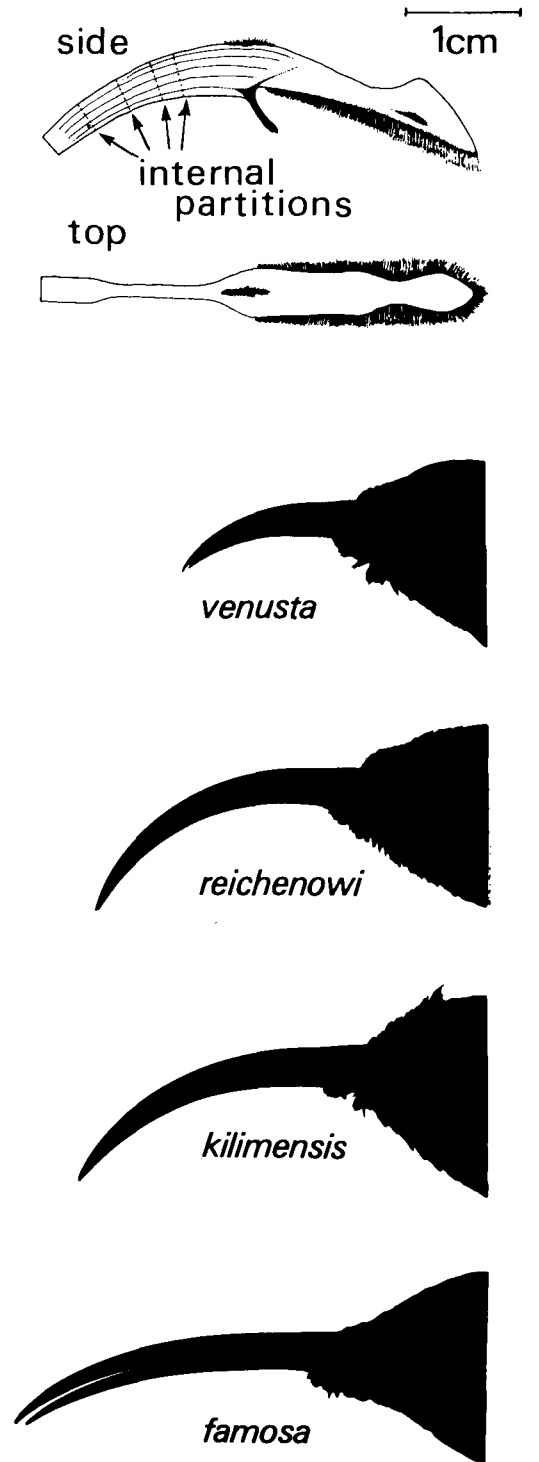


FIGURE 1. Top: general structure of a flower of *Leonotis nepetifolia*. Bottom: bills of the four species of sunbird studied.

pally to differences in bill morphology and the consequent ease of inserting the bill into the *Leonotis* corolla. *Kilimensis*' bill is moderately curved and slightly thicker than the interior

dimensions of the corolla. This sunbird inserts its bill rapidly, straightening the corolla only slightly, but deep penetration into the basal chamber is sometimes limited by the tight fit of its bill. *Reichenowi's* is strongly decurved, actually more decurved than many corollas, leading to occasional punctures of the corolla wall just in front of the basal partition. However, by pressing its bill forward against the calyx during insertion, a bird of this species can force the corolla to flex just enough to accommodate the bill and to permit penetration of the basal chamber. This action apparently requires a fraction of a second longer than insertion of *kilimensis's* straighter bill. *Reichenowi's* bill is thinner than those of the other species, permitting deeper penetration. Both *kilimensis* and *reichenowi* insert their bills with a single fast head movement, and move smoothly between adjacent flowers.

