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## ECONOMICS OF FEEDING TERRITORIALITY IN THE GOLDEN-WINGED SUNBIRD<sup>1</sup>

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**Abstract.** Feeding territories of Golden-winged Sunbirds contain enough energy to support an individual's daily energy requirements, and the amount of nectar per flower inside a territory tends to average higher than in adjacent undefended flowers. When undefended nectar levels are low (especially below 2  $\mu$ l per flower) the costs of territorial defense can easily be offset by energy saved from shortened foraging time budgets made possible by feeding at the higher average nectar levels. At higher undefended nectar levels the costs of territorial defense should not be recoverable. The balance between these costs and gains appears to define the conditions when territorial defense in this species is advantageous.

**Key words:** Aggression; behavior; energetics; foraging; nectar; sunbird; territoriality.

### INTRODUCTION

In recent years the adaptive nature of behavioral interactions between organisms has become increasingly clear. Such phenomena as coloniality, territoriality, and flocking all seem to adapt organisms to particular patterns of resource availability or predator avoidance (Crook 1965, Lack 1968, Brown and Orians 1970, Schaller 1972). Our understanding of the patterns of territoriality in birds, in particular, has benefited greatly from the concept of economic defendability (Brown 1964), which suggests that territoriality will be manifest when a needed resource is physically defensible and when the costs of defense are exceeded by the resulting gains.

It is now generally accepted that territories function to provide the aggressive individual with an adequate supply of some critical resource, often food (Brown 1964, Schoener 1968, Brown and Orians 1970). Defense of flowers by nonbreeding nectar-feeding birds, in particular, seems to be an adaptive response to limited food resource availability (Pitelka 1951, Wolf 1969, Stiles and Wolf 1970, Stiles 1971). It is a way the bird can restrict access by competing individuals to nectar that it requires, and is in this sense a very simple form of interference competition that is directly adaptive in terms of individual fitness (Gill 1974).

Nectar-producing flowers are often defendable in terms of their physical characteristics because they provide a site-specific renewable resource (Wolf and Hainsworth 1971). How defendable they are

in terms of the time and energy budgets of the territorial individual depends on the ratio of energy saved by gaining exclusive use of a feeding area to the energy expended in defending that area (Stiles and Wolf 1970, Wolf 1970). Because territoriality tends to space feeding individuals on fixed sites and to reduce the number of individuals feeding at a particular set of flowers, it should increase food availability to the defender in terms of both density (amount of nectar per flower as well as plant density) and predictability. Such changes should tend to increase the territorial individual's foraging efficiency.

Measurement of costs and gains is implicit in any evaluation of whether aggressive behavior is economical, but it has rarely been practicable in nature. However, advances in the study of nectar-feeding birds (Pearson 1954, Stiles 1971, Wolf and Hainsworth 1971, Hainsworth and Wolf 1972) have made possible the evaluation of their aggressive behavior in energetic terms. In the course of our studies of the behavioral ecology of African sunbirds (Nectariniidae), the ecological counterparts of hummingbirds, we examined several aspects of feeding territoriality of the Golden-winged Sunbirds, *Nectarinia reichenowi*, a common montane species in Kenya. Because the territories were small and easily defined, this system was amenable to measurement of the caloric costs of aggression, of the foraging behavior of the resident, and of the nectar available to it. Use of this information has enabled us to evaluate the adaptive value of territorial behavior in this species in terms of the balance of energetic costs and gains.

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FIG. 1. Stalks of *Leonotis nepetifolia* near Lake Naivasha, Kenya.

## METHODS

### Study area

Field work was conducted primarily in the vicinity of Hell's Gate near the southern edge of Lake Naivasha (altitude 1,930 m), 16 km ssw of Naivasha, Kenya. Initial, preliminary observations were made in July 1971, followed by intensive studies in March–April 1972, and July–August 1973.

The study area consisted of about 50 ha of flowering *Leonotis nepetifolia*. At times the area was occupied by over 2,000 feeding sunbirds, the largest concentration we have ever observed. In 1973 (following a prolonged period of limited rainfall) flowering *Leonotis* was reduced compared to previous years and was restricted primarily to shaded lake edge areas.

### The flower

*Leonotis nepetifolia* (Labiatae) is a common montane annual weed along roadsides and in early secondary successional fields in the Rift Valley region of central Kenya. This species is not found below 1,650 m elevation and is replaced rather abruptly above 2,300–2,450 m by *L. mollissima*, a bushy

perennial that occurs in later stages of succession than *L. nepetifolia*, particularly along the edges of montane forest. *Leonotis nepetifolia* grows after heavy local rains. An individual plant usually blooms for 1–1½ mo (depending on the continuity of the rains), and particular patches may reseed themselves and persist for several years.

The flowers are about 35 mm long, bright orange, and tubular. These features, as well as the curvature of the corolla and the lack of a lower lip, all seem to be adaptations for bird pollination. Nectar is produced and stored at the base of the corolla. Flowers are produced daily on one or more ball-like inflorescences on tall stalks (Fig. 1). Within each inflorescence open flowers are arranged in rings that appear first at the top of the ball and then progressively lower. Flowers fall out about two days after emergence. Normally, all the flowers of a ring are visited during a single sunbird visit; the sunbird simply spins around the stalk probing successively into adjacent flowers.

The concentration of sugar in the nectar was measured in the field in terms of percent sucrose equivalents with a temperature-compensated hand refractometer. Laboratory analyses (Hainsworth, unpubl. data) of the *Leonotis* nectar showed that glucose, fructose, and sucrose were the only sugars present. The caloric values of glucose and fructose solutions are about one-half that of an equimolar sucrose solution. Since the refractive indices of glucose and fructose solutions are also about one-half that of an equimolar sucrose solution, it is possible to read the refractive index of any mixed solution in terms of sucrose equivalents (Hainsworth and Wolf 1972). We assume a 100% assimilation efficiency of these sugars (Hainsworth 1974).

The sugar concentration of *L. nepetifolia* nectar averages 18% sucrose equivalents (mean 18.36, SE 0.18, range 14.7–21.7), which is an 0.52 molar solution containing 0.7 cal/μl. There is no change in average concentration during the day.

We assayed nectar production in 1973 by bagging an inflorescence immediately after a feeding sunbird visited all the flowers on it. Except in the very early morning, flowers examined just after a sunbird visit contained no nectar. Production was measured as the accumulated nectar volumes in flowers after 2 h, 4 h, or overnight. Early morning production was adjusted for residual nectar volumes. Initially in 1972 we measured nectar production by taking a baseline average nectar volume in flowers being visited by sunbirds and then measuring the difference between this value and that of bagged inflorescences. The two methods produced similar results.

