

# MATING SYSTEM AND REPRODUCTIVE BIOLOGY OF MALACHITE SUNBIRDS

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The Old World sunbirds (Nectariniidae) are essentially ecological equivalents of the New World hummingbirds (Trochilidae). Most male hummingbirds do not contribute to the nesting effort, except by providing genes, producing associated specializations in mating behavior and pair bonding (D. Snow 1963, Orians 1969, B. Snow 1973, 1974, Wolf 1975a). Sunbirds normally are monogamous and have a pair bond that apparently lasts throughout all or most of the breeding season (Skead 1967). However, very little is known about the breeding biology of sunbirds. This report documents some aspects of the reproductive biology of the Malachite Sunbird (*Nectarinia famosa*) in Kenya and provides some preliminary comparison of the mating systems of the two families of birds.

## METHODS AND MATERIALS

The nestings of Malachite Sunbirds reported here were studied in the Rift Valley of Kenya about 20 km north of Gilgil, elevation 2300 m. The principal observations were made from 30 August, when we first located the nesting birds, to 8 December 1972, when nesting activity ceased in this area.

At least the male of each of the four pairs was uniquely colored-banded and the majority of our observations was on one pair in which both sexes were banded. We recorded about 135 hr of time budget information on paired males, about 21 hr of time budget data on a single female, and over 40 hr of observations of activity by the adults at the nests. The time budget information for the males came from all stages of the nesting cycle; that for the females only from the incubation and nestling stages of the cycle. The time budgets were mostly obtained during two-to-three hr continuous observation periods, although a few periods were as short as one-half hr. Behavioral categories for time budgets were: sitting, flying, foraging, chasing, and gone (see Wolf 1975b). These time budget data were transformed into energy budgets using laboratory-derived metabolism values obtained for the slightly larger *N. killimensis* (Bronzy Sunbird, Wolf et al. 1975). All energetic values were corrected for differences in body weight of the two species; for the Malachite Sunbirds, body weight was taken at 13.5 g for males and 11.5 g for females (weights of individuals at banding were: ♂♂ 13.5–14.5; ♀ 13.2, with oviducal egg).

To estimate the availability of nectar we measured the rate of nectar production for the *Aloe graminicola* flowers around which the territories were situated (for methods and results, see Wolf 1975b). The total number of flowers and the seasonal course of flow-

ering were estimated from sample counts of flowers throughout the study area. We also counted the total number of inflorescences with open flowers (fig. 1) and the total number of open flowers on the inflorescences of 50 plants from throughout the area. The average number of flowers per inflorescence was used to calculate the total number of flowers available in the study area and also within the individual territories. Total caloric content of the territories was obtained by measuring the sugar content per unit volume of nectar of *Aloe* flowers and converting all the volumetric measures of nectar availability into caloric units using this average sugar content (see Wolf 1975b, for details and results).

## RESULTS

### THE FLOWER-*Aloe graminicola* (Liliaceae).

The blooming season of these flowers in the study area is depicted in figure 2. The intensity of flowering increased fairly rapidly from mid-September to late October and then began to decline. The change in flower availability was generated mostly by the changing numbers of inflorescences that had open flowers, but, to a lesser extent, reflected the change in the average number of flowers open per head. This general trend in flowering probably was in part a response to a similar trend in rainfall in the area. This is the period of the short rains in this part of East Africa; the rains may start in July or August and continue until early to mid-December although the amount of rain gradually diminishes in November and December (see fig. 6). Throughout the Gilgil area the patches of *Aloe graminicola* that came into bloom during our stay seemed to respond to local rainfall, generally coming into bloom a month or slightly longer after relatively heavy rains. Unfortunately there were no weather stations near the study area to measure rainfall during the nesting season.

The seasonal trend in flowering throughout the study area was composed of slightly different trends in the several sections of the area. The cause of these local differences was not apparent. Since the clumps of *Aloe* in the study area bloomed slightly asynchronously, some territorial birds had high flower availability at the start of the nesting effort, but later were faced with declining conditions



FIGURE 1. The inflorescence of *Aloe graminicola*. Note the central stem which serves as a perch for a foraging sunbird. A feeding sunbird probes into the nearly vertical, downward opening corollas. Unopened and wilted corollas both point upward so that only open, nectar-producing flowers are in a position to be probed by a sunbird perched on the central stem.

while an adjacent area had somewhat better conditions (table 1).