Famosa moves quickly around an inflorescence, but takes longer to probe a flower because it lifts its head higher during insertion, pushing harder against the dorsal lip of the corolla than either *kilimensis* or *reichenowi*. Of the four sunbirds, *famosa* has the longest and straightest bill. When inserting it, this species often requires three quick head lifts and increasingly deeper probes to straighten the corolla. When we probed a *Leonotis* flower with the bill of a *famosa* specimen we found that such action was necessary to avoid catching the sharp tip of the bill on the upper surface of the corolla or on the hard lips of the partitions.

Venusta's bill is too short for effective feeding at *Leonotis* flowers. This sunbird normally slits the base of the corolla from the outside between the second and third partitions, but even so, its bill reaches only the second chamber and does not penetrate the basal partition. *Venusta* takes a relatively long time to pierce the side of the corolla, an action which involves both finding the correct site and making quick jerky head movements to break the tissue before inserting the bill. This species spins around the stalk more clumsily than the other

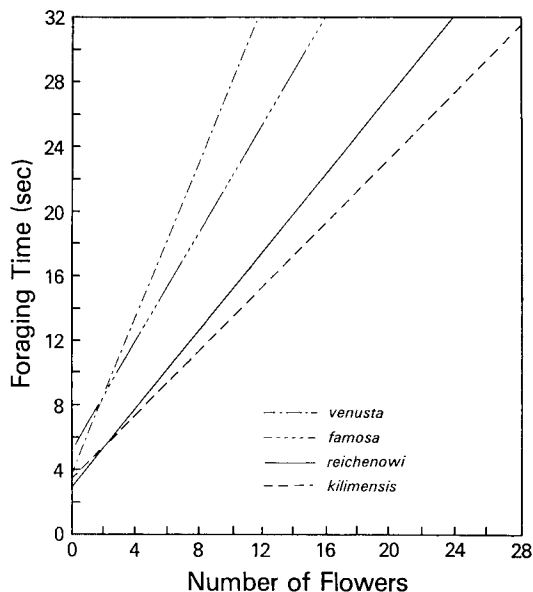


FIGURE 2. Relationships between foraging time and the number of flowers visited by male sunbirds. The slopes of the regressions indicate the average duration of one flower visit, and reflect differences in the fits between bill and corolla.

species. It also glances around more often than the other species, apparently to see whether it is about to be chased by a larger sunbird. Each of these actions involves only a fraction of a second, but they add up to a relatively long time per flower.

PARTIAL REMOVAL OF NECTAR

The sunbirds did not always remove all the nectar from the flowers they visited (Fig. 3). We found no consistent sexual differences in nectar removal, so we combined our data for both sexes of each species. The absolute amount of nectar left by the sunbirds in a flower was significantly correlated ($P < .05$) with amount available; the Spearman Rank Correlation Coefficients (r_s) were 0.95 for *reichenowi*, 0.85 for *kilimensis*, 0.82 for *famosa*, and 0.93 for *venusta*. The proportion of available nectar that was removed by *reichenowi*,

TABLE 1. Average weights (g) and bill measurements (mm) of sunbirds (*Nectarinia*) studied. Figures are means for 10 males of each species.

Species	Weight	Bill ^a length	Bill ^b curvature	Bill depth at		Bill width at	
				nostril	midpoint	nostril	midpoint
<i>kilimensis</i>	17.0	22.6	0.221	3.6	2.5	4.2	1.9
<i>reichenowi</i>	15.5	22.9	0.263	3.5	2.4	4.1	1.7
<i>famosa</i>	13.8	24.2	0.169	3.0	2.5	3.8	2.0
<i>venusta</i>	7.5	13.8	0.231	2.8	2.1	3.2	1.6

^a Measured from nostril.

^b Taken as the ratio x/y , where x is the bill length measured from the anterior edge of the nostril and y is the maximum height above the longest chord of the bill. Curvature is proportional to the calculated value.

