NECTAR LOSS BY GOLDEN-WINGED SUNBIRDS TO COMPETITORS

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ABSTRACT.—We develop a mechanistic approach to the study of resource competition among sunbirds in natural systems. Our emphasis is on the proximate impacts of actual nectar loss on the daily energy balance of nonbreeding sunbirds. We estimated nectar losses by monitoring visits to marked *Leonotis nepetifolia* flowers in Kenya during a season of low-resource availability and intense competition.

Territorial Golden-winged Sunbirds (*Nectarinia reichenowi*) lost an average of 8% of the nectar encountered per flower to competing individuals. Nonterritorial males lost a minimum of 36% and a maximum of 46% of the potentially obtained nectar to other sunbirds. Females lost more than males. We calculate that territorial and nonterritorial males had to forage 17% and 72% more each day respectively to maintain a balanced energy budget as a result of these losses. These results support earlier models of the energetic economics of territoriality and provide some insights into the problem of exploitative competition for nectar, including the nonlinearity of the competitive effect on foraging time. *Received 14 February 1978, accepted 13 February 1979.*

COMPETITION for food by related species of birds is a prevailing axiom of avian ecology (Lack 1971, MacArthur 1972, Cody 1974). Its importance also is being questioned (Wiens 1977, Connell 1978), partly because it is difficult to demonstrate, much less to measure, "competition" in bird populations, which cannot easily be manipulated. General formulations of competitive effects often have used the amount of overlap in resource or habitat use (Levins 1968, Schoener 1974), which assumes ongoing exploitative competition and is not applicable to situations with interference competition (Case and Gilpin 1974) or to situations in which the patterns of equilibrium resource use are the result rather than the cause of the interaction. Even for exploitative situations, the additional assumptions are required that equilibrium has been achieved and that the overlap on all resource states actually reduces population growth. In most natural situations it is impossible to quantify such negative effects. In some systems, however, including the bird-nectar system discussed in this paper, we can estimate some of the effects of competition on the time and energy budgets of individual birds.

Floral nectar is an important food resource for many birds. Nectarivores, which often are energy limited (Gass et al. 1976, Carpenter 1978, Gass 1978), tend to aggregate at major blooms of certain flowers and to defend some of them intra- and interspecifically (Cody 1968; Stiles and Wolf 1970; Wolf and Hainsworth 1971; Gill and Wolf 1975; Carpenter and MacMillen 1976a, 1976b; Gass et al. 1976; Kodric-Brown and Brown 1978; Gass 1978; Wolf 1978). Productive flowers assure these birds of stable resource sites that can be revisited repeatedly during the day for several weeks or longer. This makes it possible for us to monitor their visits to the flowers and to analyze foraging success and competition in terms of sequential foraging visits to known resource sites (Gill and Wolf 1977, Gill 1978).

In this paper we estimate levels of nectar uptake and loss by the Golden-winged Sunbird (*Nectarinia reichenowi*) from flowers of the mint *Leonotis nepetifolia*. The estimates of nectar loss allow us to examine 1) exploitative competition during a season of low resource availability, 2) the relative importance of interspecific and intraspecific competition, and 3) how flower defense reduces exploitative losses. We also examine the potential impact of caloric losses on foraging time requirements of individuals.

METHODS

This study was conducted in July/August 1973 and 1975 near Naivasha, Kenya at the same sites used for previous studies (Gill and Wolf 1975, 1977, 1978). Our study areas were located in the Rift Valley 150 km south of the equator at an elevation of 1,800 m. Flowering *Leonotis nepetifolia* in this region often attracts large numbers of nonbreeding sunbirds. The year of 1973 was dry and flowers were scarce in the region that summer. Many sunbirds congregated at the limited flowering *Leonotis* on the south shore of Lake Naivasha, where some of the sunbirds were strongly territorial. We obtained most of our data on territorial males at this time. We also obtained two sets of data from undefended flowers. The rest of our data from nonterritorial situations were obtained in 1975, which was a wetter year with more insects and flowers. The flowers generally were not defended by sunbirds.

One of the species regularly attracted to *Leonotis* flowers in the Rift Valley was the Golden-winged Sunbird, *Nectarinia reichenowi,* which is a large (15 g) species that often defends feeding territories (Gill and Wolf 1975). Golden-winged Sunbirds competed most intensely with three other sunbird species for the nectar of *Leonotis nepetifolia* in our study areas: the Bronzy Sunbird, *N. kilimensis,* a large, resident, montane species (17 g) that is behaviorally dominant to the Golden-winged Sunbird; the Malachite Sunbird, *N. famosa,* a medium-sized (13.5 g), montane sunbird that is (locally) highly nomadic and behaviorally subordinate to the Golden-winged Sunbird; and the Variable Sunbird, *N. venusta,* a small (7 g) subordinate species that feeds opportunistically at a variety of flowers. Elsewhere we have compared the foraging efficiency of these species at *Leonotis nepetifolia* (Gill and Wolf 1978). We also have described the flower and nectar characteristics of *Leonotis nepetifolia* (Gill and Wolf 1975, 1977, 1978; Gill and Conway 1979).