Each open flower produced about 45 calories per day and was open for about 1½ days. New flowers opened each day on an actively blooming inflorescence so that there were flowers of at least two ages on the plant, each producing nectar at about 6  $\mu$ l per hour; we found no significant age differences in production rate. Most new flowers for the day opened by noon. As a plant aged, the number of open flowers per inflorescence and the number of new flowers that opened per day declined. Toward the end of the blooming season higher proportions of flowers were parasitized or aborted and did not open properly, making access to the nectar difficult or impossible for the birds.

The flowers visited by a nesting pair as a nectar source were almost all contained within the clumps of flowers regularly defended by the male and, to a lesser extent, by the female. Table 1 gives our estimates of territory quality for the two pairs (pairs 1, 3) for which we had sufficient data. While the birds were using their territories actively our minimum estimate was that about 65,000 calories were produced on the territory per 24 hours. The

TABLE 1. Seasonal variation in quality of territories of two nesting pairs of Malachite Sunbirds.

Date	Approximate area (m <sup>2</sup> )	Number of flowers	Calories per 24 hr
Pair 1			
11 Sept.	12,000	1500	73,800
30 Sept.	12,000	2730	133,400
15 Oct.	10,000	1575	77,400
29 Oct.	10,000	1480	72,700
15 Nov.	10,000	1780	87,450
30 Nov.	10,000	1470	72,100
14 Dec. <sup>a</sup>	10,000	240	11,700
Pair 3			
15 Oct.	6,400	1340	65,750
29 Oct.	10,000	2420	118,725
15 Nov.	6,400	2322	114,010
30 Nov.	10,000	3230	158,600
14 Dec. <sup>a</sup>	10,000	600	29,500

<sup>a</sup> Pair gone from territory.

pairs left the area when availability dropped below 30,000 calories produced per 24 hours. At this time roaming individuals of *N. famosa* still foraged at the flowers, but were not territorial. The table also shows the precipitous decline in nectar availability just before the birds disappeared. As will be noted in detail later, 30,000 calories per 24 hours probably will not support a nesting pair of Malachite Sunbirds.

Configurations of territories shifted somewhat during the nesting season (fig. 3 and 4), partly as a result of the presence or absence of more dominant sunbirds, and partly because of changes in flowering intensity in the several areas along with shifts in caloric requirements of each pair. The male of pair 1 reduced his total territory size from 11 September to 15 October while the total nectar available on the new territory remained at the same level as earlier and continued at that level until just before the birds left the area.

## THE BIRDS

**Breeding Seasons.** We found Malachite Sunbirds nesting in the study area only from August to December, 1972. We did not find any evidence of nesting or pairing in concentrations of these birds within 20 km of the study area during December through April and during late June and early July, 1973, in areas of high flowering density of two species of *Aloe*. Some males in June and July, were in non-breeding eclipse plumages (see Skead 1967, for a discussion of eclipse plumages in sunbirds) and several males had testes that ranged up to 6 mm long, probably approaching or in breeding condition; fe-