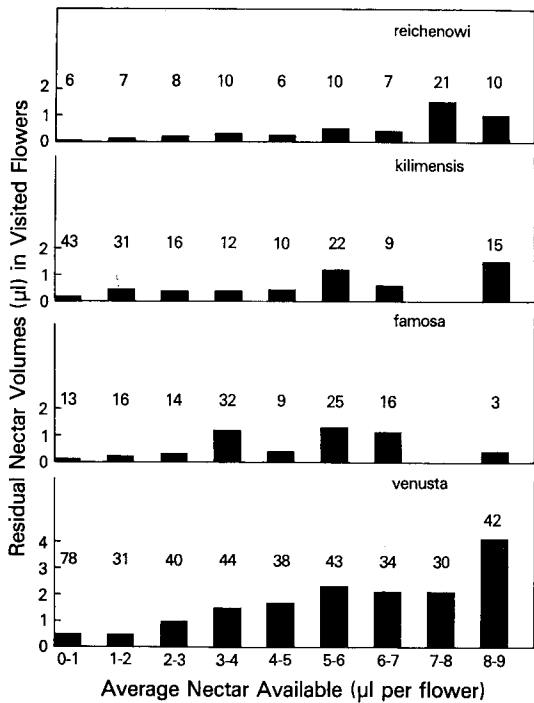


FIGURE 3. Residual nectar volumes in flowers of *Leonotis nepetifolia* visited by sunbirds. The numbers above each bar specify the average percent of the available nectar that was left in the flower.

famosa and *venusta* was not significantly correlated with the volume of nectar available. *N. reichenowi* consistently removed the greatest fraction of available nectar, averaging 90%. Our data for *famosa* at different available volumes varied from 68 to 91% removed, averaging 82%. *Venusta* consistently removed the smallest fraction of available nectar, 56–70% (average 62%) from flowers with more

than 1 µl. It did poorly at flowers with less than 1 µl, removing only 22% of the available nectar. *Kilimensis* differed from the other species in that below 5 µl per flower, the amount left was essentially constant at about 0.4 µl and thus the proportion removed increased significantly with the amount present ($r_s = 0.79$). The average proportion removed by *kilimensis* was 82%.

Does one species consistently remove more nectar from the flowers than another, independent of the amount of nectar available? We tested the differences in percent of available nectar left in flowers (Fig. 3) using a Wilcoxon Matched Pairs Signed Rank Test (Siegel 1956). For example, to compare *reichenowi* and *kilimensis*, we paired 6 and 43% at 0–1 µl per flower, 7 and 31% at 1–2 µl per flower, etc. The results of these tests confirmed that *reichenowi* consistently removed more nectar than *kilimensis* ($P < .005$), *famosa* ($P < .025$) and *venusta* ($P < .005$). *Kilimensis* removed more than *venusta* ($P < .005$), but not more than *famosa* ($P < .05$), and *famosa* removed more than *venusta* ($P < .005$).

We hypothesized that differences between sunbird species in the average percentages removed should correspond to the frequencies with which some nectar was left in the basal chamber, because that remainder is the most difficult to reach and extract. Removal of this nectar should be affected by how far the bill can be inserted into the corolla and by the accuracy of aligning the bill with the center of the basal partition. First, we established that nectar left in a flower after a sunbird visit is found either in the basal chamber alone or in both the basal and outer chambers. Then we

TABLE 2. Comparisons of regressions for duration of flower visits by male sunbirds feeding at *Leonotis nepetifolia*.

	<i>kilimensis</i>	<i>reichenowi</i>	<i>famosa</i>	<i>venusta</i>
Sample size (N)	45	193	96	65
Original data				
Slope ± se	0.99 ± 0.06	1.24 ± 0.04	1.71 ± 0.09	2.65 ± 0.19
Intercept ± se	3.40 ± 1.57	2.83 ± 1.55	5.18 ± 3.79	3.92 ± 3.72
r ²	0.87	0.86	0.80	0.75
S _{y.x}	6.42	13.93	23.16	15.52
Transformed data (log ₁₀)				
Ex ²	7.19	22.05	11.41	4.46
Ey ²	7.96	25.21	11.19	5.09
Exy	7.40	22.08	10.36	4.37
t values ^a				
<i>kilimensis</i>	—	—	—	—
<i>reichenowi</i>	0.769	—	—	—
<i>famosa</i>	2.529**	2.307*	—	—
<i>venusta</i>	5.620***	4.85***	2.806**	—