We studied competition among sunbirds feeding in large fields of high density, flowering, *Leonotis* plants (10–30 inflorescences/m^2) by marking up to 40 stalks and 100 inflorescences randomly throughout 50 m^2 undefended plots or territories. We counted the number of flowers on each marked inflorescence. We then recorded the time and identity of all visitors to the marked inflorescences during a continuous 4-h morning observation period, usually starting at 0800. We recorded the time of each visit to the nearest minute and, to reduce sampling errors, analyzed data only for observation periods when male or female Golden-winged Sunbirds visited at least 100 flowers on marked inflorescences. If two different males each visited 100 flowers, we calculated their nectar uptake and losses separately.

We assume nectar accumulates at 0.7 $\mu l \cdot flower^{-1} \cdot h^{-1}$ from 0700–1100 and 0.35 $\mu l \cdot flower^{-1} \cdot h^{-1}$ from 1100–1300. The average production/accumulation rates in intact flowers without nectar varied from 0.57 to 0.87 $\mu l \cdot flower^{-1} \cdot h^{-1}$ (Gill and Wolf 1975). Some of this variation was the result of sampling error; some reflected real differences. Nectar production may vary with age of inflorescence or flower, sun exposure in old plants, and high nectar volumes in some flowers (Gill and Conway 1979). We were unable to control all these variables in our studies of nectar production and especially in our monitoring studies of marked inflorescences. We assume instead that sunbirds experienced averages close to our average values because

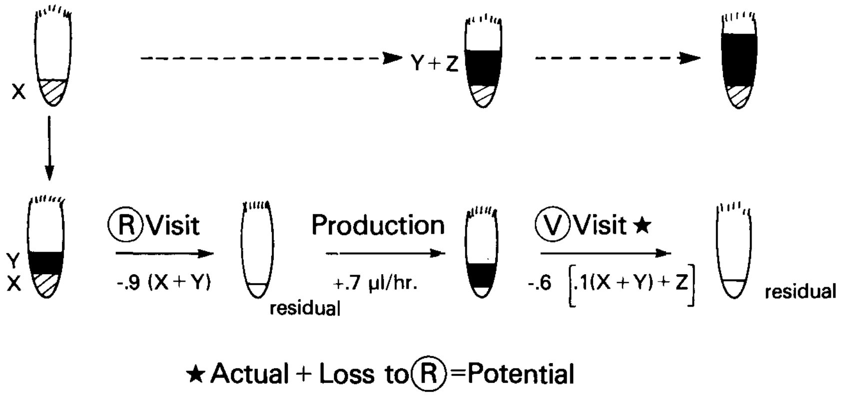

Fig. 1. Diagrammatic scheme for estimating nectar uptake and losses from marked, monitored, *Leonotis nepetifolia* flowers. X is the average volume in flowers on the study plot at the beginning of the 4-h observation period. Y and Z are volumes accumulated during the observation period at an average rate of 0.7 μl·flower^{-1}·h^{-1}. When a sunbird visits a marked flower, it removes a known fraction of the amount of nectar present, 90% in the case of *N. reichenowi* Ⓡ and about 60% in the case of *N. venusta* Ⓥ.

of the large number of flowers they visited in the course of normal foraging. The average of 0.7 μl·flower^{-1}·h^{-1} was a consistent result obtained in both 1973 and 1978.

We measured the nectar in 50 flowers, one per inflorescence, at the beginning of the observation period. We then translated the field data on time and identity of visitors to marked inflorescences, the number of flowers on those inflorescences, and the starting nectar volumes into estimates of *Actual Uptake, Loss to Competitors,* and *Potential Uptake* (Fig. 1).

Actual Uptake from previously unvisited flowers (U_o) in microliters was calculated as

$$U_{oj} = \sum_{i=1}^{n} R_j(V + tA)m_i,$$

where V is the average nectar volume per flower at the start of the observation period, t is the time in hours since the start of the observation period, A is the nectar accumulation per hour since the start of the observation period, m_i is the number of flowers on the ith inflorescence, and R_j is the usual fraction of available nectar removed from these flowers by each sunbird species (denoted by the subscript j). R_j is assumed to be 0.90 for *N. reichenowi,* 0.82 for *N. kilimensis* and *N. famosa,* and 0.62 above 1 μl per flower for *N. venusta* or 0.22 below 1 μl per flower (see Gill and Wolf 1978).

Actual Uptake from inflorescences that were visited previously during the observation period (U_v) was calculated as

$$U_{vj} = \sum_{i=1}^{n} R_j(L + tA)m_i,$$

where L is the residual nectar left in the flower by a previous visitor and tA is the nectar accumulation since the last visit. Considering all flower visits during the course of the observation period, Actual Uptake per flower by subclass k of *reichenowi* individuals then is

$$U_k = (U_{ok} + U_{vk})M_k^{-1},$$

where M_k is the total number of flower visits by that subclass during the observation period.