Nectar production rates average about 0.7 μl per

flower per hour in the morning (0700–1100 h) (Fig. 2). Midday (1100–1300 h) production rates average lower, about  $0.3 \mu\text{l}$  per flower per hour. Average nectar production increases again in the early afternoon—on some days to as high as  $0.7 \mu\text{l}$  per flower per hour, but on other days to only about  $0.4 \mu\text{l}$  per flower per hour. These measurements of nectar production rates represent overall averages of large sets of flowers that vary in age and probably also in nectar output.

The total nectar energy production per flower per day (0700–1800 h) is obtained from our nectar production rate data. A flower producing nectar at average rates should produce 4.0 cal per day (Table 1). On days with consistently high production this could increase to about 4.4 cal per day, but on days of poor nectar production this may drop to 3.3 cal per flower per day.

We measured nectar volumes in individual *Leonotis* flowers by squeezing the nectar from the base of the corolla into a 25- $\mu\text{l}$  capillary tube. Nectar availability was measured by cutting inflorescences (1972) or randomly plucking single flowers from inflorescences (1973) throughout a territory and calculating the average nectar volume per flower. We counted the number of flowers on a territory by tallying the number of inflorescences with 1, 2, 3, etc. flowers.

#### The birds

Flowering *Leonotis* serves as a nectar source for sunbirds, often in large aggregations. The sunbirds include most of the species found at montane altitudes in Kenya, and occasionally some species from adjacent lowlands. One sunbird, *Nectarinia reichenowi*, the Golden-winged Sunbird, is closely associated with flowering *Leonotis* and feeds only infrequently on other flower species. This sunbird is restricted to highland areas of East Africa above 1,650 m (Mackworth-Praed and Grant 1960) and has a geographical distribution similar to that of *Leonotis*. A large species (15 g), it differs conspicuously from other sunbirds in having a more decurved bill and large yellow patches in the wing and tail, as well as an unfeathered groove extending

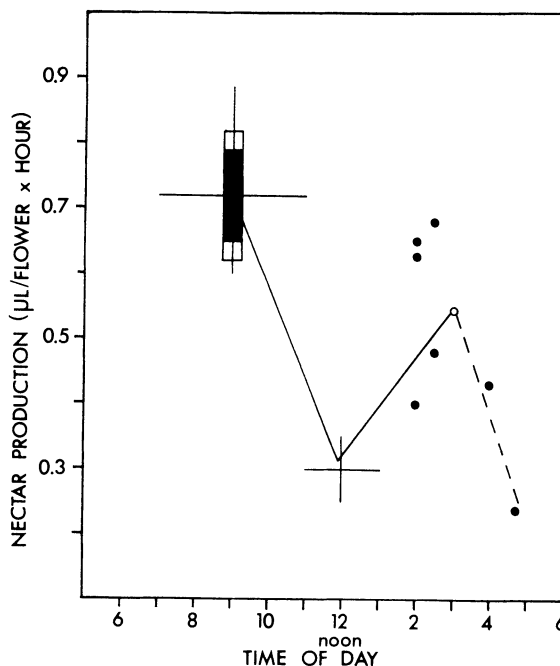


FIG. 2. Nectar production rates of *L. nepetifolia*. Horizontal bar = mean for time covered; vertical bar = range; open rectangle = one SD from mean; closed rectangle = 95% confidence interval.

from the base of the bill up the forehead. This groove apparently carries pollen of *Leonotis* (Friedmann and Stager 1969).

We delimited territories by watching a territorial individual. Many of these were marked with unique color band combinations, but even unmarked birds could be followed continuously for several hours because of the small size of the territory. After a preliminary observation period the territory boundaries were delimited with a string or marked with small pieces of tape. These markers were adjusted as necessary after subsequent observations. The flowers were counted and the territories measured after the morning observation period was completed.

Golden-winged Sunbirds are normally active from 0700–1700 h. Time budgets were calculated from the amount of time spent Sitting, Chasing, Foraging, Flycatching, Perch Changing, and Gone (Stiles 1971,

TABLE 1. Daily nectar production of *Leonotis* flowers

Time periods	Average			High			Low		
	$\mu\text{l}/\text{h}$	h	cal	$\mu\text{l}/\text{h}$	h	cal	$\mu\text{l}/\text{h}$	h	cal
0700–1100	0.70	4	2.0	0.80	4	2.2	0.60	4	1.7
1100–1300	0.30	2	0.4	0.30	2	0.4	0.30	2	0.4
1300–1600	0.55	3	1.2	0.65	3	1.4	0.40	3	0.8
1600–1800	0.25	2	0.4	0.25	2	0.4	0.25	2	0.4
Total			4.0			4.4			3.3

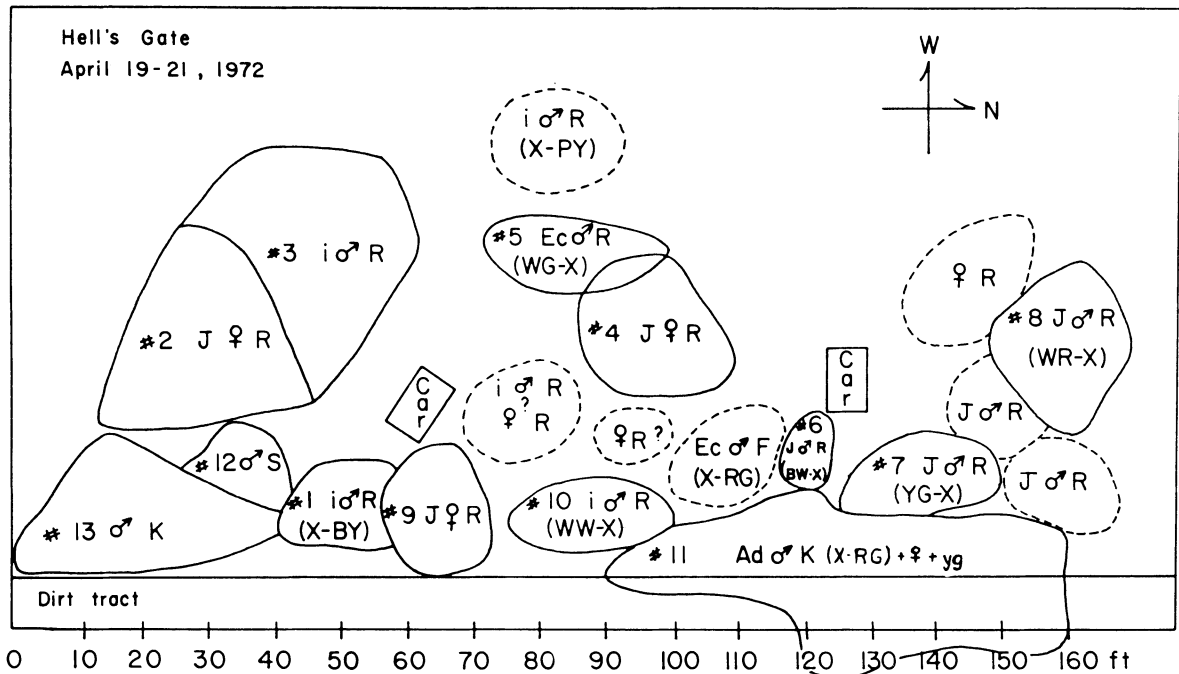


FIG. 3. Map of feeding territories defended by Golden-winged Sunbirds (R), Scarlet-chested Sunbirds (S), and Bronzy Sunbirds (K). Other symbols indicate age (ad. = adult, j = juvenile), sex class, color band combinations, and plumage (ec. = eclipse, a nonbreeding plumage common to many ♂♂).