^a Significance at .05 (*), .01 (**), .001 (***)

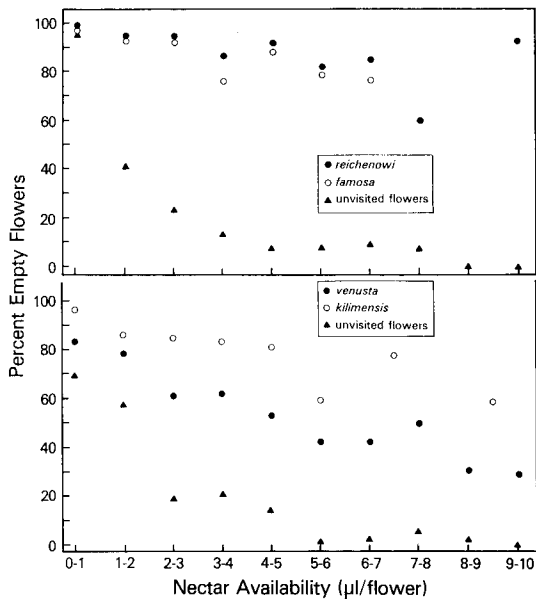


FIGURE 4. Frequencies of empty visited and unvisited flowers. The percentages were obtained from the same set of data used to prepare Fig. 3. The frequencies of empty, unvisited flowers for *reichenowi* and *famosa* were not significantly different, so values from the *reichenowi* series are shown here. The values for unvisited flowers on the lower graph are from *venusta* data sets.

examined flowers visited by *reichenowi*, *famosa* and *venusta* before 08:30, when nectar levels per flower were predictably high, and we established the frequency of the presence of any residual nectar in the basal chamber for each species. As predicted, *venusta* left nectar in this part of the flower more often (70%) than *famosa* (41%) or *reichenowi* (28%) ($X^2 = 38.3$, 2 df, $P \ll .001$). We were unable to obtain these data for *N. kilimensis*. These data do not indicate whether some nectar was also left in the second chamber, or the absolute amounts of nectar left in different parts of the flower, all of which require further study.

A similar result is obtained by comparing the frequencies of empty flowers in the original data with residual volumes (Fig. 4) instead of absolute amounts of nectar that remain, as in Fig. 3. The frequency of empty unvisited flowers was the same for *famosa* and *reichenowi*, and increased hyperbolically at low average availabilities of nectar. *Reichenowi* consistently emptied a slightly higher percentage of the flowers it visited than did *famosa*, but both species emptied fewer flowers at higher nectar availabilities. *Venusta* emptied a much lower proportion of visited flowers than the other species, especially at higher nectar volumes, despite the fact that the per-

centage of empty, unvisited flowers on these paws was slightly lower than we found for *famosa* and *reichenowi*.

It seemed likely that a bird's ability to remove nectar from the basal chamber would be affected by curvature of the bill, a straight bill being less likely than a curved bill to penetrate the basal chamber. We simulated this situation by sucking up nectar from intact flowers with fine-bored, 10 μ l capillary tubes inserted into the corolla. We compared the effectiveness of a strongly curved tube bent to match the bill of *N. reichenowi*, and a slightly curved tube bent to match the bill of *N. famosa*. Using the curved tube we removed all the nectar from the basal chambers of about 98% of the flowers we "visited." Using the straighter tube we removed all the nectar from the basal chambers of only 57% of the flowers we visited. No procedural bias was apparent to a critical observer. If anything, we tried harder to get the nectar with the straight capillary tube, and thought we had been more thorough than proved to be the case. This minor experiment merely demonstrates the functional importance of differences in bill curvature.