Losses to Competitors (*C*) by Golden-wing subclass *k* to competitors of category *j* were calculated as the amount of nectar obtained by previous visitors of category *j* from flowers visited by Golden-wings, corrected for Golden-wing's removal fraction (0.9, and divided by the total number of marked flowers they visited during the observation period, or $C_j = 0.9\ U_jM_k^{-1}$. Total losses to all competitors by Golden-wing subclass *k* then were

$$C = 0.9\left(\sum_{j=1}^{n} U_j\right)M_k^{-1}.$$

We partitioned losses among previous visitors to the same flower and did not attribute such losses simply to the last preceding visitor.

The distinction between previous visits to a particular flower by the same or different individuals affects these calculations of nectar lost to competing individuals. If a flower was visited twice by unbanded and otherwise indistinguishable sunbirds, it is possible either that they were the same individual, in which case no competitive loss occurred, or else that they were different individuals, in which case some nectar was lost by the second visitor to a competitor. Because we are concerned with losses by Golden-wings, this problem only involved loss to other Golden-wings of the same sex. We usually could not distinguish different unbanded female Golden-wings. Many different male Golden-wings were distinguishable, however, by differences in plumage color, molt, age characters, length of tail, etc. To account for unmarked foragers, we calculated both maximum and minimum values for conspecific, consexual loss. Maximum loss (C_x) assumed that all prior visits by indistinguishable individuals were, in fact, by different individuals and thus resulted in true competitive losses. Minimum losses (C_n) assumed that all previous visits to particular flowers by indistinguishable individuals were, in fact, by a single individual and thus did not include nectar obtained on these flower visits as losses.

Potential Uptake (*P*) was the sum of Actual Uptake plus all Losses to Competitors, or $P = U_k + C$. It was thus the amount of nectar a subclass of Golden-wings would have obtained from the flowers it visited *if* no other individuals had fed previously at those flowers.

We assumed that all flowers on an inflorescence had the same volumes (Gill and Wolf 1977) and that all were visited. Sunbirds feeding at *Leonotis* flowers perched below the inflorescence and spun around quickly inserting their bill into each adjacent flower. They normally visited every flower only once. Sometimes, however, the sunbirds rejected a marked inflorescence after 1–4 flowers (see Gill and Wolf 1977). We did not include the flowers on rejected paws or their nectar content in any of the final calculations, because this is one way sunbirds avoid the impacts of competitive nectar losses. The costs of rejection are minimal (Gill and Wolf 1977).

LIMITATION OF METHODS

It seems prudent to consider potential limitations of some of our analytical assumptions. First, we assumed average nectar production rates, with the knowledge that there is some variation and that there may not always be a midday drop in

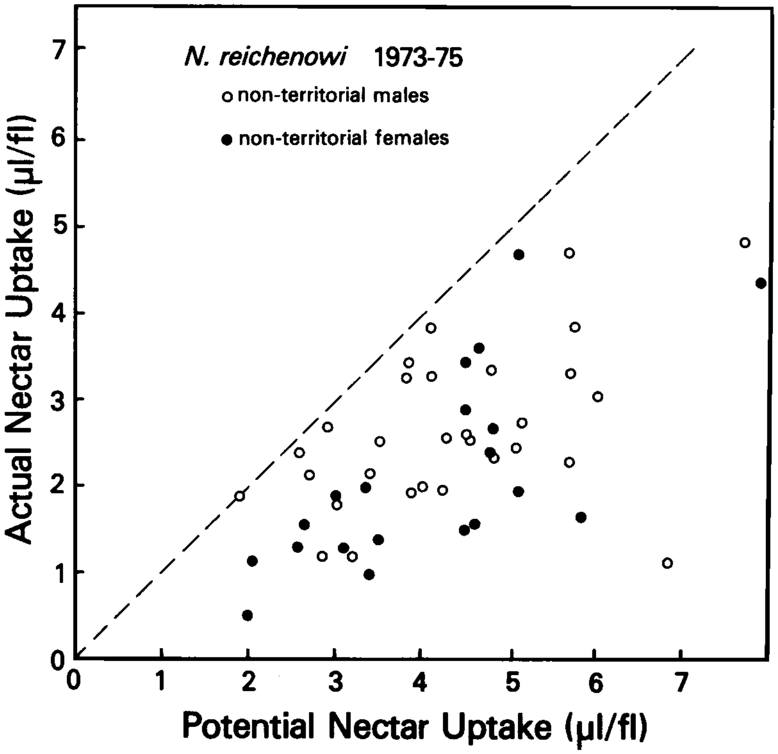

Fig. 2. Impact of nectar losses to competing sunbirds on nectar uptake of nonterritorial *N. reichenowi*. The Potential Uptake is the amount that would have been obtained from marked flowers if other distinguishable sunbirds had not also visited those flowers some time earlier during the observation period. Deviation from the line of equality is proportional to the extent of the average loss during a 4-h observation period.

nectar production. If the average production really was 1 $\mu l \cdot flower^{-1} \cdot h^{-1}$ instead of 0.7 $\mu l \cdot flower^{-1} \cdot h^{-1}$, both Potential and Actual Uptakes would be slightly higher than we estimated. But the average accumulation period between visits in our nonterritorial data was 72 min, meaning that the average intake per flower would have been only 0.36 μl higher than we estimated. This is within our calculated confidence limits. If nectar production from 1100 to 1300 really was 0.7 $\mu l \cdot flower^{-1} \cdot h^{-1}$, then the most a flower could accumulate would be 0.7 μl more than we calculated, if it produced for a full 120 min before a visit at the end of the observation period. Such flowers would normally comprise only a minor fraction of the total number of flower visits used to calculate the means, and this departure from our assumption would not cause a significant change in the mean values of Potential and Actual Uptake.