Wolf and Hainsworth 1971) during morning observation periods of from 30 min to 3 h. Activity during these periods is assumed to be typical of a 10-h day (though see below). We recorded times using stopwatches read to the nearest 1.0 s. The percentages calculated for each category exclude from the total time that portion of the observation period when the sunbird was Gone.

We converted time budgets to energy budgets using known per gram metabolism of the similar-

sized *N. kilimensis* (Bronzy Sunbird) in four different activity levels (Wolf et al. 1975), and an average body weight for male *N. reichenowi* of 15.0 g. Standard metabolism, calculated from the equation  $\text{ml O}_2/\text{g} \cdot \text{h} = 7.93 - 0.17 T (^{\circ}\text{C})$ , is used for overnight metabolism, assuming a constant overnight temperature of 15°C from 1700 to 0700 h. Values from this equation are similar to those calculated from the thermal conductance equations of Herreid and Kessel (1967) using a body temperature of 41°C. Sitting costs are calculated from the equation  $\text{ml O}_2/\text{g} \cdot \text{h} = 13.3 - 0.33 T (^{\circ}\text{C})$ , separately for each of the 10 daylight hours from 0700 to 1700 using dry bulb shade temperatures. Calculated values for Sitting costs are 1.5–1.7 times standard metabolism at the same temperature (Wolf and Hainsworth 1971). Foraging costs are calculated from the equation

$$\text{ml O}_2/\text{g} \cdot \text{h} = 11.7 + 0.4 (\% \text{ time flying}),$$

which regression was obtained from metabolism studies of *N. kilimensis* that were actively hopping and flying. Sunbirds feeding on *Leonotis* in our study areas spent about 5% of a foraging bout in active forward flight and the rest hopping and feeding. The calculated cost of foraging is 1,027 cal/h for *N. reichenowi*. In all calculations we assume an RQ of 5.0. Flight costs are calculated as 3,000 cal/h for *N. reichenowi*.

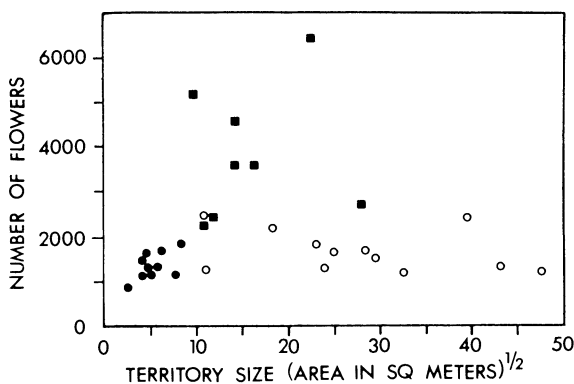


FIG. 4. Variation in the size and flower number of territories of the Golden-winged Sunbird. Open circles = territories studied in March 1972; closed circles = territories studied in April 1972; squares = July 1973 territories.



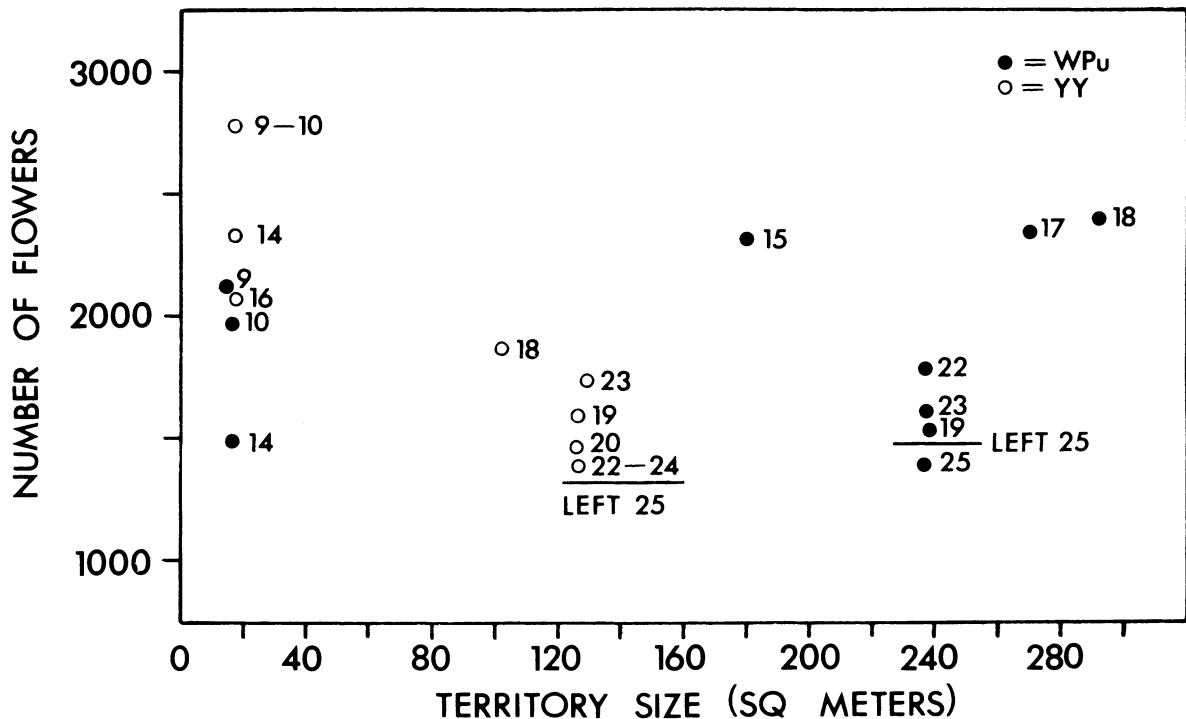


FIG. 5. Temporal changes in territory size and flower number of two Golden-winged Sunbirds. Numbers are dates in July 1973.

