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NONRANDOM FORAGING BY SUNBIRDS IN A PATCHY ENVIRONMENT¹

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Abstract. Sunbirds (*Nectarinia* spp.) feeding at the East African mint *Leonotis nepetifolia* encounter great variations in the nectar contents of flowers blooming in dense fields. The dispersion patterns of nectar are attributable to nectar removal from some flowers by the sunbirds themselves in earlier foraging and also to intrinsic floral variations. The problem facing the foraging sunbird is to increase its foraging efficiency (net energy gain per unit time) by avoiding recently visited, empty flowers and by visiting flowers with greater than average nectar volumes.

Sunbirds patterned their foraging in 3 major ways. First, they used initial flowers probed on an inflorescence as an assay of what the rest of the flowers in that inflorescence contained and they rejected inflorescences with little nectar. Such rejection increased nectar intake per flower by as much as 15%. Second, territorial sunbirds preferentially fed at unvisited inflorescences, increasing nectar intake 25% relative to random foraging. This was accomplished at least in part by foraging at different heights on successive foraging bouts. Third, flight distances to the next flower changed in response to immediate reward levels in some species but not in others. In general, sunbirds feeding at *Leonotis* responded less to reward levels by differential turning and movement than some other organisms, possibly reflecting different prey distributions or boundary constraints on their foraging.

Key words: *Coevolution; foraging efficiency; Kenya; Labiatae; Leonotis nepetifolia; Nectar; Nectarinia; optimal foraging; patchy environments; predation; sunbirds.*

INTRODUCTION

Consumers normally encounter nonrandom, clumped dispersion patterns of food items in the course of daily foraging (Gibb 1958, Taylor 1961, Wiens 1976). A consumer's response to variations in prey density or quality can affect its foraging efficiency (rate of net gain) (Schoener 1971, Charnov et al. 1976). Moreover, the more accurately the consumer senses the distribution and availability of its prey types, the more efficiently it should be able to forage. The higher its foraging efficiency, the more likely it will achieve a balance or positive daily energy budget and thus maintain good health or successfully undertake high-cost activities like reproduction or migration. Time not used in foraging also is available for hiding from predators, avoiding local climatic extremes or for breeding, all of which may improve an individual's fitness. Thus, to the degree that individuals respond differently to the same pattern of prey dispersion or patchiness, there will be selection favoring those that forage most effectively. Because of this, understanding how consumers exploit environmental mosaics has become increasingly interesting to ecologists.

Nectar, a caloric resource contained and replenished in flowers that usually are conspicuously displayed (Faegri and van der Pijl 1971, Hainsworth

and Wolf 1972, Heinrich 1975, Wolf et al. 1975), can be exploited by flower-feeding birds with increasing efficiency as the nectar content of the flower increases (Wolf 1975, Wolf et al. 1975). Therefore, if other costs are equal, natural selection should favor individuals that forage in ways that bias their foraging visits towards flowers with greater than average nectar content to increase the net reward above that achieved by foraging randomly. To so forage, a bird must either remember which flowers or areas were previously visited, or else respond to encountered variations in the nectar content of flowers in ways that move the bird away from flowers with little nectar but keep the bird at flowers with much nectar.

This study was undertaken to determine if sunbirds (Nectariniidae) forage randomly within arrays of flowering *Leonotis nepetifolia*, a common East African mint (Labiatae) that is an important source of nectar (Gill and Wolf 1975a, b). In this paper we show that sunbirds may pattern their foraging in at least 3 ways that improve rates of nectar intake above those expected from random foraging. We also consider in a preliminary way the detailed nature of the patterning and the conditions under which it was manifest.

METHODS

We obtained these data during 1973–1975 in the Rift Valley of central Kenya on 4 species of montane sunbirds feeding at flowers of the weedy mint, *Leonotis*

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nepetifolia. We studied the Bronzy Sunbird (*Nectarinia kilimensis*; 17 g), the Golden-winged Sunbird (*Nectarinia reichenowi*; 15 g), the Malachite Sunbird (*Nectarinia famosa*; 13.5 g), and the Variable Sunbird (*Nectarinia venusta*; 7.5 g). The 2 smaller species usually were not territorial, and fed primarily at undefended flowers. The 2 larger species often defended feeding territories containing 1,500–2,500 flowers or 200–300 inflorescences (Gill and Wolf 1975a). Much of our study involved watching the feeding patterns of uniquely color-marked, resident individuals that fed repeatedly in the same group of *Leonotis* flowers.

Leonotis flowers are arranged in a ring on ball-like inflorescences that we call "paws" (Fig. 1, Gill and Wolf 1975a). The plants consist of 1- to 2-m-tall stalks with up to 5 paws at ≈ 0.25 m intervals. *Leonotis* plants grow densely in open fields, often 10–30 paws/m². A flowering paw may contain 1–30 open flowers, depending on its age. A flower lasts 1–2 days and new ones open daily. Flowers produce 0.7 microlitres of nectar per flower-h ($N = 8$, $SE = 0.04$) from 0700–1100 h and ≈ 0.3 μ l/h from 1100–1300 h. The nectar contains sugar in a concentration equivalent to 0.52 (range 0.42–0.61) molar sucrose or 2.93J/ μ l (for details see Gill and Wolf 1975a). We measured average nectar volumes available to the sunbirds by extracting nectar from the base of the corollas of single flowers with a 25- μ l capillary tube. To minimize destruction of plants at which the sunbirds were feeding we usually picked 1 flower from each of 50 paws distributed throughout the area of immediate study. We occasionally measured the nectar in all flowers on a random sample of paws, which provided estimates of within- vs. between-paw variance in nectar volumes of *Leonotis* flowers.

We marked with small pink flags ≈ 35 stalks (50–100 paws) throughout a territory or feeding area and we counted the number of productive flowers on each paw on these stalks. We monitored all visits to the marked paws by the resident and other sunbirds for at least 4 h, starting at 0800 h. The time of each visit was recorded to the nearest minute. The visit times and frequencies by a known individual to the marked paws during a continuous observation period of one day comprised a "data set." We compared the observed frequency of visits to marked paws to the frequencies expected if the probabilities of visiting various paws were equal and independent of previous visits. We used the expected Poisson distribution of visit frequencies as the model of random paw visitation (**Appendix A**). We statistically compared the observed and expected frequency distributions by the *G*-test (Sokal and Rohlf 1969:563). If the data were not significantly different ($P > .05$) from the Poisson distribution, we call them "Poisson" or "nonpatterned." If the data were significantly different ($P < .05$) from a Poisson distribution, we called them "Nonpoisson" or "patterned."

Direct measures of the average amount of nectar available to a sunbird were obtained in samples of 50 flowers at the beginning and end of, but not usually during, the observation period to avoid disruption of natural feeding patterns. Average nectar volumes per flower during the observation were calculated indirectly from known visit times to marked flowers. The amount of nectar in an unvisited flower was assumed to be the average volume at the beginning of the observation period plus the nectar that accumulated due to production up to the specified time. The amount of nectar in a flower that had been visited was assumed to be the amount left after the first visit plus the accumulated volume. The average of all these values for marked flowers was then calculated for each hour. The average amount of nectar that would have been obtained during the observation period by a randomly foraging sunbird is:

$$\sum_{i=1}^n \bar{a}_i m_i / \sum_{i=1}^n m_i$$
 where \bar{a}_i is the average availability value from each hour (*i*) and m_i is the number of marked flowers visited in that hour.