A potentially more serious problem is our use of average starting volumes. This assumption requires that the large number of flowers visited by the sunbirds averages out the starting volumes in relation to the probabilities of visitation by other sunbirds. This is reasonable. Distortions will result, however, if the sunbirds biased their visits towards fuller flowers, as territorial sunbirds sometimes do (Gill and Wolf 1977). Paw rejection also results in a similar bias away from low-yield flowers and may increase nectar gains on first visits to marked inflorescences above the assumed average starting volumes, thus increasing Uptake values (Table 1). Cor-

TABLE 1. Nectar Uptakes and Competitive Losses by Golden-winged Sunbirds (*Nectarinia reichenowi*) feeding at *Leonotis nepetifolia,* from data sets involving 100 or more flower visits. Losses expressed as percent of total potential nectar uptake ± standard error of the mean. Standard errors of percent loss data were calculated using arcsin transformations.

	Territorial	Nonterritorial	
Nectar	Males	Males	Females
Potential Uptake (μl/fl)			
Mean ± SE	3.89 ± 0.34	4.35 ± 0.24	4.10 ± 0.32
N, Range	15, 2.2–6.8	30, 2.6–7.7	20, 2.0–7.9
Actual Uptake (μl/fl)			
Mean ± SE	3.54 ± 0.37	2.67 ± 0.13	2.26 ± 0.24
N, Range	15, 1.2–6.4	30, 1.1–4.9	20, 1.1–4.4
Losses (% Potential) to			
N. reichenowi ♂♂	2.2 ± 0.48	min. 9.7 ± 1.35 max. 20.2 ± 2.01	22.8 ± 1.93
N. reichenowi ♀♀	4.1 ± 0.97	8.7 ± 0.92	min. 0.0 max. 8.4 ± 1.21
N. famosa	0.9 ± 0.27	9.1 ± 1.17	11.0 ± 1.30
N. venusta	0.7 ± 0.31	7.6 ± 1.03	10.4 ± 1.61
Other species	0.4 ± 0.25	0.6 ± 0.22	0.4 ± 0.15
Total	8.3 ± 1.23	min. 35.8 ± 2.37 max. 46.4 ± 1.96	min. 44.0 ± 2.35 max. 52.4 ± 2.85

rection for this error should increase the calculated percent losses due to competition, because first visitors get the most per flower and do the greatest damage to the foraging efficiency of subsequent visitors. Although the impact of each of these factors on the final calculations is diluted by the fraction of the total flower visits that were not affected, these factors should be considered in more detail in future studies. Their possible importance does reemphasize the final point that our calculations for this system are probably minimum estimates.

RESULTS

Nonterritorial situations.—Golden-winged Sunbirds usually lost a substantial amount of the potentially available nectar to competitors (Table 1, Fig. 2) during our morning observation periods. The minimum losses (C_n/P) during a morning varied from 0 to 83%, and averaged 36% for males and slightly higher (44%) for females. Competitors depressed average nectar levels in flowers visited by males from 4.4 μl/flower to 2.7 μl/flower (based on 30 data sets with 9,338 flower visits). Competitors depressed average nectar levels in flowers visited by females from 4.1 to 2.3 μl/flower (based on 20 data sets with 6,251 flower visits). There was no significant correlation in either sex between the percentage lost each morning and the Potential Uptake (Fig. 3).

Levels of intraspecific and interspecific competition were similar. Males lost a minimum of 18.4% ± 1.78% to other Golden-wings, the rest to Malachite (9.1%) and Variable sunbirds (7.6%). Losses by males to females were moderate (8.7%). Females lost a minimum of 22.8% to conspecifics (males only) and also suffered substantial losses to Malachite (11%) and Variable sunbirds (10.4%).

Maximum losses (C_x/P) by male Golden-wings to conspecific males might have been as high as 20.2% because of problems inherent in working with some unmarked individuals. We suspect, however, that these extra "losses," totalling 10.5%, mostly