We measured the time a sunbird took to feed at *Leonotis* flowers by counting the number of flowers visited by an actively foraging bird within a measured time period. The total time in seconds accumulated on a stopwatch was divided by the number of flowers visited to obtain an average time per flower.

## RESULTS

### *Territory characteristics*

Golden-winged Sunbirds often establish feeding territories centered on flowering *Leonotis*. These territories are spatially limited sites in which the resident restricts use of the resources by other individuals (Rand 1967, Wolf 1969). Usually such territories involve only a single resident individual. Occasionally, however, a female coexisted with a male on a large territory and participated in its defense. Such sharing may relate to a complex, prolonged pattern of pair formation, but this phenomenon needs further study. Feeding territories may be defended by all age and sex classes of the Golden-winged Sunbirds, including juveniles. They are defended both intraspecifically and interspecifically against all sunbird species in the area. How effective the defense is depends in part on the dominance relationships of the intruding individual, e.g., persistent individuals of the slightly larger Bronzy Sunbird may feed successfully. Territorial individuals

usually defend their feeding territories throughout the day. The same male may defend the same set of flowers for several weeks, e.g., X-RG was territorial in the same place from 29 March to 15 April 1972. YY-YX and WPU-YX each defended their particular flowers continuously for 15 days in July 1973.

Spatial relations of the feeding territories of Golden-winged Sunbirds under conditions of high sunbird density at Hell's Gate are illustrated in Fig. 3. In this situation, most of the *Leonotis* was defended by Golden-winged Sunbirds, but a few territories were defended by *N. kilimensis*, *N. famosa*, and *N. senegalensis*.

Territory sizes varied greatly, ranging from 6.7 to 2,300 m<sup>2</sup> (Fig. 4). In March 1972 the territories along the edge of the *Acacia* woodland were larger and more variable in size than in April 1972, when the sunbirds were concentrated in peak densities in the open fields of *Leonotis*. Territories by the lake in July and August 1973 were intermediate in size. Regardless of territory size in 1972 the number of flowers counted on a territory tended to be between 1,000 and 2,500 (Fig. 4). This was also true for two territories that we followed for several weeks in 1973 (Fig. 5). In 1973 we counted the territories in a different area with few sunbirds (Fig. 4). The flower numbers in these were considerably higher

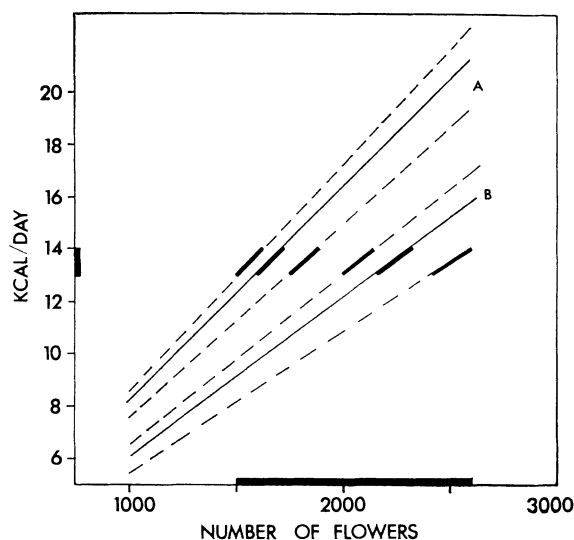


FIG. 6. Relation between flower number and total energy availability. Solid line indicates average daily production of nectar containing 4.0 cal per flower. Upper and lower dotted lines indicate production extremes of 4.4 and 3.3 cal per flower day. A—initial volume 6  $\mu$ l of nectar per flower at 0700 h; B—initial volume 3  $\mu$ l of nectar per flower at 0700 h.

(2,500–5,000) than in the other territories studied, possibly because of either the low level of competitive pressure or a difference in the quality of the plants.

As the rate of emergence of new flowers declined, reducing flower density, males increased the size of their territories, incorporating parts or all of adjacent territories. This was well illustrated by the changes in size and flower number observed on the terri-

ties of two males (YY-YX and WPu-YX) in July 1973 (Fig. 5). YY increased the size of his territory from 17 to 106 m<sup>2</sup> on 18 July, when the number of flowers on the previously defended area dropped below 2,000. He expanded it again the next day to 125 m<sup>2</sup> and defended that area until 25 July, when only 1,300 flowers remained. WPu expanded his territory on 15 July after the number of flowers in his core area dropped below 1,500 on 14 July and then again the next 2 days, keeping flower numbers more or less constant. When a peripheral clump of flowers that he used dried up on 21 July, he contracted his territory. On 25 July, when there were fewer than 1,500 flowers on this territory, he left, but established a new territory nearby, part of which included the area once defended by YY.

The diurnal energy content of a territory depends on (1) the total number of flowers, (2) the average production rate per flower during the day, and (3) the average energy contained in a flower at the start of the day. The average production rate per flower per day varied from 3.3 to 4.4  $\mu$ l, while the average initial nectar volumes varied between 3 and 6  $\mu$ l per flower. Figure 6 illustrates estimated nectar available per day in territories as a function of these conditions. Approximately 1,500–2,500 flowers are required to provide 13–14 kcal each day (Fig. 6); this corresponds to the sunbird's daily energy requirement.

#### Time and energy budgets

We obtained 21.5 h of time budget data from territorial Golden-winged Sunbirds defending *L. nepetifolia* territories (Table 2). Territorial indi-

TABLE 2. Time budgets of territorial Golden-winged Sunbirds<sup>a</sup>

Date(s)	Individual <sup>b</sup>	Total time (min)	Present (min)	Percent of time present spent				Changing perch
				Sitting	Foraging	Flycatching	Chasing	
1972								
29–30 March	X-GR	am	360	345	64.8	29.1	2.4	2.3
		pm	360	358	51.8	46.3	0.8	1.1
14–15 April	X-GR		208	198	67.2	26.7	2.0	2.8
		STUB	60	56	68.2	25.1	1.4	3.3
19 April	#1	♀	30	30	77.6	17.4	2.7	2.2
			30	30	68.6	28.8	1.1	1.4
			30	20	77.6	18.6	1.6	2.1
			30	30	68.5	28.6	0.1	2.7
			30	30	63.1	33.0	1.3	2.5
			30	30	75.5	22.0	0.0	2.5
20 April	#1	♀	30	29	76.5	19.5	1.1	2.8
			30	25	66.9	30.1	0.4	2.7
			30	30	79.2	16.9	1.1	2.8
			30	30	68.1	26.0	0.3	5.6
19–20 April	(combined)		300	284	72.0	24.2	1.0	2.8

<sup>a</sup> All from morning observation periods except one afternoon data set for X-GR on 29–20 March.