FORAGING COSTS AND RATE OF NET CALORIC GAIN

The rate of caloric expenditure by sunbirds while foraging depends on the proportion of time spent flying versus perching (Wolf 1975). Previously, we estimated the percentage of a foraging bout spent flying between inflorescences to be about 5% in high-density *Leonotis* fields (Gill and Wolf 1975a). Supporting data for *reichenowi*, *famosa* and *venusta* are presented in Table 3. In low-density situations, where inflorescences average 7/m², this figure increases to 10 or more percent (see Table 3).

Foraging costs also depend on the size of each species, which we designate below as a variable, *i*. Assuming 5% flying time while foraging, we estimate foraging to cost 0.34 cal/s for *N. kilimensis* from laboratory studies of activity metabolism (Wolf et al. 1975). We converted this estimate to values for the other species of different metabolic weight by multiplying by $(\text{wt species } i/17 \text{ g})^{0.72}$; this assumes that weight-dependent metabolism is proportional to $(\text{wt})^{0.72}$ (Calder 1974). Differences in wing disc loadings (see Feinsinger and Chaplin 1975) could increase the estimated difference in foraging costs between large and small species. This is because large species tend to have higher wing disc loadings,

TABLE 3. Proportions of foraging times spent flying.

Date	Sunbird	Inflorescence ^a density	Number of foraging bouts	Percent time flying ($\bar{x} \pm se$)
23 July 1974	<i>venusta</i>	21.5	35	4.61 \pm 0.52
		12.3	52	4.86 \pm 0.37
	<i>famosa</i>	21.5	9	6.00 \pm 0.93
		12.3	22	5.31 \pm 0.58
13 July 1978	<i>reichenowi</i> and <i>kilimensis</i>	21.5	11	4.54 \pm 0.49
	<i>reichenowi</i>	13.3	7	4.94 \pm 0.32
	<i>famosa</i>	6.8	13	11.85 \pm 1.10

^a Number of flowering inflorescences per square meter.

at least in hummingbirds, and hence higher flight costs than smaller species. No data are currently available on sunbird wing disc loadings, but they should make only a minor contribution because of the lesser importance of flying while foraging, as compared to hummingbirds.

To compare the foraging efficiencies of different sunbirds we converted the extraction data developed above into estimates of net gain per unit foraging time. Net caloric gain (G_{net}) for species i is estimated in terms of calories per second as

$$G_{net} = G - M_i = \frac{0.7 N R_i}{D_i} - M_i \quad (1)$$

where G is the absolute rate of nectar uptake, N is the nectar volume per flower in microliters, R is the average fraction of available nectar removed, D is the average duration of a flower visit in seconds, M is the metabolic cost/s of foraging defined above, and 0.7 is the caloric value of one microliter of nectar of *Leonotis nepetifolia* (see Gill and Wolf 1975a). Alternatively, we might calculate the unitless ratio of caloric gains to metabolic costs (G_{eff}), i.e. gain per unit cost or

$$G_{eff} = 0.7 N R_i / D_i M_i \quad (2)$$

but (1) is a more meaningful estimate of foraging efficiency for these systems (Pyke et al. 1977, DeBenedictis et al. 1978).

As shown in Table 4, *kilimensis* and *reichenowi* achieved similar rates of net caloric gain, which were considerably greater than those of the other two species. *Kilimensis*' faster rate of bill insertion more than compensated for its slightly lower removal fraction. *Famosa*'s rate of net gain was about half that of the two larger species. Its foraging costs were almost the same, but its slower rate of visiting flowers had a major effect on the calculations. *Venusta*'s rate of net gain was 25–28% of that of

the two largest species and about 45% of *famosa*'s rate of net gain. Its foraging costs were 40% less than those of *famosa*, which compensates for some but not all its deficiencies in extracting nectar. Slight differences in bill morphology tend to override the effect of differences in body size on foraging efficiency.