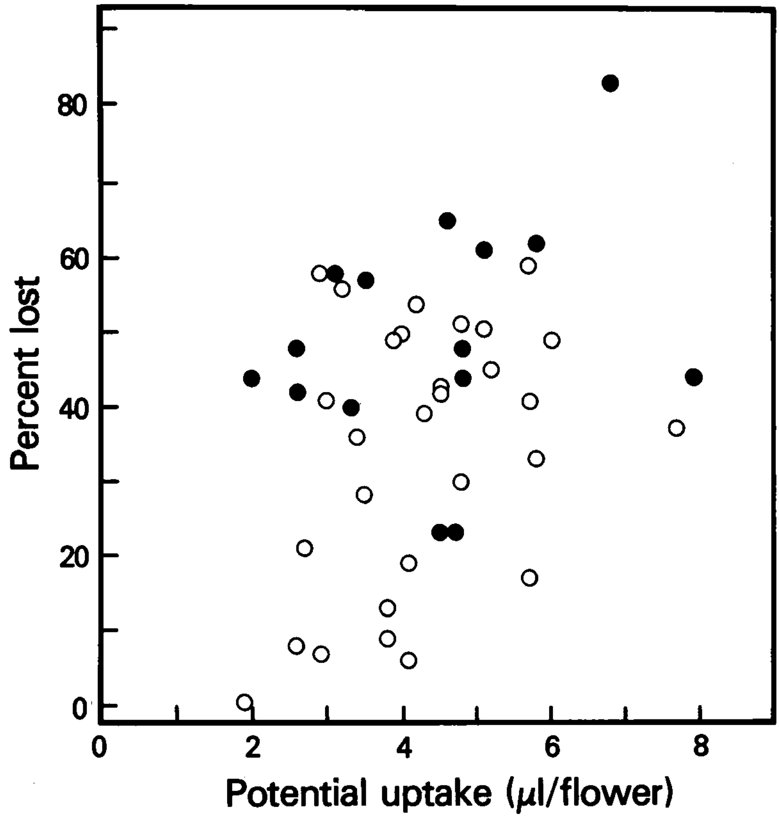

Fig. 3. Relationship between percent of nectar lost by nonterritorial Golden-winged Sunbirds and the maximum (Potential) uptake. Open circles indicate males; closed circles indicate females. Each point represents the average for one morning observation period.

involved nectar obtained on prior visits to particular flowers by the same individual. When known individuals fed repeatedly at the same flowers, their prior visits accounted for intakes or "losses" of the same magnitude as the amounts lost to "indistinguishable" individuals by unmarked males (see below, Table 2). Furthermore, because we were able to distinguish many different males, the chances were slight that additional, undistinguishable males were feeding in our plot, and the probabilities that any two of these would visit the same flowers were extremely low.

Minimum losses by females to other females were zero, because we assumed the presence of only a single feeding female during the observation period to calculate C_n. If all revisits to particular flowers were by different females, maximum losses to females were only 8.4%. Real losses to conspecific females were presumably between these two limiting estimates but were considerably less than among males. Thus we conclude that exploitative competition was greater among males than among females.

Territorial situations.—Territorial male Golden-wings lost some nectar to intruders that were not displaced before they fed. Average nectar volumes in flowers visited by territorial males were depressed by such competitors from 3.9 μl/flower to 3.6 μl/flower (based on 15 data sets with 8,991 flower visits). These losses were

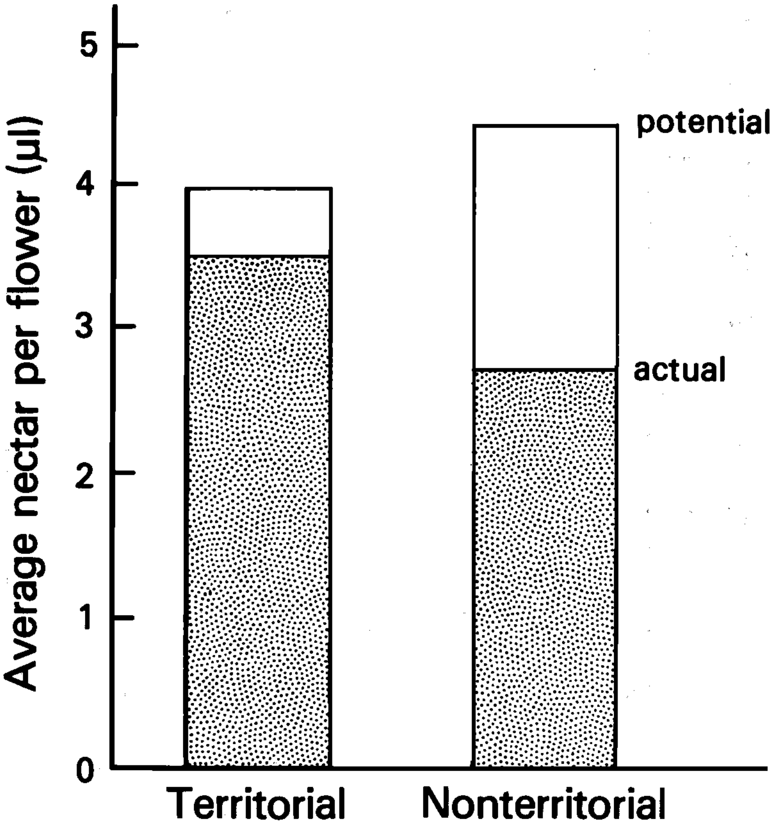

Fig. 4. Comparison of exploitative nectar losses by territorial and nonterritorial male Golden-winged Sunbirds. The territorial data were obtained mostly in 1973, the nonterritorial data in 1975. Average losses shown here were 8% for territorial males and 36% for nonterritorial males.

minor, however, the average total being only 8.3% compared to the minimum by nonterritorial males of 35.8% (Table 1, Fig. 4). No nectar was lost to competitors on four of the 15 mornings for which we have adequate data. Most of the nectar loss (6.3%/8.3%) was to conspecific individuals, especially to females (4.1%), which often fed persistently in a territory. A minor amount was lost to Malachite and Variable sunbirds, which were more easily displaced from the territory. On one day, a male Bronzy Sunbird fed briefly without interference and removed 4.5% of the territorial male's Potential Uptake, but no significant amounts of nectar were lost on other days to this dominant species. Actual Uptakes by territorial males varied from 1.2 to 4.4 μl per flower ($\bar{U}$ = 3.6 μl). The lowest values, below 2 μl/flower, occurred just prior to abandonment of territories.