Sunbirds feeding at *Leonotis* flowers perch below the inflorescence and spin around inserting their bill quickly into adjacent flowers around the paw. They rarely (<1%) revisit flowers on a paw during a visit and normally visit every flower. Nectar intake was calculated from the nectar content per flower on the paw times the number of flowers on a paw assuming all flowers on a paw were visited (see following). We also assume that *N. kilimensis* and *N. reichenowi* removed 90% of the nectar in any flower, *N. famosa* removed 82%, and *N. venusta* removed 62% above 2 μ l per flower and 22% below 2 μ l per flower (*personal observation*). The average intake per flower

during the observation period is:
$$\sum_{p=1}^8 i_p / \sum_{i=1}^n m_i$$
 where i_p = intake from flowers on the *p*th paw. The sum of the nectar volumes "obtained" included nectar lost to intruders that visited the same flowers prior to the visit by the territorial male under study. This was necessary from the standpoint of how nectar intake related to the pattern of foraging *per se*, which reflects the choice of paws visited independent of competitive losses. Nectar loss to competitors will be the subject of another paper.

We studied foraging movements of nonterritorial sunbirds in 1974. We tagged up to 13 *Leonotis* paws visited in succession by a sunbird and then characterized each in terms of the number of flowers in the paw, height above the ground, distances to preceding and subsequent paws and angular relations to preceding and subsequent paws. We also measured distances to all paws within a circle defined from the first of two paws as the center and the radius as the distance from the center to the second paw. We counted flowers on all paws within this circle. Movement direction in the

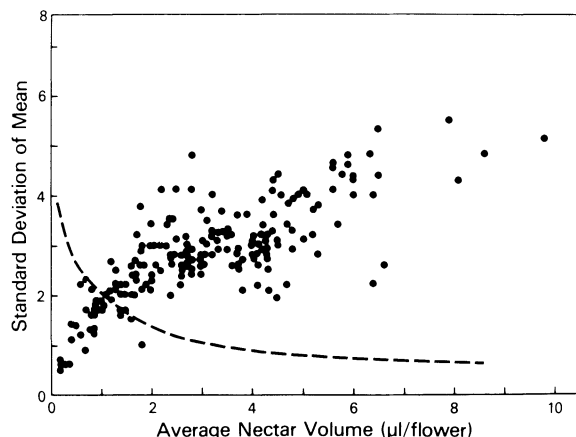


FIG. 1. Relation between standard deviations and means of nectar volumes from samples of 50 *Leonotis* flowers, 1 per paw. Calculated regression is $\ln y = 0.58 + 0.4 \ln x$ or $y = 1.79x^{0.4}$. The dashed line indicates the average values of the coefficient of variation (SD/\bar{X}) relative to the mean.

horizontal plane was evaluated as the angle of departure from a stalk relative to the direction of arrival. If the directions were the same, the departure direction was scored as 0° ; if the bird left the stalk at right angles relative to its arrival, the departure direction was scored as $+90^\circ$ (right) or -90° (left). We considered the sunbird to have changed foraging height if it moved >0.25 m vertically between successive paws.

RESULTS

Variations in nectar content of *Leonotis* flowers

We present here a synopsis of the patterns of nectar variability that a foraging sunbird will encounter. First, nectar volumes in *Leonotis* flowers in 1972 and 1974 were normally more different between paws than between flowers on the same paw (F -test; P always $<.05$). Table 1 illustrates the results of our most extensive data taken throughout the day on 18 March 1972. The ratio of variance between paws:variance within paws changed during the day and was greatest in the late morning.

Most of our data on nectar volume variability in-

TABLE 1. Analysis of variance of *Leonotis* flower nectar volumes on 18 March 1972. All values of F are significant ($P < .001$), indicating greater variability between paws than within paws.

Time	\bar{X}	s^2	Sum of squares		F	df
			Between paws	Within paws		
0700	16.2	14.4	1,014.00	967.82	9.20	14,123
0900	5.6	36.2	3,447.51	1,725.56	18.41	14,129
1100	4.0	47.4	6,071.45	627.75	87.50	14,126
1300	3.4	40.6	4,014.36	1,731.74	21.19	14,128
1500	1.9	34.5	4,093.94	878.55	43.27	14,130
1700	0.9	6.2	413.82	425.53	8.61	14,124

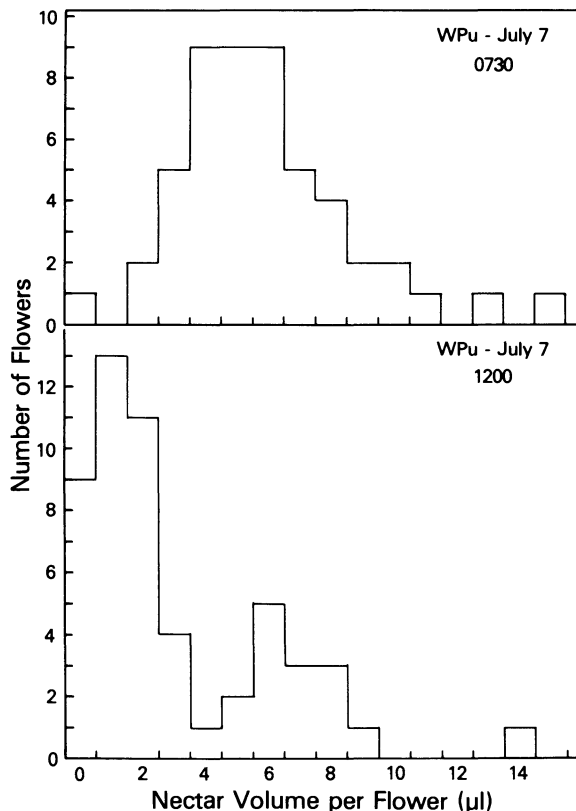


FIG. 2. Nectar contents (μ l) of *Leonotis* flowers defended and used by a male Golden-winged Sunbird (WPU) on 7 July 1973. Feeding during morning lowered average nectar volume from 7.0μ l at 0730 to 3.0μ l at 1200 and greatly reduced the proportion of flowers with 4 or more microlitres of nectar.

volve samples of 50 flowers, 1 from a paw. The general pattern of standard deviations relative to the means of these samples is illustrated in Fig. 1. As average nectar levels decline (during the day) the variation in paw quality also declines, rapidly below 2μ l of nectar per flower. However the variation relative to the mean, expressed as the coefficient of variation *increases* rapidly below 2μ l per flower.

The relative frequency of high vs. low nectar volumes usually declines during the morning as a result of sunbird feeding. Figure 2 illustrates the effect of morning feeding by a territorial Golden-winged Sunbird (WPU - 7 July 1973) on the relative numbers of flowers with high and low nectar volumes. It illustrates variability between paws that a sunbird could encounter while foraging and the dramatic change in the pattern of resource availability for these sunbirds over short time periods.