DISCUSSION

Our study indicates that in sunbirds, as documented or suggested for other nectarivores, morphological features of the bill and the corolla determine relative foraging efficiency. The relative lengths of bill and corolla affect not only a bird's ability to reach the nectar chambers, but more importantly, the actual rate of nectar uptake mediated through the amount of nectar obtained per tongue lick (Hainsworth 1973, Schlamowitz et al. 1976). The curvature of the corolla increases difficulty of access to the nectar chamber for relatively straight-billed species, and thereby increases the time required for insertion of the bill, as demonstrated in this study by the comparison of *famosa* and *reichenowi*. The importance of precise match between curvatures of bill and corolla is increased in *Leonotis nepetifolia* by the internal partitions which hinder deep probing by straight-billed species. Bill width and depth affect ability to penetrate narrow corollas. However, bill stoutness and therefore strength may increase feeding success at other flowers, such as those of the mistletoe *Phragmanthera dshallensis* (Gill and Wolf 1975b) which require forceful splitting.

The sunbirds we studied at *Leonotis nepetifolia* also feed at the flowers of *Aloe graminicola* (Liliaceae; Wolf 1975, Wolf and Wolf 1976). Because the corolla of the aloe is straighter than that of the mint, the relative foraging times of *N. reichenowi* and *N. famosa* are reversed. *Reichenowi* takes more than twice as long as *famosa* to extract a given quantity of nectar from a flower (Wolf and

TABLE 4. Comparative foraging ability of four sunbirds at *Leonotis nepetifolia*.

	<i>kilimensis</i>	<i>reichenowi</i>	<i>famosa</i>	<i>venusta</i>
Foraging cost (M^*) (cal/s)	0.34	0.32	0.29	0.19
Flower visit rate (D) (s/fl)	0.99	1.24	1.71	2.65
Fraction of nectar removed (R)	0.82	0.90	0.82	0.62 ^b
Gross caloric gain (G^c) (cal/s)	2.90	2.50	1.68	0.82
Net caloric gain (G_{net}) (cal/s)	2.56	2.18	1.39	0.63

^a Symbols as in equation (1).

^b Above 1 μ l per flower.

^c Calculated as 3.5 R/D; these values assume all species encounter 5 μ l of nectar per flower.

Wolf 1976: Fig. 7), and the difference in their rates of net energy gain is enhanced by the difference in their body sizes. *N. venusta*, like *reichenowi*, feeds slowly at *Aloe*, but because it is so much smaller, its foraging efficiency is nearly equivalent to that of the larger *famosa*. However, it can exploit only *aloe* flowers with high nectar volumes because of its short bill.

We consider a single average time per flower visit to be representative of each species at normally encountered nectar volumes. Nectar volume can have only a minor effect on the duration of a flower visit, because *Leonotis* flowers rarely contain large amounts of nectar; the average volume ranged from 0.5 to 6.0 μ l per flower and was usually about 3 μ l per flower by midmorning (see Gill and Wolf 1977: Fig. 2). Experimental data (Schlamowitz et al. 1976) suggest that large, long-billed sunbirds such as *kilimensis*, *reichenowi* and *famosa* can extract 4 μ l of nectar per tongue lick from corollas 30 mm long, and that they normally lick 4–5 times per second. Thus, 1–2 licks will drain 4–8 μ l of nectar from a single *Leonotis* flower, which is more than most flowers contain. This suggests that there should be little difference in feeding time at flowers with 0–8 μ l of nectar and that there will be increments of only 0.2 s for each additional 4 μ l per flower. The tongues of small, short-billed species apparently have disproportionately lower volumes (Schlamowitz et al. 1976). In species such as *venusta*, nectar volumes may have a greater effect on duration of flower visits, which will be disproportionately longer at high nectar volumes. This variable also may contribute to *venusta*'s long time per flower.