<sup>b</sup> Territories were occupied by a single ♂, or as indicated a ♀.

TABLE 3. Caloric energy budget of territorial Golden-winged Sunbirds<sup>a</sup>

Date	Sit	Forage	Fly			Total
			Changing perch + flycatch	Chase	Sleep (14 h)	
29–30 March <sup>b</sup>	2,592 (20)	2,989 (23)	1,140 (9)	690 (5)	5,649 (43)	13,060
14–15 April						
X-GR	2,688 (21)	2,742 (21)	960 (7)	840 (7)	5,649 (44)	12,879
STUB	2,728 (22)	2,578 (20)	690 (5)	990 (8)	5,649 (45)	12,635
19–20 April <sup>c</sup>	2,880 (24)	2,485 (20)	300 (2)	840 (7)	5,649 (47)	12,154

<sup>a</sup> Calories for each category calculated from time budget data in Table 2. Percent of total energy budget indicated in parentheses.

<sup>b</sup> Morning only.

<sup>c</sup> Calculations based on combined average time budget figures.

viduals normally spend 90%–100% of their time on their territories. When the short observation periods are combined, the birds were present 95% of the time, although individuals may be absent for as much as one-third of the shorter time periods. Foraging time averages about 24% (range 17%–33% in the morning) of total time present on a territory. Foraging time was longer (46%) in our one set of afternoon time budgets. Only about 1% of their time was spent Flycatching. Defense measured as actual chases comprised 1%–3% of the time budget.

Chase rates were highly variable, principally because of the hour-to-hour (or even minute-to-minute) fluctuations in the number of nonterritorial intruders trying to feed in a particular area. On 19–20 April under conditions of extremely high overall density, chase rates averaged 74 chases per hour (range 34–192) or about 3% of the time budget. Chases usually last only 1–2 s. Under conditions of lower sunbird density in July 1973, chase rates averaged 18/h (range 1–55) or less than 1% of the time budget.

Converted to energy budgets the time budget data suggest territorial Golden-winged Sunbirds utilize about 13 kcal/24 h (Table 3). Foraging costs were about 20% of the total 24-h expenditures or 40% of the daytime costs. Defense costs (= Chase) were about 6% of the total 24-h expenditure or 12% of the daytime costs. The value of 13 kcal/24 h is clearly an approximation based on a variety of assumptions including (1) that short-term time budgets reflect the bird's activities throughout the day, (2) that ambient temperature is a reasonable index of the bird's temperature relations with its environment, and (3) that body temperature is not lowered at night (cf. Cheke 1971, Wolf et al. 1975), which means that we may be overestimating Sleeping costs. If the figure for afternoon foraging time budget of 46% is typical, a minor increase of about 300 cal per day would have to be accommodated, but this is well within the range of error and observed vari-

ation. At present we do not have enough information on the occurrence or physiology of nocturnal body temperature drops in sunbirds to include possible savings in our estimate of total daily costs. Our approximation of total daily energy requirements corresponds well to the general relation between body size and existence energy (Kendeigh 1970). This value of 13 kcal also seems to be matched by that available on territories with 1,500–2,500 *Leonotis* flowers. Such close correspondence between requirements and availability gives us further confidence in the assumptions and metabolism equations used. In addition to nectar, Golden-winged Sunbirds of course eat insects, which supply both supplemental energy and critical amino acids, fatty acids, etc. not normally found in nectar in large quantities (Percival 1961, cf. Baker and Baker 1973).

#### *Nectar availability*

The amount of nectar in a *Leonotis* flower is determined by the length of time elapsed since the last visit by a sunbird and the rate of nectar production during that time. A flower that has never been visited will contain what nectar has accumulated since it emerged. A flower that has been frequently visited will be empty or nearly so. In large samples of flowers, as are present on a sunbird territory, the average amount of nectar per flower is determined by the average frequency of visitation per flower. Defense of a set of flowers should reduce the number of individuals feeding at those flowers, reduce the frequency that flowers are visited, and therefore increase the amount of nectar that accumulates in the average flower. If these result from territorial defense, nectar volumes inside a territory could average higher than nectar volumes in adjacent undefended areas.

We examined this possibility on 31 March–1 April (Fig. 7) and 21–23 April 1972 (Fig. 8), under conditions of high sunbird density and rigorous territorial



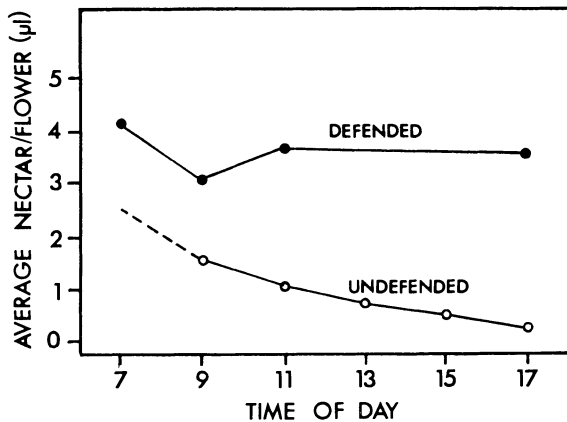


FIG. 7. Temporal patterns of nectar availability in flowers inside territories (defended) compared to adjacent undefended flowers on 31 March–1 April 1972.

defense. The samples were taken on successive days because we had observed little day-to-day variation in nectar production levels at this time, and assumed this to be true for the days in question. No differences in territorial activity, sunbird density, or weather conditions were apparent on these successive days. Average nectar volumes outside the territories were 2–4 times lower than inside the territories. Differences between defended vs. undefended nectar volumes at the same time of day were tested with a *t*-test (using the average value of each inflorescence).

In the data from 31 March to 1 April, the average nectar volumes inside vs. outside a territory were significantly different ( $P < .005$ ) at 0900, 1100, and 1700 h. The 1700-h nectar volumes were both measured on 31 March. In the data from 21 to 22 April, average nectar volumes inside territories were significantly higher than those outside territories ( $P < .005$ ). The average nectar volumes inside territories on 21 and 23 April at 0700 and 1200 h (using combined 1100- and 1300-h samples for 23 April) were not significantly different ( $P > .05$ ).