Paw rejection

Since paws vary in the average nectar content of the flowers on them, sunbirds might respond to differences between paws in ways that increase the rate of energy intake. Early in our studies we noticed that

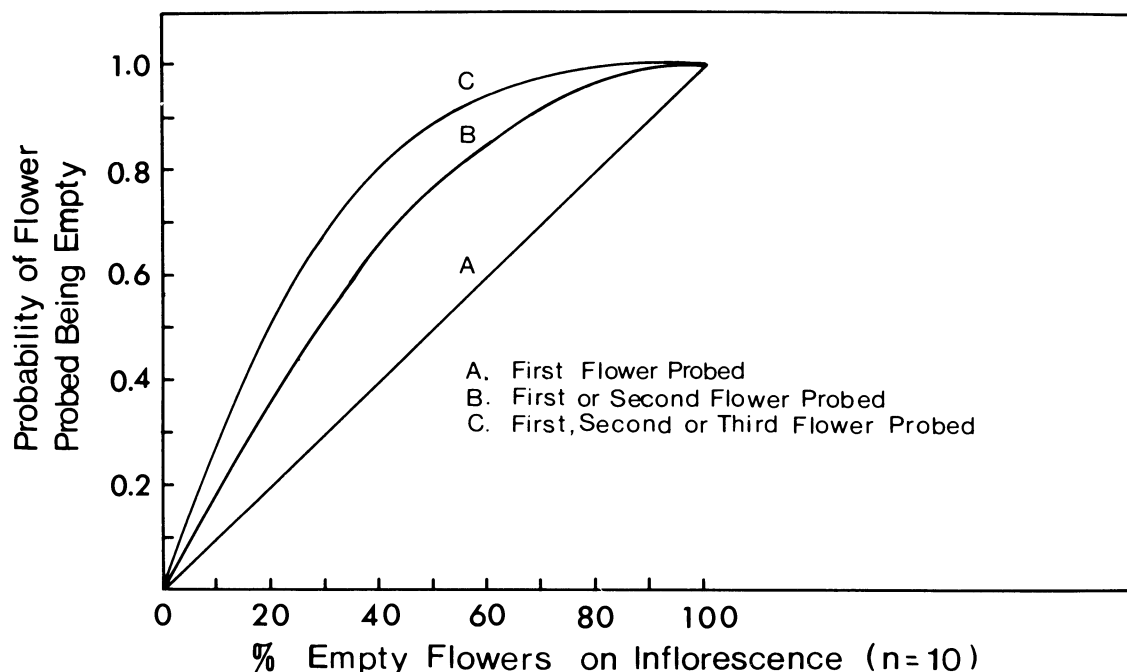


FIG. 3. Relation between probability of finding an empty flower on an initial probe and percentage of empty flowers on the inflorescence. This assumes that the sunbird does not visit additional flowers after finding an empty one. The figure suggests that sunbirds should almost always encounter an empty flower in 1 of the first 3 flowers probed on a *Leonotis* paw with 50% or more empty flowers.

sunbirds often left a paw, predictably ones that had been recently visited, after probing only a few flowers (mode of 2, Table 2). We called this behavior "paw rejection."

To see if rejected paws contained less nectar than accepted paws, we measured nectar volumes in unvisited flowers. We considered a paw rejected if the sunbird left the paw after 1–4 flower visits prior to visiting all the flowers on the paw. We considered a paw accepted if the sunbird visited 4 or 5 flowers and had to be chased off by us before it visited any more. The average amount of nectar in unvisited flowers on an accepted paw was significantly higher ($P \leq .005$) than on a rejected paw (Table 3). The proportion of unvisited flowers that were nearly empty ($\leq 0.4 \mu\text{l}$ of nectar) was also significantly greater (Mann-Whitney U , $P < .0001$) on rejected paws (57%) than on accepted paws (14%). By rejecting paws with low average nectar volumes per flower, a sunbird increased the average amount of nectar it obtained per flower. If 25% of the paws visited were rejected (see below), a sunbird

would increase its intake per flower by as much as 15% over feeding at all flowers on each paw visited.

We hypothesized that sunbirds foraging at high nectar volumes reject paws upon probing an empty flower among the first few flowers tested on a paw. The probability of finding an empty flower varies as a function of the proportion of empty flowers on a paw and the number of flowers tested. It is analogous to drawing blindly without replacement from a bag containing unknown proportions of black-and-white balls until 1 white ball is found. If X is the number of empty flowers on a paw, and N is the total number of flowers on the paw, the probability of the first flower being empty is

TABLE 3. Nectar volumes in flowers on rejected and accepted *Leonotis* paws. A mean value of nectar/flower was calculated for unvisited flowers on each paw. The data here collected on 7 July 1974 are based on the sum of the means from different paws.

Species	Paw state	Paws (n)	Av. nectar/un-visited flower μl	z^1	P
<i>N. reichenowi</i>	Accepted	23	4.68		
	Rejected	22	2.51	2.99	.0014
<i>N. famosa</i>	Accepted	13	4.50		
	Rejected	23	2.38	2.59	.005

¹ Mann-Whitney U -test with transformation of U statistic to z , (Siegel 1956).

TABLE 2. Incomplete *Leonotis* paw visitation: number of flowers visited before leaving a *Leonotis* inflorescence with 10 or more flowers.

Species	Number of flowers visited							
	1	2	3	4	5	6	7	8
<i>Nectarinia reichenowi</i>	11	12	5	5	0	3	0	1
<i>Nectarinia famosa</i>	9	19	4	3	2	1	1	0

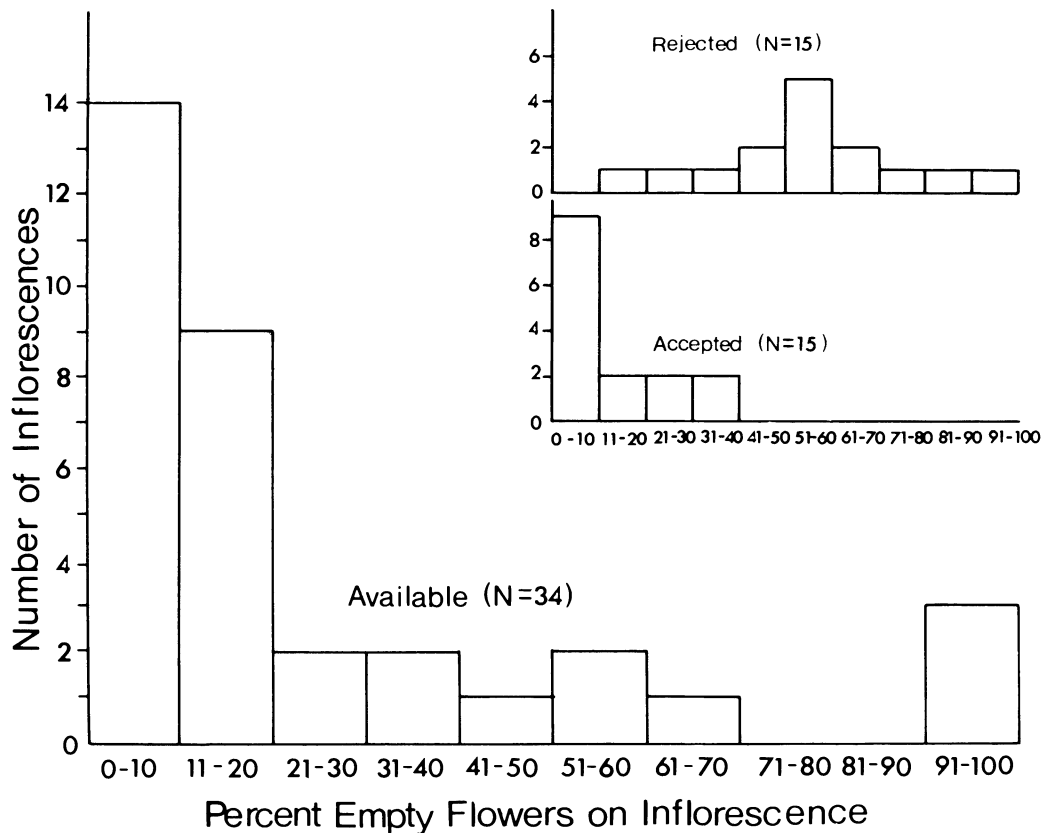


FIG. 4. Variation in percentages of empty flowers on inflorescences available to, accepted by and rejected by sunbirds.