Our data on residual nectar volumes in visited flowers suggest that three of the sunbirds removed approximately a constant proportion of the nectar available per flower. Conceivably the sunbirds behave within an inflorescence according to the theorem of marginal value (Krebs et al. 1974, Charnov 1976). If a sunbird treats each flower within

an inflorescence as a patch, and all the flowers on an inflorescence as a small universe of patches, consider the following. The nectar content of the first few flowers probed on an inflorescence indicates the average quality of the rest of the flowers on that inflorescence (Gill and Wolf 1977). If the flowers contain much nectar, the amount obtained per tongue lick will decrease as the content of the flower declines, especially as the easily reached nectar in the outer chambers is depleted. This process is analogous to the decline with time in the rate of prey capture within a patch (Krebs et al. 1974). When the rate of nectar uptake per lick declines below the average expected within an inflorescence, it should be advantageous for the sunbird to move quickly to the next adjacent full flower. If this process is essentially independent of other paws the sunbird should leave more nectar in flowers on paws with high nectar availability than in flowers on poor paws. This would produce the result we observed.

Average conditions at other paws probably have some effect, e.g. when most paws are empty the sunbird should really drain each flower on a good paw and the marginal value theorem operates on a different scale. When little nectar was available, the sunbirds seemed to probe more deeply and remove more nectar from the basal chamber. Conversely when nectar is plentiful at other paws, the sunbird should reject poor paws more often (see Gill and Wolf 1977) or be more sensitive to declining nectar volumes per lick. Differences between species in their ability to reach nectar in the basal chamber would affect their definition of an "empty" flower and thus affect frequencies of paw rejection, as we previously speculated (Gill and Wolf 1977).

We presume differences in bill structure to be adaptive because they affect the rates of food handling, and consequently, the rates of food ingestion. While ornithologists have long recognized the functional specializations of major bill types, we are just beginning to demonstrate the functional effects of minor

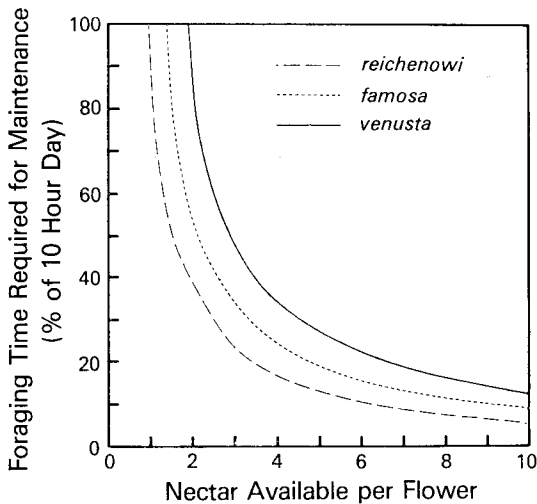


FIGURE 5. Calculated foraging time budgets required by sunbirds when feeding at flowers of *Leonotis nepetifolia* to maintain balanced daily energy budgets. The curves for the three species reflect the interactions of differences in average times per flower, average amounts of nectar removed from a flower and total daily energy requirements. The advantage given by *reichenowi*'s long decurved bill is clear, despite its larger size and higher total energy requirements.

variations of bill dimensions. The adaptive consequences of slight bill differences such as between sexes not only affect patterns of foraging and prey choice, but also lend strong functional support to models of the microevolutionary steps involved in spectacular radiations of bill form (see Bock 1970).

Differences between species in the rate of net caloric gain achieved while feeding on *Leonotis* nectar affect the foraging time required each day to maintain a balanced energy budget. A lower foraging efficiency means more flower visits and a greater proportion of the daylight hours that must be spent foraging. Otherwise, small birds such as these nectarivores must draw upon bodily reserves which are limited and easily exhausted (King 1972). We have calculated for *reichenowi*, *famosa* and *venusta*, the theoretical relationship between the foraging time required to balance daily energy expenditures, and the average nectar volume per flower (Fig. 5). These calculations are based upon the formulae developed earlier for *reichenowi* (see Gill and Wolf 1975a) using values of variables presented in Table 4 of this paper. The relative positions of the hyperbolic curves permit useful comparisons of the different species as they feed in a highly controlled, theoretical situation. Required foraging time is correlated with achieved foraging efficiency. For example, *venusta* must forage twice as long as