Known individuals feeding repeatedly at the same flowers lowered their own foraging efficiency. They revisited the same inflorescences 3–5 times during a morning, which increased the number of flower visits but not the total amount of nectar they obtained. Thus, they reduced their average uptake per flower visit. If we divide the total nectar uptake by a color-marked Golden-winged Sunbird by the minimum number of different flowers it visited, we can estimate the sunbird's hypothetical uptake per flower without revisitation (Table 2). We exclude from this analysis se-

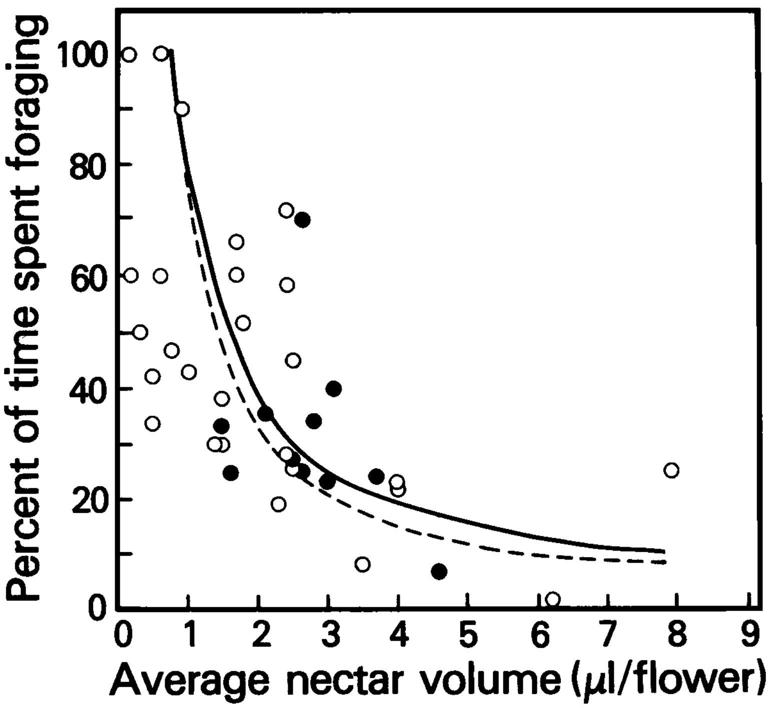

Fig. 5. Relation between foraging effort of male Golden-winged Sunbirds and average nectar availability per flower. Open circles represent 1-h observation periods; closed circles indicate 4-h observation periods. Nectar availability was measured in a sample of 50 flowers. The solid line is the calculated power curve fit for these data, or $Y = 44.27X^{-.58}$. The dashed line is the relationship assumed in previous studies (Gill and Wolf 1978).

quential visits to the same flowers by a marked individual that were interrupted by visits of another individual, because waiting to feed at those flowers would not have increased the nectar obtained.

Territorial male Golden-wings reduced their average uptake per flower by 29% (range 10–63%) because of multiple visits to the same flowers (Table 2). Marked sunbirds accounted for rather few of the flower visits we recorded in nonterritorial situations. In the eight analyzable cases, they reduced their average uptake per flower visit by 24% (range 7–60%) by revisiting certain flowers. The difference between territorial and nonterritorial males is not significant.

A bird must forage longer each day to maintain its 24-h energy balance when its rate of net caloric gain is lower (King 1974, Wolf et al. 1975). Accumulating adequate reserves to cover overnight energy expenditures is an especially important component of daily foraging effort (King 1972, Wolf and Hainsworth 1977). Elsewhere we have estimated the foraging time requirements for different average nectar levels encountered by Golden-winged Sunbirds feeding at the flowers of *Leonotis nepetifolia* (Gill and Wolf 1975, 1978). Our field data (Fig. 5) support the negative hyperbolic form of this relationship.

Moreover, the calculated curve fit for the data is nearly identical to the relationship we have assumed in earlier studies (Gill and Wolf 1978). While not suggesting a significant difference between the two, we remind you that to the degree the sunbirds

TABLE 2. Effect of flower revisitation by known individuals on average nectar uptake per flower.

		Number of flower visits[a,b]		Nectar uptake (μl/fl)[b]		
	N	Potential minimum	Actual	Potential with no revisits	Actual	Percent reduction
Territoral	15	467 ± 67	678 ± 89	4.8 ± 0.37	3.4 ± 0.33	29.0 ± 2.5
Nonterritorial	8	332 ± 36	478 ± 72	3.8 ± 0.51	2.7 ± 0.26	24.4 ± 6.3

[a] The difference between Actual and Potential minimum is the number of revisits to particular flowers. The Potential minimum is the number of different flowers visited at least once.