X/N . The probability of the second flower being empty **when** the first flower is not empty is:

$$[X/(N-1)] \cdot [(N-X)/N].$$

The joint probability of finding an empty flower on the first probe or finding an empty flower on the second probe when the first flower contained nectar is:

$$(X/N) + \{[X/(N-1)][(N-X)/N]\}.$$

Therefore, the sum of the probabilities of leaving a paw immediately after finding an empty flower, when 1 of the first 3 flowers is empty is:

$$\begin{aligned} & \frac{X}{N} + \left[\left(\frac{X}{N-1} \right) \left(\frac{N-X}{N} \right) \right] \\ & + \left\{ \left(\frac{X}{N-2} \right) \left(\frac{N-X}{N} \right) \left[\frac{(N-1)-X}{N} \right] \right\}. \end{aligned}$$

The relationship between this probability function and the proportion of empty flowers on a paw (Fig. 3) indicates that if 50–60% of the flowers on a paw (flowers per paw fixed at 10 for convenience) are empty, 1 of the first 3 flowers probed will be empty $\approx 90\%$ of the time. Therefore, a sunbird that rejects because it finds an empty flower in 1 of the first 4 probes should reject $>90\%$ of the paws with more than 50% empty flowers and a decreasing fraction of those with fewer empty

flowers. The characteristics of the paws that were rejected and accepted in 1974 (Fig. 4) support this prediction. Thus, paw rejection could have been based on a system of sampling probabilities using the first few flowers to predict what the other flowers on the paw contained. Rejection did not seem to take into account the probability that some paws with one of the initial flowers empty contained only a few empty flowers and therefore probably should have been accepted. Instead the decision was apparently biased by the conditional probability that if one of the first flowers probed was empty, the paw was more likely to be bad than good (Schlaifer 1959).

Paws should not be bypassed or rejected when the costs of continued foraging are unlikely to be offset by improved gains (Pulliam 1974, Gill and Wolf 1975b, Charnov 1976). The costs of moving to another *Leonotis* paw are usually minimal because of the high density of flowering *Leonotis*. The time required is ≈ 2 s, the same as visiting 1 or 2 more flowers on a paw. The energetic cost of rejection is thus ≈ 6.7 joules for *N. reichenowi* (assuming 12.55 kJ/h for flight; see Gill and Wolf 1975b; Wolf et al. 1975). Therefore, the cost of rejection can be recovered by moving to a paw with flowers containing just a total of $2 \mu\text{l}$ ($\approx 293 \text{ J}/\mu\text{l}$) more than would have been found on the rejected paw. When *Leonotis* flowers are less dense, costs of rejection

TABLE 4. Frequency of *Leonotis* paw rejection by sunbirds. Nectar availability in microlitres/flower is based on a 50-flower sample, 1 per paw. The number of paws visited is indicated in parentheses after percent rejected.

Date	Time	Mean nectar availability	Median % empty flowers per paw	Percent paws rejected		
				<i>N. reichenowi</i>	<i>N. famosa</i>	<i>N. venusta</i>
1974:						
7 July	0900–1130	3.14	15	25 (203)	30 (91)	
21 July	0730–1130	6.38	...			24 (156)
22 July	0700–1100	6.40	...		28 (88)	31 (289)
						28 (286)
						> 30 (575)
1975:						
5 July	1500	0.20	...	8 (271)
8 July	< 0900	2.08	20	20 (417)
	1300	0.80	41	7 (310)
12 July	1030	2.47	28	25 (223)	36 (174)	42 (170)

tion will be higher and we would expect less frequent rejection at comparable nectar volumes.

When the average nectar per flower is low or most of the flowers in an area are empty, sunbirds also should be more tolerant of paws with empty flowers (Krebs et al. 1974, Charnov 1976) because the costs of moving probably will not be offset by the improved intake. In 1974, when average nectar volumes were high, we found that the sunbirds rejected 24–31% of the paws they visited (Table 4). In 1975 *N. reichenowi* rejected 20–25% of the paws visited in the morning compared to 7–8% in the afternoon (Table 4). The difference on 8 July was significant ($\chi^2 = 23.60$; $P < .001$) and corresponded to a drop in average nectar volumes from 2.08 μl to 0.80 μl per flower. The rejection of paws thus resembles the leaving of poor foraging patches by chickadees (Gibb 1962, Tullock 1971, Krebs et al. 1974, Smith and Dawkins 1971). The threshold for rejection of a patch was higher in rich habitats than in poor habitats as predicted (Krebs et al. 1974, Charnov 1976) but giving up time (\approx rejection probability) was more sensitive to the initial test of the patch condition than is evident in the foraging behavior of chickadees, either because search time is minimal in this sunbird system, or because initial tests are more accurate predictors of patch quality.

On 12 July 1975 we compared rejection frequencies of all 3 species feeding in the same place (Table 4). *Nectarinia reichenowi* rejected paws less often (25%) than *N. famosa* (36%) and *N. venusta* (42%). These differences are significant ($\chi^2 = 12.83$; $P < .01$) and probably reflect differences in ability to remove low nectar volumes from *Leonotis* flowers, i.e., definitions of “empty” differ among species.

Independence of visits to different paws

We obtained 28 data sets specifying visit frequencies to marked paws by a known individual, 20 in 1973, 8 in 1975 (Table 5). Two of the data sets from 1973 involved a male *N. kilimensis* (X-RG), the rest involved male *N. reichenowi*. In 7 of the 28 data sets the resident sunbird fed at but did not defend the marked paws. The fre-

quency distributions of visits per paw in 6 of these 7 data sets were not significantly different from the expected Poisson distribution. One differed significantly from the Poisson distribution due primarily to more than the expected number of paws in the 2-visit category, i.e., the sunbird (TS-8/1) revisited some paws too often for random foraging. The variance in this data set was still less than the mean ($s^2 = 1.05$, $\bar{x} = 1.54$) and the observed frequencies for other categories of 1, 3, 4, and 5 visits per paw were close to expected, but too many paws were visited at least once.

Of the remaining 21 frequency distributions of visits to defended flowers, 11 (52%) were significantly different from the Poisson distribution. The principal contribution to G was from fewer paws than expected in the 0-visit category and more paws than expected in the 1-visit category. Thus, significant patterning resulted from preferential visits to flowers that had not been visited earlier in the observation period. In some cases, the observed frequencies in the 2-visit category were higher than expected, but in only 1 case was this category's contribution to the statistic sufficient to change significance at the .05 level. The higher propor-

TABLE 5. Distributions of sunbird visits to marked *Leonotis* paws.