reichenowi at average nectar availabilities of 3 μ l just to survive. Differences in foraging times for these species will be greater if subordinate species such as *venusta* encounter less nectar per flower than aggressive dominant species such as *reichenowi*. If a sunbird forages longer than the time specified for a particular nectar availability, it will be able to accumulate energy for fat storage, or increase its total daily costs without incurring a negative energy budget.

The advantages of smaller body size and lower foraging costs should increase as average times of searching or flying between flowers increase. If flight time increases linearly as the average distance between flowers increases, then the rate of net gain should decrease asymptotically, more rapidly for larger species, particularly if flight costs are proportional to $(wt)^{0.97}$ rather than to $(wt)^{0.72}$ (Tucker 1974). Our preliminary calculations suggest that a small sunbird such as *venusta* should be able to maintain a positive rate of net caloric gain at patches with half the flower density required by a larger sunbird such as *reichenowi*. Low flower density increases the importance of differences in weight-dependent costs relative to differences among species in nectar extraction abilities. This sets up a possible basis for coexistence of different-sized nectarivores. Often, the smaller of two coexisting hummingbirds is a mobile exploiter of scattered flowers, while the larger species is a sedentary, territorial exploiter of locally dense flowers (Lack 1971, Feinsinger 1976, Wolf et al. 1976, Montgomerie 1978, Wolf and Gill, in press).

In addition to metabolic costs, differences in body size affect dominance relations, with smaller species being subordinate (Stiles and Wolf 1970, Wolf 1970, Morse 1974). To the degree that exploitative losses make some aggressive displacement advantageous (Case and Gilpin 1974, Gill and Wolf 1975a, Gill 1978), there may be selection for increased size, which increases the advantages of behavioral dominance. The selective disadvantages of the increased costs of larger size may be compensated for, in part, by improved access to richer resources, but whether such access increases as 0.72 times weight is unknown. Higher costs should result in increased specialization on flowers at which foraging efficiency is high and perhaps in tighter coevolutionary relationships with bird-pollinated plants. The enhanced dominance of larger individuals reinforces their feeding priority at such preferred flowers (Wolf et al. 1976). Their greater fasting endurance (Calder 1974) also counteracts

some of the uncertainty of finding adequate specialized foraging in seasonal environments. Small size will be advantageous when minor exploitative losses do not favor aggression or when flowers are few or widely dispersed.

SUMMARY

Four species of montane sunbirds, *Nectarinia kilimensis*, *N. reichenowi*, *N. famosa* and *N. venusta*, commonly feed together at flowers of the mint *Leonotis nepetifolia* in Kenya. Differences in bill dimensions of these sunbirds affect both the rate of nectar extraction and the proportion of available nectar that is removed from the flower. These results are consistent with the apparent fit between the bills and the length and curvature of the corolla, which affects the ability to reach nectar in a basal chamber partly protected by a corolla partition. Differences in body size affect foraging costs and render the species more similar, but not equivalent, with respect to rates of net caloric gain at this flower.

ACKNOWLEDGMENTS

We are indebted to the Office of the President for official permission to do research in Kenya, to R. Leakey, A. D. Forbes-Watson, D. Angwin, G. Backhurst, of the National Museums of Kenya for their assistance and sponsorship, and to L. Mackie, R. Terry, and B. Terry for hospitality. C. Conway, T. Halverson, S. Lanyon, S. Peters, and M. Stolper assisted in the gathering and analysis of data. F. R. Hainsworth, L. Gass and P. Feinsinger made many helpful criticisms of this paper. The National Science Foundation (GB 40108, GB 28956, DEB 76-04152) supported these studies.

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