[b] Values shown are means ± SE.

actually feed longer than the minimum predicted time at a particular nectar availability, they improve their daily energy budgets and may be able to accumulate surpluses as storage. Wolf (1975) obtained a similar relationship between foraging time and the average nectar obtained from *Aloe* flowers. These data support the important assumption that foraging time of these sunbirds is a variable influenced by average nectar availability.

The Competitive Losses, i.e. the differences between Potential and Actual Uptake, will influence the total foraging time required to maintain a balanced 24-h energy budget (Wolf et al. 1975). If the values we have calculated for our observation periods are representative for the entire day, we can calculate how much the foraging time would have to increase to account for the Losses to Competitors. For nonterritorial males the Potential Uptake would require 15% of the daylight hours spent foraging, while the Actual Uptake requires 25%, an increase of 72%. For females, the increase is 116%, from 16% foraging time for the Potential Uptake to 35% foraging time for the Actual Uptake (Fig. 6). Territorial males required only a 17% increase from 18% to 21%. Values for individual birds range from no increase to 812% increase, from 8.2% foraging time for Potential Uptake to 65% foraging time for Actual Uptake.

DISCUSSION

Sunbirds feeding at *Leonotis nepetifolia* in the Rift Valley in July/August are subject to varying amounts of competition for food. This is a season of generally poor flower availability in the highlands, and large numbers of young expand population sizes following breeding during the rains in April/May (Van Someren 1956). Consequently, many Golden-winged Sunbirds and Malachite Sunbirds move into the valley and congregate in large numbers in fields of flowering *Leonotis nepetifolia,* even though this is not the flowering plant they prefer (Gill and Wolf 1978; Gill unpubl. data). Their intrinsic foraging efficiency is greater at other flowers such as *Aloe graminicola* (Liliaceae) and *Leonotis mollissima,* and they tend to breed in association with these flowers rather than with those of *Leonotis nepetifolia.* They feed at *Leonotis nepetifolia* in July because other flowers are not available.

The level of exploitative competition experienced by Golden-winged Sunbirds under these conditions often is substantial and apparently necessitates a major increase in the foraging time required for self-maintenance. Changes in foraging time budgets are nonlinear, because they depend on the Potential Uptakes as well as the absolute levels of losses. Losses at high starting volumes may have virtually no effect on the time budget, while the same loss at a low starting volume may require a

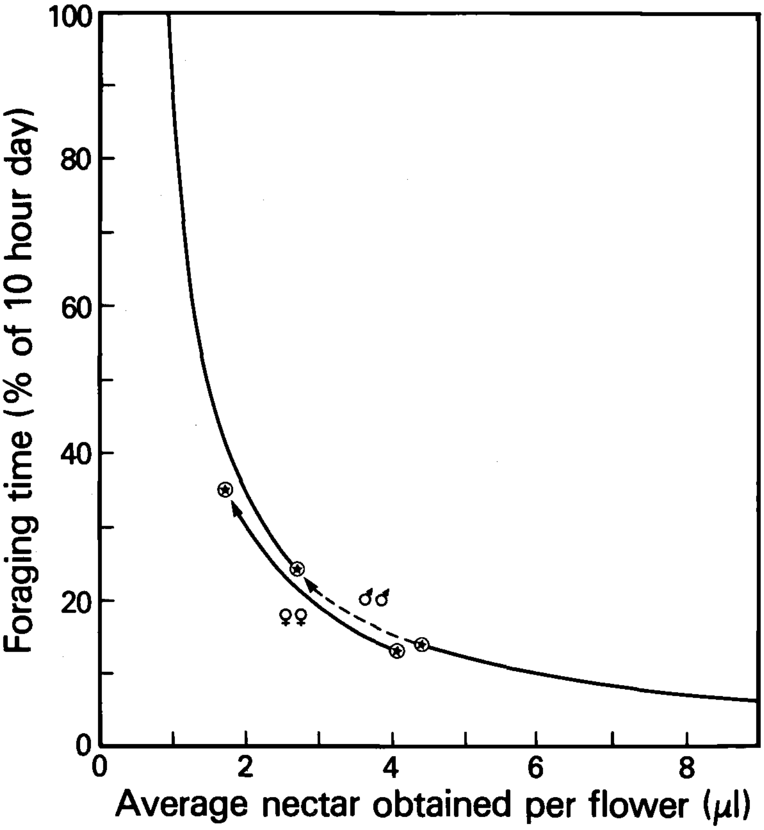

Fig. 6. Impact of nectar losses on foraging time budgets by nonterritorial *N. reichenowi* to competitors. The foraging time budgets here are hypothetical values required to maintain a balanced energy budget. Loss of nectar decreases the average obtained per flower visit and increases the number of flowers that a sunbird must visit to obtain a specified amount of energy each day, including the costs of the additional foraging. Because females are smaller, their costs are lower, and they can forage less each day than males at a particular nectar volume. Females tend to lose more nectar to dominant individuals, however, and must forage longer each day.

major increase in foraging time. Perhaps the extreme conditions of nectar availability correspond to definitions of "limiting" versus "nonlimiting" resources, but we must recognize that the ecological consequences of varied resource availability involve graded continua. Although these values are calculated here only for Golden-winged Sunbirds, similar measures are possible for all species, the general shape of the curves remains the same, but the constant and exponent of the equation will vary with body size and bill-corolla interactions (Wolf et al. 1975, Gill and Wolf 1978). The basic similarity of the curves, however, means that this type of exploitative competition has a nonlinear effect on foraging time.