Data set	Distribution of visits	
	Poisson	Nonpoisson
Nondivisible		
Nonterritorial	3	
Territorial	5	3
Divisible		
Nonterritorial		
Entire morning	3	1
(early morning)	(3)	(1)
(late morning)	(2)	(2)
Territorial		
Entire morning	5	8
(early morning)	(5)	(8)
(late morning)	(2)	(11)
Total data sets	16	12

TABLE 6. Estimated nectar intake by territorial sunbirds. The contents (in microlitres) of flowers on rejected paws are included as is nectar actually lost to intruders. See text for details and assumptions of the calculations. The difference between average nectar contents of visited flowers and available flowers is significant ($P < .001$) for Nonpoisson data sets but is not significant ($P > .3$) for Poisson data sets.

Data set	Flower no.	Total nectar	Average nectar volumes (microlitres/flower)	Visited flowers	Available flowers	Difference
Nonpoisson						
YY—7/23	696	3,273	4.7 (4.8) ¹	2.8	1.9	
WPu—7/22	423	1,639	3.9 (3.9)	3.4	0.5	
—7/23	561	3,100	5.5 (5.9)	5.0	0.5	
—7/24	619	2,804	4.5 (4.9)	3.4	1.1	
—7/26	655	1,884	2.9 (3.0)	2.1	0.8	
RG—8/3	469	1,498	3.2 (3.2)	2.2	1.0	
—8/4	238	1,142	4.8 (4.8)	4.3	0.5	
PO—8/3	445	1,468	3.3 (3.3)	3.0	0.3	
GB—7/6	497	2,221	4.5 (4.5)	3.5	1.0	
GW—7/13	1,042	2,942	2.8 (2.9)	2.2	0.6	
		Average	4.0	3.2	0.8	
		Weighted average ²	3.9	3.0	0.9	
Poisson						
YY—7/22	480	1,436	3.0 (3.1)	2.6	0.4	
—7/24	747	2,994	4.0 (4.4)	3.2	0.8	
WPu—7/27	1,722	3,644	2.1 (2.2)	1.3	0.8	
PO—8/4	483	2,163	4.5 (4.5)	4.7	-0.2	
YPu—8/3	450	1,683	3.7 (3.8)	4.4	-0.7	
GB—7/7	768	1,908	2.5 (2.5)	2.5	0	
GW—7/14	1,363	1,905	1.4 (1.4)	1.0	0.4	
		Average	3.0	2.8	0.2	
		Weighted average ²	2.6	2.2	0.4	

¹ Values in parenthesis are average volumes for flowers on accepted paws only. The difference between the two values is thus the improved intake per flower visited attributable to rejection of some flowers.

² Sum of products of flower number \times average nectar volume per flower in each data set, \div by total flower number.

tion of birds approaches a significant difference (Fisher's exact test; $P = .08$).

The fact that any frequency distributions of sunbird visits to marked paws fit a Poisson distribution is perhaps surprising because of the way sunbirds moved between adjacent paws rather than randomly selected paws within the defended area. But the small size of the territories, the high mobility of the sunbirds within their territories and the intensity of foraging (20–30% of each hour; about 120 paws per h) apparently combine to equalize the probabilities of visits to paws in different parts of the territory, except for biases involving the vertical dimension (see below).

The nectar encountered per average flower was higher in Nonpoisson foraging than in Poisson foraging (Table 6). To control for day-to-day variations in nectar availability, we compared the nectar content of flowers on paws visited by territorial birds with the average content of flowers a randomly foraging bird

TABLE 7. Distribution of sunbird visits to marked *Leonotis* flowers in divided data sets.

Early morning visits	Late morning visits	Entire morning visits	Data sets (n)
Nonpoisson	Nonpoisson	Nonpoisson	5
Poisson	Nonpoisson	Nonpoisson	3
Poisson	Poisson	Nonpoisson	1
Poisson	Poisson	Poisson	2
Poisson	Nonpoisson	Poisson	2
Nonpoisson	Poisson	Poisson	1
Nonpoisson	Nonpoisson	Poisson	3
TOTAL			17

would be expected to visit (see Methods). Poisson foraging increased the nectar volumes encountered by $\approx 0.2 \mu\text{l}$ per flower in 7 data sets (7% increase), or $0.4 \mu\text{l}$ per flower if the differences are weighted by the number of flowers visited in each data set. Nonpoisson foraging increased the nectar volumes encountered by $\approx 0.8 \mu\text{l}$ of nectar (25% increase) per flower in 10 data sets. (We could not calculate these figures for all data sets because of missing data.) We tested these data against the null hypothesis of no difference between the amount of nectar in flowers on paws actually visited and the average amount of nectar available in the flowers on randomly visited (marked) paws (see p. 1285). The null hypothesis was not rejected for Poisson foraging (Wilcoxon matched pairs signed rank test, $T = 7$, $P > .05$; $N = 7$; Siegel 1956; paired t statistic, $t = 1.03$, $df = 6$, $P > .3$; Steel and Torrie 1960). The null hypothesis was rejected for Nonpoisson foraging using the same 2 statistics (Wilcoxon test: $T = 0$, $P < .01$, $N = 10$; paired t -test: $t = 5.59$, $df = 9$; $P < .001$). These statistics support the conclusion that nonrandom paw visitation as practiced by these sunbirds was advantageous because it increased the energy yield per flower visited.

The territorial sunbirds involved in these data sets rejected 5.8% (range 0–16%) of the marked paws they visited. Rejection rate was only slightly lower in Nonpoisson data sets (5.1%) than in Poisson data sets (6.6%), not enough lower to suggest that patterned foraging reduces rejection probabilities. But territoriality and nearly exclusive use of a particular set of flowers apparently reduces the frequency of visiting paws with empty flowers. By such rejection, the territorial sunbirds increased the average nectar encountered per flower visit by an additional 2.7%. Thus the combination of rejections and patterned foraging improved nectar volumes encountered by 25–30%.

Seventeen (8 Poisson and 9 Nonpoisson) of the 28 data sets were sufficiently large that we could divide them in half and separately analyze visit patterning in the early and late morning and compare these results to those for the total observation period (Tables 5 and 7). Four of these data sets involved undefended flowers. Twenty-two of the 34 (65%) frequency distributions for these shorter time intervals were significantly

different from Poisson distributions, including some nonterritorial data. The directions of departure were similar to those mentioned for the full data sets, except that frequently there were fewer revisits (2-visit category) than expected. In contrast to the full data set, TS—8/1; (see p. 1289) did not revisit paws more often than expected during short time intervals. Six of the 8 full Poisson data sets included some significant patterning over shorter time intervals (Table 7). Sunbirds patterned their visits less often in the early morning (9/17) than in the late morning (13/17), when nectar volumes average lower and, interestingly, when the variance between paws relative to the mean is higher (see p. 1286), but this difference was not significant (Fisher's exact test; $P = .11$).

If a sunbird forages nonrandomly in the early morning, subsequent late-morning foraging may tend to erase departures of the frequency distribution from a random model unless the late-morning visits are dependent on the early morning visits. If they are independent, the proportion of all paws shifted from a particular category in the first frequency distribution will correspond to that category's observed relationship to the expected. For example, if the observed frequency in a particular category was higher than expected, a disproportionately high number (relative to other categories) will be visited in the late morning. The net result of this sampling phenomenon will be a final, combined frequency distribution that more closely approximates the expected frequency distribution for the full data set. Keeping this in mind, our data suggest that the sunbirds were patterning their paw visits primarily over short time intervals, and that visits in the late morning were independent of previous visits to those paws. In most data sets the observed frequency of revisited paws was close to the expected, which supports this conclusion. Also the average time interval between revisits in Poisson (119 min) and Nonpoisson foraging (144 min) was not significantly different.