If the frequency of visits to the average flower is reduced by defense, the rate of cropping of nectar should also be lower and the average amount of nectar per flower should decline less rapidly in the course of the day than in undefended areas. This is the pattern we observed on 31 March–1 April (Fig. 7), when X-GR was defending a rather large number of flowers (2,700). The average amount of nectar per flower inside territories with fewer flowers declined more rapidly on 21 and 23 April (Fig. 8). Nectar volumes in undefended areas were lower at 0700 h and then were nearly constant at minimal values. We cannot rule out the possibility that the defended plants were of better quality in

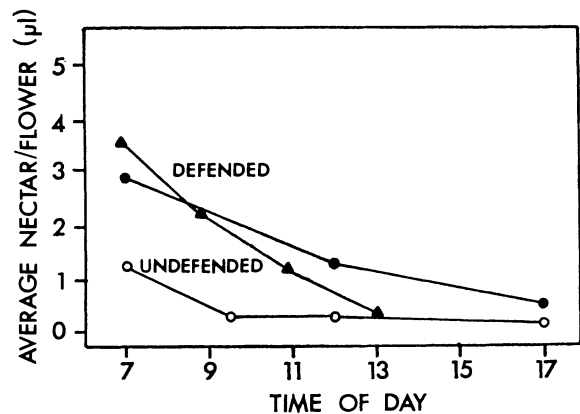


FIG. 8. Temporal patterns of nectar availability in flowers inside territories (defended) compared to adjacent undefended flowers on 21–23 April 1972. Closed circles 21 April; open circles 22 April; closed triangles 23 April.

terms of flower or nectar production than the undefended plants in the adjacent interstitial space, but this is unlikely because of the overall uniformity of the *Leonotis* patch. Also it seems probable that plants with more nectar would have been visited preferentially by other sunbirds if they had not been defended, and their nectar depleted to levels equivalent to the other flowers in the area.

#### Foraging efficiency

The cost of foraging at a single flower for a Golden-winged Sunbird was calculated as the average time per flower times the cost per unit time, which we assume to be 0.29 cal/s. An actively foraging sunbird averaged 1.5 s (range 0.9–2.3) per flower (Fig. 9), which costs 0.44 cal. Caloric gains per flower are a function of the average number of microliters of nectar obtained times 0.7 cal/μl. The achieved foraging efficiency is the ratio of calories gained to calories spent (Wolf et al. 1975). Thus, when a Golden-winged Sunbird feeds at *L. nepetifolia* flowers with 2.0 μl of nectar and takes 1.5 s/flower, it achieves a foraging efficiency of 3.2 (i.e., 1.4 cal/0.44 cal), or a net gain of 0.64 cal/s.

A sunbird that forages 25% of the daylight hours ( $10 \times .25$ ) must achieve an average efficiency of about 5 to obtain 13,000 cal, i.e., 13,000 cal/(2.5 h  $\times$  1,027 cal/h). This is the efficiency required to accumulate enough energy while foraging to cover all energy costs incurred during a 24-h day. A lower efficiency of about 4 would be adequate if the sunbird foraged slightly more each day than assumed here.

The relation between achieved foraging efficiency and nectar per flower is illustrated as a function of several different times per flower in Fig. 10. If the

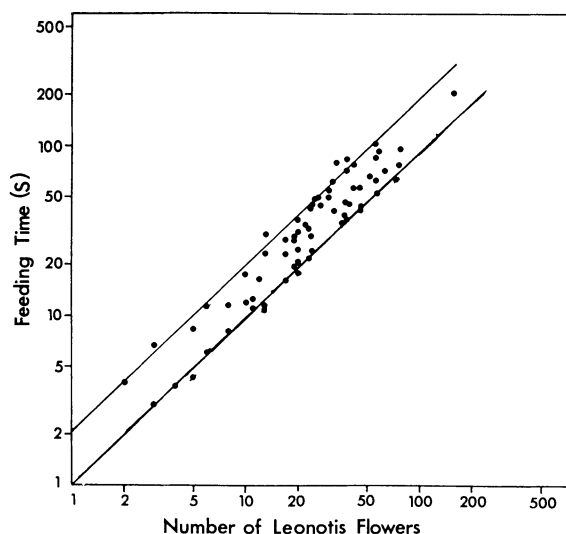


FIG. 9. Relation of total feeding time of Golden-winged Sunbirds to number of *Leonotis* flowers visited, including time between flowers. Data are for actively foraging individuals. The upper and lower lines indicate averages of 2 and 1 s per flower respectively.

bird averages only 1 s per flower it can achieve an efficiency of 5 at lower nectar levels than can a bird averaging 2 s per flower. The variation in average times per flower could be due to (1) the distance between plants or number of flowers on an inflorescence, (2) intensity of foraging, or (3) the amount of nectar extracted from the flower. We have not yet been able to separate the relative influence of these variables, except for an absence of any significant correlation between time per flower and the amount of time nectar had accumulated in the flower, which provided time measures for nectar volumes in the range illustrated in Fig. 10. For the observed range of foraging rates, *Leonotis* nectar levels of between 1.7 and 4.2  $\mu\text{l}$  enable a Golden-winged Sunbird to operate at an efficiency of 4–5.

#### Economics of defense

Actual defense costs of territorial Golden-winged Sunbirds tend to be about 900 cal per day ( $3\% \times 10 \text{ h} \times 3,000 \text{ cal/h}$ ). If the principal result of the defense investment is higher nectar volumes in the defended flowers it is appropriate to consider the relation between such nectar volumes and foraging costs.

A theoretical relation between foraging time budgets and nectar availability is illustrated in Fig. 11, where foraging is considered to be the percent of the 10 daylight hours required to obtain 13,000 cal of nectar. This model assumes that changes in foraging costs are balanced by changes in costs for other activities, such as defense, breeding, etc. Re-

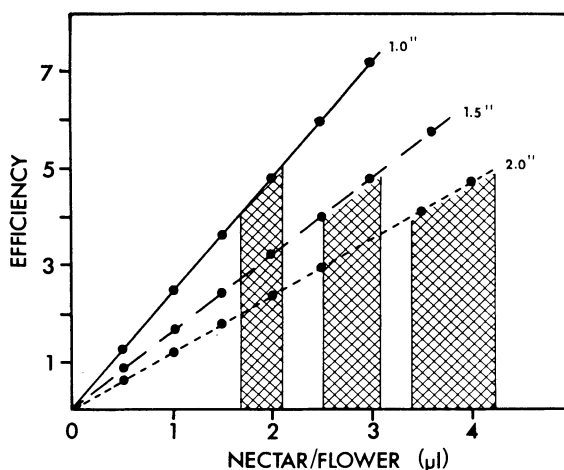


FIG. 10. Relation between foraging efficiency and amount of nectar per flower. Efficiency is calculated as the ratio of calories per flower assuming 0.7 cal/ $\mu\text{l}$  of nectar divided by foraging costs of 0.44 cal/s. Illustrated are three typical foraging times per flower (1.0, 1.5, and 2.0 s). Efficiencies of 4–5 are theoretically required to maintain a neutral 24-h energy budget.

laxing this assumption provides additional support of our arguments. The model also assumes that foraging efficiency is a positive linear function of nectar volume per flower at least over the range of low nectar volumes typical of *Leonotis* flowers. Our present data support this assumption. The relation between foraging time in hours ( $T_f$ ) and a particular average nectar level ( $N_x$ ) is

$$T_f = \frac{13 \text{ kcal} \times 1.5 \text{ s/flower}}{N_x \mu\text{l/flower} \times 0.7 \text{ cal}/\mu\text{l} \times 3,600 \text{ s}}$$

or

$$T_f = \frac{7.74}{N_x}$$

At low nectar volumes required foraging time increases rapidly, whereas at high nectar volumes required foraging time changes little with changing nectar volumes. If average time per flower increases at the higher nectar volumes, efficiency would be lower and the actual required foraging time would be slightly higher than is shown.