Ecologists usually conceptualize competition among organisms as the effect of individuals on the ability of others to survive and reproduce. The Lotka-Volterra equations assume that the addition of individuals produces a linear decrease in the growth rate of the affected population (McNaughton and Wolf 1979). Somewhat more complicated equations (e.g. Smith, 1963, and Wiegert, 1975) incorporate nonlinearities into the effect of competition and probably are more realistic (Smith-Gill and Gill 1978). The potential causes of nonlinearities are many, ranging from a subset of conditions that are nonlimiting (Caperon 1967) to variations in the impact of the limiting resource with changing resource and/or population density. Before we can incorporate these interactions into a more general model of community and ecosystem organization, it is important to recognize and understand their possible causes.

We do not yet know how much nectar loss affects an individual's survival or reproductive success. We assume that these must be negatively related to the minimum foraging time required for self-maintenance, because the longer a bird forages simply to maintain itself, the less time it has for reproductive activities, and the less able it is to avoid adverse climatic exposure or predation hazards, to undertake high-cost activities that jeopardize energy balance, or to build up its energy reserves (Schoener 1971, Gill and Wolf 1978, Gill 1978, Wolf 1978). In other systems the fitness of potentially polygamous males seems to be correlated with low foraging time budgets, which in turn are made possible by high territory quality (Verner and Englesen 1970).

Aggressive interference buffers the individual against some negative effects of competition for nectar. A nectar-feeding bird can both "guarantee" the nectar required for maintaining its daily energy balance and also ensure certain levels of foraging efficiency by becoming territorial when the caloric costs of aggression are recoverable through improved foraging efficiency (Gill and Wolf 1975). Most of our data from territorial versus nonterritorial situations were obtained in different years when different conditions prevailed. In 1975, Golden-wings were able to obtain 2.7 μl of nectar/flower visit without defending those flowers. Our previous model for the economics of territorial defense suggested that, under these conditions, a territorial Golden-wing must obtain 4.0 μl/flower (at 2% defense time) to 5.5 μl/flower (at 3% defense time) from defended flowers to justify the costs of such aggression. Territoriality should not have been advantageous under these conditions because Potential Uptake itself averaged only 4.4 μl/flower, i.e. the nonterritorial behavior of the Golden-winged Sunbirds was consistent with our model's predictions. Conditions did vary from day to day, however, Occasionally, average Actual Uptake from undefended flowers was as low as 1–1.5 μl/flower, which should encourage occasional territoriality, as we observed.

The inefficiency of revisits seemed to be about equal among nonterritorial and territorial individuals in terms of percent reduction of nectar volumes. Revisits and their consequent inefficiency may have any of at least three separate causes. First, the birds may not be able to keep track of where they have recently visited. This should be less of a problem for territorial birds feeding in localized areas (Gill and Wolf 1977). Second, to meet short-term energy demands the birds may not be able to forage at a flower once a day. These birds forage about once every 15 min and visit several hundred flowers on a foraging bout. To maximize efficiency the bird would have to let the nectar accumulate until it had nearly reached the maximum total accumulation for that flower's life span. A sufficiently clever bird on a territory with enough flowers could make the rounds of the flowers just as they reach the maximum accumulation. Any mistakes from this perfect timing would reduce the efficiency, as mentioned above. The third reason is also important in this regard. The longer a bird waits to visit a flower, the greater the chance that another bird will visit that flower and deplete the nectar. Thus, a foraging bird should have some optimal revisit timing that incorporates both the accumulation rate and the increasing probability of loss at the flowers. Reduced foraging efficiency that results from revisitation as a response to the probabilities of competition should be considered an additional cost of exploitative competition.

Local instability characterizes the sunbird-flower system examined in this paper as it does many nectar-feeding bird assemblages (Wolf and Gill 1979). In the first place, fields of *Leonotis nepetifolia* in the Rift Valley are a recent by-product of modern agricultural methods and maize crop rotations in this area; it is unlikely that *Leonotis nepetifolia* was nearly as abundant prior to the expansion of agriculture at these altitudes in the last 50–100 years. Second, these aggregations of feeding sunbirds last only 1–2 months at any locality, largely because that is the flowering period of the plants themselves (Gill and Conway 1979). Also, there is considerable daily or weekly turnover of individuals within the aggregation, even though some individuals do remain for weeks. Stable coexistence of the different species is a more complex function of their relative success on a larger geographical and temporal scale than we studied in this one situation. Ultimately, we must take into account the variety of seasons, localities, flower systems, and mixtures of competing species usually encountered in the course of the annual cycle. Yet, in some years, the Rift Valley *Leonotis* systems probably are what Fretwell (1972) has called the "limiting season."

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