To determine whether the sunbirds preferred paws with higher flower numbers, we compared the average number of flowers on marked paws that were visited (A) to the average number of flowers on all available marked paws in a feeding area (B). In 24 of 25 data sets, A was greater than B (average increase 12%; range 2–37%). The difference between A and B was significant (t -test; $P < .05$) in only five of these but the overall trend is significant (sign test; $P < .001$).

Patterns of foraging movement

A consumer can also increase its rate of prey capture, or nectar uptake by moving in response to variations in resource density (Tinbergen et al. 1967, Croze 1970, Cody 1971, Smith 1974a, b, Charnov et al. 1976). If resources are clumped in distribution, the consumer can tend to move away from areas of low resource density and remain in areas of high resource density by turning more and moving shorter distances after a

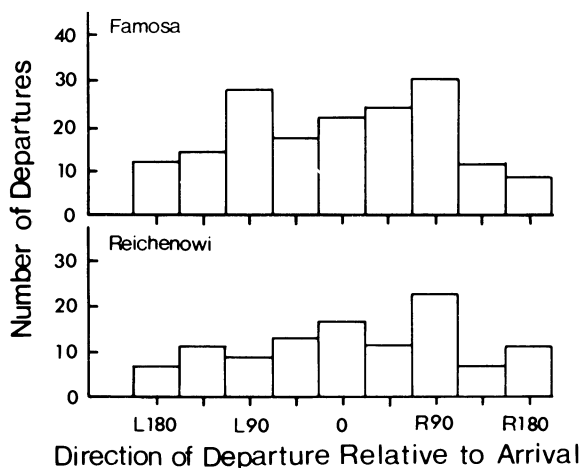


FIG. 5. Departure directions relative to arrival directions of sunbirds feeding at *Leonotis nepetifolia*. Data include all moves to a new stalk from both accepted and rejected paws. Most moves involved a turn; there was no pronounced modal peak at 0°.

positive reward. The consumer should thereby minimize the proportion of revisited resource points and should avoid places visited by other consumers (Pyke 1977, Cody 1971), increasing its foraging efficiency.

In 1974 we studied the movements of nonterritorial sunbirds. Most of the departures from a paw were at a pronounced angle relative to the arrival direction (Fig. 5). There was no pronounced modal peak at 0° in these data, suggesting that departure direction was usually independent of arrival direction. The mean departure direction following paw rejection was not significantly different from the mean departure direction following paw acceptance (Table 8). There was also no significant tendency to alternate turn directions.

The modal distance moved by sunbirds between successively visited paws was 0.3–0.4 m (Fig. 6). The average distance moved after paw rejection was significantly higher than after paw acceptances in *N. famosa* and *N. venusta*, but not in *N. reichenowi* (Table 8). Both *N. famosa* and *N. reichenowi* moved to a new stalk more often than they stayed on the same stalk (Table 8). *N. famosa* moved significantly more often ($P < .05$) to a new stalk after a rejection than after an acceptance, whereas *N. reichenowi* did not.

Sunbirds often moved horizontally while feeding despite options of moving vertically to higher or lower paws on the same or an adjacent stalk. About 80% of the moves were in the same plane (Table 8). The frequency with which birds changed height was not influenced by acceptance or rejection (χ^2 , $P > .50$) suggesting height changes were independent of immediate reward levels.

We also noted whether a sunbird bypassed a better paw on each move between paws. A "better" paw was one with as many or more flowers in the same depart-

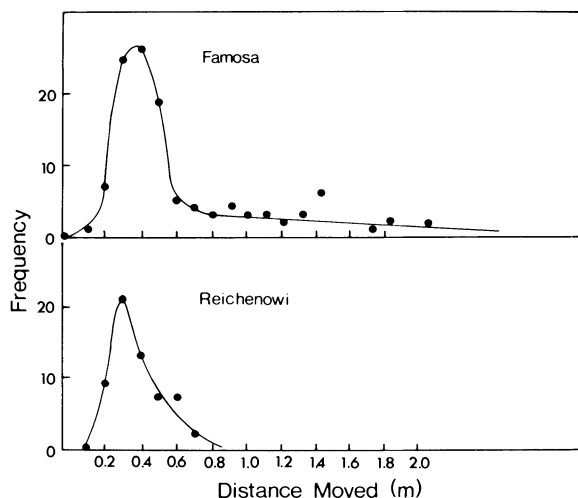


FIG. 6. Distances between visits to successive *Leonotis* paws. Curve fitted by eye.

ture quadrant as the paw to which the sunbird actually went. We did not include better paws in different potential departure directions as we could not be sure these were in the visual field of the bird making a decision where next to go. All other factors being equal (e.g., nectar per flower, which is presumably unknown to the nonterritorial birds on which the data were collected), a sunbird should not bypass such a paw for one farther away if it is going to maximize foraging efficiency. In fact, sunbirds bypassed better paws $\approx 30\%$ of the time (Table 8). The better paws that were bypassed tended to be at the same height as the others so they were not subject to a stratification bias. Also sunbirds did not bypass better paws significantly more often after a rejection than after an acceptance (Table 8). These data indicate that the sunbirds are not: (1) perfect in recognizing the closest, largest inflorescence; or (2) using inflorescence size (i.e., the number

of flowers on the inflorescence) as an index of quality. Regardless of the reasons for the bypasses, it must be remembered that each bird showed some departure from what we would have considered to be the best possible short-term behavioral pattern.

On 16 July 1975 we measured the heights of paws visited by a color-marked male *N. reichenowi* (YX-GB) on different foraging bouts during the morning. We tested for differences in average heights of these bouts which varied from 124.7 cm to 160 cm, using a one-way analysis of variance. The differences among bouts were significant ($F = 2.48$; $df = 7, 51$; $P < .05$), indicating that foraging height differed more among bouts than within bouts. If patterning of foraging bouts with respect to height tended to bias visits to previously unvisited paws in the course of the morning then the final distribution of visits to marked paws of particular heights should approximate the actual height distribution of those marked paws. We compared these distributions for the 7 possible 1975 data sets using a 2-sample Kolmogorov-Smirnov test (Siegel 1956) and found no significant differences.

DISCUSSION

Three factors contribute to spatial variations of nectar availability in a field of flowers. First is the distribution of the resource sites themselves, flowers, which also can change in time as new inflorescences bloom and as the total number of flowers increases and declines. Second is the rate of nectar renewal in individual flowers, itself a variable (Faegri and van der Pijl 1971, Heinrich 1975, Gill and Wolf 1975a, Stiles, 1975). In flowers with high nectar production and infrequent consumer visits, uneven resource removal may contribute only slightly to variable nectar volumes, but this second factor interacts strongly with the third factor, consumer exploitation. Not only do previous visits lower absolute levels of nectar availability, which may

TABLE 8. Movements of sunbirds between successive *Leonotis* paws

Species:	Departure direction		Distance moved (m)		Change stalks			Change height			Bypass better paw		
	N	$\bar{X} \pm SE$	N	$\bar{X} \pm SE$	Yes	No	χ^2	Yes	No	χ^2	Yes	No	χ^2
<i>N. famosa</i>													
Accepted paws	136	-0.33 ± 8.6	121	$0.54 \pm .05$	98	26	4.73*	23	101	0.03	30	71	1.43
Rejected paws	27	-8.33 ± 14.0	40	$0.91 \pm .15$	27	1		5	20		4	19	
	163	-1.66 ± 7.6^1											
<i>N. reichenowi</i>													
Accepted paws	78	9.87 ± 11.6	62	$0.50 \pm .08$	57	8	.04	13	65	0.55	17	38	1.79
Rejected paws	20	9.25 ± 1.6	22	$0.61 \pm .11$	17	2		2	18		7	7	
	98	9.74 ± 10.1^1											
<i>N. venusta</i>													
Accepted paws	27	6.11 ± 18.0	52	$0.44 \pm .05$									
Rejected paws	14	28.57 ± 25.2	27	$0.66 \pm .09$									
	41	13.78 ± 14.4^1											

¹ Rejected and accepted paws combined.