Doubling nectar per flower from 1 to 2  $\mu\text{l}$  or from 2 to 4  $\mu\text{l}$  should cut the required foraging time in half, from 77% to 38% and from 38% to 19%, respectively. A sunbird that averages 2  $\mu\text{l}$  per flower should forage only 3.8 h instead of 7.7 h at 1  $\mu\text{l}$  per flower. Foraging costs 1,027 cal/h compared to 400 cal/h for Sitting, and 7.7 h of Foraging should cost about 7,907 cal. A sunbird that forages for 3.8 h and sits for the remaining 3.8 h would spend about 5,423 cal, or save about 2,484 cal per day.

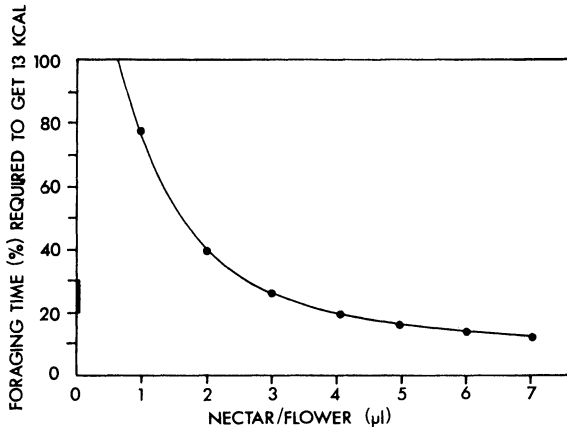


FIG. 11. Relation of foraging time budget to nectar availability. All foraging times calculated as proportion of 10 daylight hours required to obtain 13,000 cal worth of *Leonotis* nectar assuming 1.5 s/flower for each foraging bout.

Such gross energy savings are calculated for several additional pairs of nectar volumes in Table 4. It is apparent that at high nectar volumes unitary changes in nectar availability will have only a slight effect on the foraging time budgets (Fig. 11) and thus result in much smaller savings.

The net savings vary with the defense level required to achieve the specified difference in nectar availability. Defense costs about 300 cal for each percent of the 10-h day that is involved. The difference between these costs and the gross energy savings are the net energy savings. It is clear from Table 4 that the defense costs may equal or exceed the immediate savings from time budget changes, especially if undefended nectar volumes are over 2  $\mu$ l per flower. Higher defense efforts become uneconomical at the higher undefended nectar volumes.

Alternatively we can ask how much higher nectar volumes must be in a defended area ( $N_2$ ) compared to those available in undefended areas ( $N_1$ ) in order to justify a particular level of defense. To calculate this we specify that the net savings each day from

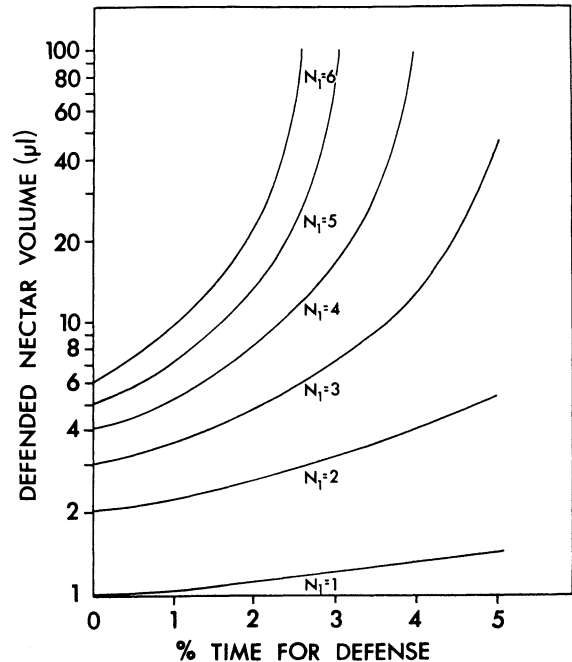


FIG. 12. Changes in nectar availability required to justify particular defense levels and costs. Each point indicates the nectar level inside a territory that is required relative to undefended areas (specified for each member of the family of curves) to balance defense costs with energy savings from reduced foraging activity.

a shortened foraging time budget must equal the daily defense costs, or

$$C_d = T_{f1} C_f - [T_{f2} C_f + (T_{f1} - T_{f2}) C_s]$$

where  $C_d$  are daily defense costs at 300 cal for each percent of the 10-h day,  $C_f$  are the foraging costs at 1,027 cal/h, and  $C_s$  are the sitting costs at 400 cal/h.

Substituting  $T_f = 7.74/N_x$  and the above values for  $C_f$  and  $C_s$  we obtain

$$C_d = 4,853/N_1 - 4,853/N_2$$

or

$$1/N_2 = 1/N_1 - C_d/4,853.$$

TABLE 4. Energetic effects of time budget changes that reflect changes in nectar availability due to defense

Available nectar volumes ( $\mu$ l)			Net savings defense levels <sup>b</sup>				
Undefended	Defended	Gross savings <sup>a</sup>	1%	2%	3%	4%	5%
1	2	2,426	2,066	1,706	1,346	986	626
2	3	809	449	89	- 271	- 631	- 991
2	4	1,216	856	496	136	- 224	- 584
3	4	408	48	- 312	- 672	-1,032	-1,392
3	6	809	449	89	- 271	- 631	- 991
4	6	401	41	- 319	- 679	-1,039	-1,399

<sup>a</sup> Calories per day; calculated for the Golden-winged Sunbird using the relation between average nectar volumes and time budget required to obtain 13,000 cal per day. Text gives representative calculation.

<sup>b</sup> Calories per day; calculated for the Golden-winged Sunbird by subtracting the cost of defense (300 cal for 1% time budget) from the gross savings.