* $P < .05$.

make aggressive exclusion of competing individuals economical (Gill and Wolf 1975a), but previous visits also change the frequency distribution of nectar per flower (Fig. 2, Gill and Wolf 1975b). This is especially important in systems with large numbers of flowers relative to the number visited by an individual bird in the course of a single foraging bout. To the degree that birds tend to forage at adjacent flowers within limited time periods, spatial patchiness will increase. To the degree that birds preferentially select flowers with high nectar availability, they may lower the variance in nectar volumes (Fig. 1) as well as spatial patchiness, as preferential foraging by crows on closely spaced prey lowers average density (Croze 1970). But as long as some flowers or groups of flowers are both renewing nectar and remain unvisited, high variance will be maintained.

Sunbirds have several ways of responding to local variations in nectar content of flowers. The different responses are probably used in alternative situations. Territorial sunbirds can favor unvisited flowers because they feed repeatedly in the same group of flowers and mostly relate to their own previous flower visits. However, proximate response systems such as paw rejection and movement rules should be more important to nonterritorial sunbirds, which are less restricted to a particular group of flowers and which must relate a posteriori to the visits of other sunbirds feeding in the same places.

Two important problems confront the consumer foraging on spatially variable food: (1) How can it maximize encounter rates with profitable prey; and (2) what patterns of spatial variation will it encounter and respond to? The first is a problem of optimal foraging rules for a particular situation. The second is a problem of learning and probability assessment. At this point, we are unable to define all important costs of natural foraging by sunbirds at *Leonotis* and thus we are not concerned with establishing optimality criteria for this system. Instead we focus on ways that sunbirds can increase nectar per flower over average levels.

Foraging rules that increase prey encounter rates seem to be "area-restricted searching" and "giving-up time." When the prey distribution is clumped, a predator should move in ways that keep it in a clump and move rapidly between clumps of prey (Tinbergen et al. 1967). This can be accomplished most simply by turning more sharply and moving shorter distances when a prey item is encountered than when a prey item is not encountered. Such behavior is well documented for a variety of organisms (references in Charnov et al. 1976, p. 252) including some birds (Smith 1974a, b, Croze 1970). This behavior requires the predator only to assume that the dispersion pattern of its prey is clumped and to remember the angle of arrival at a foraging stop, and perhaps the average distance moved.

In the sunbird-*Leonotis* system reported here, some tendency toward area-restricted searching was evident in the foraging of *N. famosa*, but none was evident in *N. reichenowi*. Overall, such foraging behavior seemed to be less important in sunbirds feeding at *Leonotis* than has been found in bees (Pyke 1977) and thrushes (Smith 1974a, b), either because the sunbirds were feeding in areas of relatively higher average reward levels, or because their foraging spatially was more tightly bounded. If the acuteness of turning reflects the relative size of the reward just encountered, it is logical that birds or bees feeding in areas of low density or highly clumped prey should usually move straight ahead until they encounter a patch of prey. Alternatively, sunbirds feeding in a field of flowers full of nectar as was the case in 1974 during this study, should turn frequently and minimize distances moved. Territoriality also limits the directionality of foraging movements both for individuals feeding within the confines of small defended areas and for nonterritorial individuals or species feeding in the interstitial areas between the territories. Continued straight movement would take the territorial bird away from the higher nectar volumes of its defended area (Gill and Wolf 1975a) and would take the nonterritorial bird into a territory where its foraging would be disrupted by aggressive displacement. Sunbirds therefore should usually be constrained by boundary effects and naturally feed in a highly localized manner.

Giving-up time is the idea that a predator should leave a patch when the rate of prey encounters in the patch falls below the average for the habitat (Krebs et al. 1974, Charnov et al. 1976, Charnov 1976). Carrion crows give up searching at low rates of prey encounters (Croze 1970) but apparently this was independent of prey density. Experiments with chickadees (Krebs et al. 1974) support the model's predictions in greater detail. The predator need know only (a) that its prey is clumped and (b) the average density or encounter rate of that prey in a habitat. As the average density for the habitat increases, the predator should give up more easily, i.e., be less tolerant of locally poor foraging. Giving-up time may also decrease as level of satiation increases. Rejection of *Leonotis* paws seems to be similar to a giving-up time system that increases net energy gain per unit time and that is sensitive to average levels of nectar per flower in the field, though further study is needed to develop this variable in terms of optimal foraging. Our data do indicate some differences between species in the way they react to, and probably sense the quality of a particular patch. Insofar as this reflects intrinsic, species-specific feeding efficiencies, it supports the idea of consumer-defined quality gradients (Gill and Wolf 1975a, Wolf et al. 1976).

A third way the predator can increase its rates of encountering profitable prey is to pattern its own foraging over a period of time in ways that maximize

visits to productive sites that were not previously visited. To some degree this is a natural consequence of area-restriction and giving-up time systems. It is hypothesized to be an adaptive advantage of some kinds of flocking in birds (Morse 1970, Cody 1971). However, monitoring the foraging sites of other individuals must be very difficult if not impossible except on a most proximate basis, but often it should be feasible for an individual to pattern its foraging relative to its own previous foraging in systems with even minor delays in replenishment rates. This is a problem of memory adjusted to specific renewal probabilities. Birds can home precisely over long distances and time periods and are capable of detailed retention of landmarks, places, and territorial boundaries (Welty 1962, Emlen 1975), but how refined this capacity may be with regard to remembering hundreds of specific flowers in a *Leonotis* patch, for example, is not known. Hummingbirds do visit nectar feeder locations after an extended absence (and removal of the feeder) (Miller and Miller 1971a) and under certain conditions orient by cues of spatial location rather than color (Miller and Miller 1971b). But while feeding at complex inflorescences, hummingbirds make mistakes; i.e., revisit flowers within the same foraging sequence—5–10% at *Delphinium* (Pitelka 1942), 2% at *Penstemon* in Arizona (*personal observation*). It is not clear how much, if at all, exact location memory influences foraging behavior of sunbirds. To the degree that reward-related turning behavior is demonstrated, limited memory of immediately preceding flight directions must be involved (Pyke 1977). To the degree that successive foraging bouts are nonrandomly located in different strata or sections of the *Leonotis* field, memory of the locations of previous foraging bouts must be involved.

Our data suggest that sunbirds pattern their foraging mainly over short (1–2 h) time spans, possibly because of memory limitations. It often should be continuously advantageous to feed at unvisited flowers as long as these are available. However, economic considerations such as increasing rarity of unvisited flowers and renewed nectar in previously visited flowers may also be important determinants of longer term patterning. It does seem clear that effective patterning of visits is most feasible by a bird that is feeding repeatedly at the same limited set of flowers with limited use by other birds. The traplining behavior of some hummingbirds (Feinsinger 1976:265) apparently is 1 form of well-patterned flower visits to predictably renewed nectar at scattered productive flowers. To our knowledge no one has found a hummingbird visiting a series of discrete traplines on successive foraging bouts. In fact, the details of trapline foraging using color-marked birds remain to be described, or even confirmed. The flowers on a trapline are not defended. Therefore a trapline would only be economical when the number of flowers on the trapline is limited and the probability of

visits to these flowers by competing individuals is low. The timing of visits to a flower should be a compromise between maximizing nectar accumulation and minimizing loss to other individuals. Similarly effective patterning of visits to large numbers of flowers should be most feasible for territorial birds that minimize disruption of the spatial pattern of nectar availability by other competing individuals. However, there may be a point where too many chases prevent a territorial individual from patterning effectively. If so, this is another cost of territoriality.

The second of the 2 major problems confronting the consumer is the assessment of food availability so that it can forage in the best way. Predators should tend to concentrate their searching nonrandomly in areas of relatively high profitability (Royama 1970) and studies of the foraging behavior of chickadees (Smith and Dawkins 1971, Tullock 1971, Smith and Sweatman 1974) show that they do so forage. But how do they learn which areas are most profitable? How do they learn what is the average prey density in an area so that giving-up time in a patch can be adjusted appropriately? The experiments of Smith and Sweatman (1974) indicate that chickadees learn to hunt selectively where the rates of capture are highest. At first, when the chickadees were naive about the distribution of prey in an aviary, they searched in short bouts and often moved from area to area. After 11–20 trials, however, they learned to hunt persistently in the better areas. The only information available to the chickadees were immediate capture rates and learned associations between past capture rates and spatial positions in the aviary. The immediate response to reduced prey densities in the best area, as would be a natural consequence of intense foraging, was to shift their preference to the second best area. None of the chickadees foraged perfectly, i.e., spent all their time in the best area. It is logical that such predators should spend some time monitoring the variations in prey availability and adjust their foraging accordingly, i.e., they should sacrifice short-term optimal foraging for longer-term effectiveness when the distribution of prey is likely to change (Krebs et al. 1977). This is what Heinrich (1976) has called “minoring” in bumblebees, but the degree to which it is a normal part of natural foraging is not known.

Charnov (1976) has suggested that an organism should make a decision about when to leave a patch in relation to the average patch quality throughout the habitat. However, this is a special, limiting case when the number of patches sampled approaches infinity or the mean value of habitat patch quality has no variance, i.e., every patch is of the same quality. In reality there is some variation around the mean patch quality. It becomes important to understand how the pattern of this variation (i.e., the frequency distribution of patch quality) around the mean influences the perception of the environment by the organism. In most cases, the

organism also has a limited foraging area in which foraging causes a change in the mean and variance of patch quality, which in turn causes a change in foraging behavior, i.e., patch acceptance and rejection. We have suggested that the sunbirds alter their view of the mean value of the environment within a period of 4 h or less since the rate and "rules" of patch rejection changed within that time interval. Unpublished experiments with hummingbirds (*personal observation*) suggest the possibility that information is integrated primarily from one foraging bout to the next in a laboratory situation. Smith (1974a,b) and Baker (1973) have both shown relatively short time periods over which behavior patterns associated with patch exploitation can change.

Even in these cases, the relative importance of past and present information is unclear. We suspect that the birds probably continually integrate information from present foraging into their perception of the environment as it has been accumulated through past foraging episodes. The importance of a current episode in changing the perception of the environment presumably depends on the deviation of the event from the mean value as perceived at that time and the variation around that mean. In the sunbirds, not only is there a mean and variance of environmental quality, but the values of each of these parameters changes through time as a result of the foraging activities of the birds. In this case, the ability to integrate information from relatively short-term sequences of foraging episodes to achieve a view of the environment is probably extremely important in the ultimate foraging capabilities of these birds.

An important difficulty with much of patch exploitation information from natural situations is that the investigators must arbitrarily define a patch and this definition may have no close correlation with how the foraging individual perceives the patchiness of its environment. In fact, we suspect that, as with short-term reassessments of average environmental quality, the forager has short-term shifts in its definition of patch boundaries, at least in most situations. In our earlier study of sunbirds foraging at mistletoe flowers on *Acacia* branches (Gill and Wolf 1975b) we suggested a patch-foraging hypothesis to explain the observations, but it was clear that we could not define either a priori or a posteriori what a bird perceived as a patch (Gill and Wolf 1975b). In the patch-rejection studies reported in this paper we have found a situation where our definition of a patch probably corresponded closely to that of the bird.

Finally, the decision process of a foraging organism is coupled not only to its view of its external environment, but also to its internal environment, especially feedback relations between an energy storage compartment and environmental information. Hummingbirds tend to accumulate energy at approximately a constant rate throughout the day (Wolf and

Hainsworth 1977). Even under conditions of deprivation, the birds may show different changes in foraging behavior depending on the size of the energy storage compartment and, perhaps more importantly, what the bird views the size of the compartment should be at that time of the day (*personal observation*). Clearly this relationship will vary among foraging organisms as many, if not most, will not show the gradual accumulation of energy at a constant rate that the birds do. However, this feedback is viewed as an important component of meal control in humans and rats (Toates and Booth 1974) and also hummingbirds. We expect that it will play an important role also in the response of a foraging bird to a particular environmental cue. This becomes especially important if the response to a similar cue varies as a consequence of the feedback from the storage compartment. Note that this internal environment may be the major integrative mechanism for the perception of the external environment.

Future research on optimal foraging ecology must inevitably blend with the data base of learning theory in the psychological sciences. Patterns of response to reward reversals are comparable to changing prey availabilities at particular locations, and psychological studies of the "depression effect" demonstrate the impact on responses to present rewards of the difference between past and present reward levels (Bitterman 1975). Recent studies of the nectar foraging behavior of the Hawaiian honeycreeper (*Loxops virens*), show that they too avoid recently visited flowers, in ways similar to the laboratory paradigm of alternation learning (Kamil 1977). Not only can animals learn probabilities of recurrence and respond appropriately, but different animals seem to vary (adaptively?) in their abilities to learn and in their responses to different reward patterns (Bitterman 1975). An organism's intrinsic capability for remembering and projecting details of its past foraging will obviously affect how optimally it can exploit a particular condition of prey availability.

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APPENDIX A

Suppose that a sunbird visits paws at a rate, $p\Delta t$, such that the chance of visiting 2 or more paws in the time interval Δt becomes vanishingly small as Δt approaches 0. Suppose that the sunbird feeds from exactly N paws, and that on each feeding visit that the chances of visiting a particular paw are equal and independent of the previous visit then the chance of not visiting a particular paw during the time interval Δt is equal $1 - p\Delta t/N$; the chance of visiting a particular paw is equal $p\Delta t/N$; and the chance of visiting 2 or more paws is negligible. Let $p(n, t)$ be the probability distribution function of exactly n visits to a paw up to time t . Then,

$$p(n, t + \Delta t) = p\Delta t/N p(n-1, t) + (1 - p\Delta t/N) p(n, t); \\ (0, 0) = 1$$

from which an equation for the probability generating function, $P(z, t)$, may be derived as:

$$dP(z, t)/dt = (p/N)(z - 1)P(z, t); P(z, 0) = 1.$$

Hence, the generating function is:

$$P(z, t) = e^{(pt/N)(z-1)}$$

which is the generating function of a Poisson distribution with mean equal to pt/N .