In Fig. 12 we graph  $N_2$  against percent time spent on defense for different undefended ( $N_1$ ) nectar volumes. It is clear that when undefended nectar levels are 1–2  $\mu\text{l}$  per flower, defense costs are justified by small-to-modest increases in nectar availability. But when undefended nectar levels are over 3  $\mu\text{l}$  per flower, a substantial, unattainable difference may be required. As undefended nectar levels increase, therefore, even minor defense expenditures become uneconomical.

#### DISCUSSION

This study shows that the impact of increased nectar volumes on foraging time budgets may be an important consequence of territorial defense of flowers. Energetic gains can be a direct result of shortened foraging times and substitution of less expensive activities. If for some reason foraging time budgets remain constant, then the energetic gains can be specified by the increased nectar uptake per unit of time foraging. As long as the energetic gains of increased foraging efficiency exceed the costs of territorial defense, the territories may be said to be economically defensible. When defense costs become too high relative to these gains the sunbirds should not be territorial. We have observed in both the *Leonotis-N. reichenowi* and *Aloe-N. famosa* systems (Wolf 1975) that when short-term intruder frequency becomes unmanageable the sunbirds may temporarily cease defending their territories or else contract the defended area to a smaller core area. Similar short-term flexibility in aggressive defense is apparent in hummingbirds and seems related to intruder pressure and nectar availability considerations (Stiles and Wolf 1970). When nectar levels are high and not depleted rapidly by feeding sunbirds, Golden-winged Sunbirds should not be territorial. This condition was illustrated to us on 18 March 1972 when nectar levels started at 6  $\mu\text{l}$  per flower in the early morning and declined gradually during the day. The Golden-winged Sunbirds in the area were not territorial until after 1500 h, when the average undefended nectar levels dropped below 2  $\mu\text{l}$  per flower.

We have stressed the importance of energy savings rather than time savings because caloric considerations reduce activities that have different costs to a common denominator. One minute of active territorial defense is energetically equivalent to about 3 min of Foraging or about 8 min of Sitting at 25°C. Conceivably, additional gains result from the time savings per se, i.e., time to engage in breeding activities or to hide from predators. The importance of territory quality to parental time budgets has been indicated for hummingbirds (Stiles 1971, 1973, Wolf and Hainsworth 1971). In the feeding territories

of nonbreeding Golden-winged Sunbirds, however, the major time trade-off seems to be between Foraging and Sitting.

Foraging time budgets are known to vary in relation to energy requirements (Gibb 1956, Verbeek 1964), climatic conditions (Ricklefs and Hainsworth 1968, Ricklefs 1971), territory quality (Stiles 1971, Wolf and Hainsworth 1971), and food availability or quality (Hainsworth 1974, Wolf et al. 1975). As long as projected total intake is fixed over some time period, the curve relating foraging time to food availability should be hyperbolic. Intake over short time periods may be limited or fixed by stomach (and crop) capacities or other physiological feedbacks, such as blood glucose levels. Data for short-term adjustments of foraging time by one sunbird in relation to nectar uptake per flower conform to this hyperbolic curve (Wolf 1975).

Some variation in total daily energy budgets is to be expected as a function of total foraging costs. As foraging costs increase so should total costs. The equation for foraging time required to balance daily costs for the Golden-winged Sunbird is  $T_f = 11,000 / (1,680 N - 627)$  (Appendix I). Use of this equation rather than one assuming that changes in foraging costs are balanced by changes in other costs increases foraging time more rapidly at low nectar volumes but has little effect above 2  $\mu\text{l}$  per flower.

Our calculations throughout have been based on the assumption that sunbirds are visiting the flowers in their territory randomly with respect to previous visits to particular flowers. This assumption means that a foraging sunbird is obtaining on the average the amount of nectar per flower that we measure by plucking flowers from throughout the territory. If the sunbird can avoid flowers it visited on a previous foraging bout, then it will increase the average amount of nectar it obtains per flower. We now have preliminary evidence that sunbirds sometimes preferentially avoid flowers they visited previously, thereby increasing foraging efficiency. Such patterning is most feasible for a resident individual, which can monitor continuously a particular set of flowers and keep track of its visits to them. It would be difficult for a nonresident individual to monitor both its own visits and those of individuals feeding at the same flowers.

Territory size should influence the economics of its defense, in addition to being a reflection of individual requirements and environmental conditions (Schoener 1968, 1971). If intruder pressure is inversely related to territory quality, chase frequencies may be less on large territories with low flower density. But any resulting savings would be partly offset by the increased costs of each chase (Gibb 1956).



If flower density does not decrease with territory size, increasing defense costs may set the upper size limit. Foraging costs should increase as the distance between food plants increases, which should make large territories with low flower density less often defensible than small compact territories with high flower density. However, the frequency of flower revisitation should decrease with increasing flower numbers, resulting in greater obtained nectar volumes or foraging efficiency. Territories with many flowers such as we observed in 1973 should thus be advantageous as long as intruder pressure stays low.

Territoriality is only one form of aggressive social organization that occurs under particular conditions of resource availability and competitive pressure. The energetic costs of nonterritorial foraging strategies are still poorly understood, even though models of the influences of cost/reward ratios have been developed (Schoener 1971, Pulliam 1974). But presumably patterns of aggressive social organization other than territoriality, such as dominance hierarchies and individual distance also have definable costs and gains and conform to Brown's (1964) concept of economics.

The energetic consequences of body size will be of special interest in this regard, because the pattern of aggressive behavior is partly a function of a species' position in the size-related interspecific dominance hierarchy. Large dominant species tend to be sedentary and defend the richest food sources, whereas small subordinate species are displaced into more expensive mobile foraging behaviors without major defense costs. The degree to which a species can sustain a particular strategy should depend on its weight-dependent costs.

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#### APPENDIX I

To calculate foraging time required to obtain as many calories as are spent in a 24-h period, let

$\alpha$  = calories gained per hour of foraging or 1,680  $N$ , where  $N$  is the number of microliters of nectar per flower. The figure of 1,680 is obtained

assuming 0.7 cal/ $\mu$ l of nectar and 1.5 seconds of foraging per flower,

$T_f$  = foraging time in hours,

$T_s$  = sitting time in hours,

$c_f$  = foraging costs per unit time or 1,027 cal/h,

$c_s$  = sitting costs per unit time or 400 cal/h at 25°C, and

$C$  = other costs or 7,000 cal (6,000 cal overnight + 1,000 cal miscellaneous).

Then      Caloric Gains = Total Costs  
or       $\alpha T_f = c_f T_f + c_s T_s + C$ .

But, since  $T_s = 9.5 \text{ h} - T_f$ , and substituting the above values for the Golden-winged Sunbird,

$$1,680 N T_f = 1,027 T_f + 3,800 - 400 T_f + 7,000$$

or

$$T_f = 10,800 / (1,680 N - 627).$$