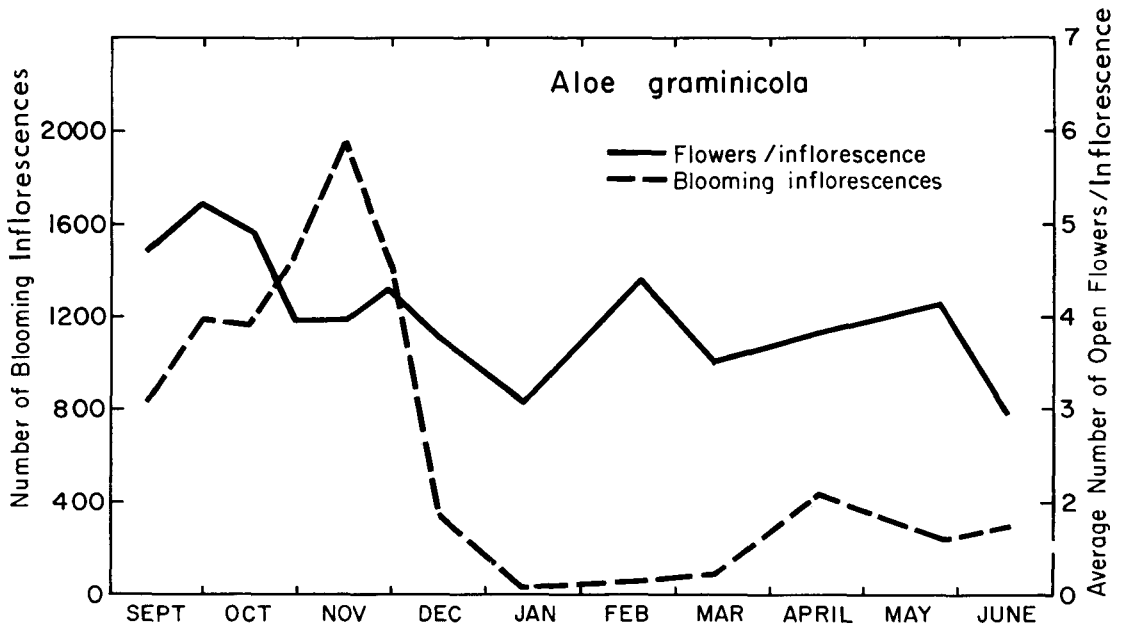


FIGURE 2. Seasonal change on the study area of total inflorescences that contained one or more open flowers and of average number of open flowers per blooming inflorescence. The relatively small variation in average flowers per inflorescence means that most of the seasonal variation in total flowers per territory results from variations in number of inflorescences in bloom.

males had granular ovaries, probably preparatory to breeding. While clearly not definitive, our findings indicate that in this part of Kenya in 1972 and early 1973 Malachite Sunbirds probably nested almost exclusively during the period of rainy weather that extended from August to early December, 1972.

On 30 August at least two pairs were nesting—pair 1 was feeding a nestling and the female of pair 2 was actively nest-building. We found no evidence of an earlier nesting attempt by pair 2 and estimated that the nesting season started in late July. We subsequently found an old nest of pair 4 that probably was used during August. By the end of the study at least four pairs had attempted to nest in the study area. Two pairs successfully brought off young and the other two pairs apparently were unsuccessful. The locations of the respective territories are indicated in figures 3 and 4.

The course of nesting events for the four pairs is illustrated in figure 5. Nearly daily information was available only for pairs 1 and 3 and we have indicated the lack of information for the other two pairs by question marks in the figure. Pair 1 apparently attempted three successive nestings, although neither bird was banded at the end of the first nesting attempt. Subsequent observations showed that this first nest was in the same territorial area as the two subsequent nests of

pair 1. Pair 2 apparently attempted only the single nesting, after which the pair split up. The male remained in the area throughout the study period and several times appeared to be interacting regularly with females, but we never found an evidence of a second nesting attempt. The male of pair 3 carved out a viable territory after pair 1 shifted its territory somewhat and after several Bronzy Sunbirds stopped feeding regularly at the *Aloe* flowers. After establishing a territory he paired with an unbanded female and nesting started. The delay in the onset of nesting of pair 3 seemed to be related only to the delay by the male in obtaining a territory.

We have little data on the nesting of pair 4, except that they apparently brought off at least two sets of two young. A nearby nest still in good condition and apparently recently used suggested that pair 4 nested successfully three times during the season.

*Nest building.* The nest was constructed solely by the female. Three nests that we were able to follow closely took 10, 16 and 16 days to complete. The female of pair 1 took 10 and 16 days to build her second and third nests, respectively, while the female of pair 3 took 16 days to complete her only nest. We have data on the delay between the end of one nesting and the start of building for the next nest for the last two nests of pair 1. The female started her second nest within six days

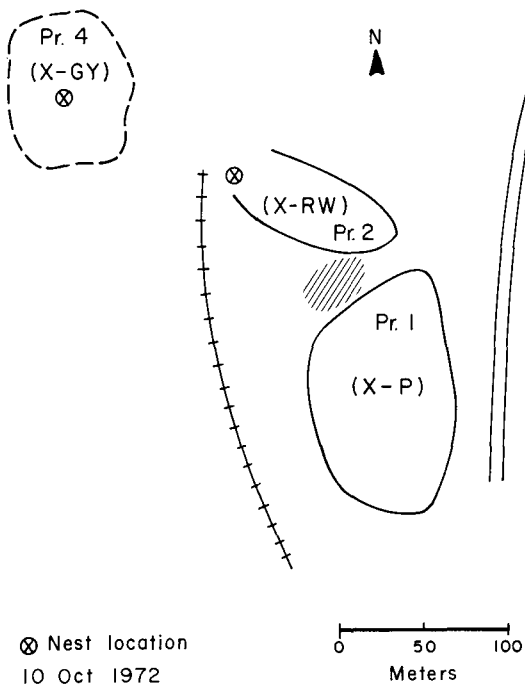


FIGURE 3. Territorial boundaries of three pairs of nesting Malachite Sunbirds present in the study area on 10 October, 1972. Slash lines indicate area used by several Bronzy and Malachite sunbirds. Some aggression occurred in this area, but no territory was established on this date. By 11 October, the male of pair 3 had established a territory including this area. The letters in the territories indicate the color code of the banded male of each pair.

after the young left the first nest. The young was no longer in the area. The third nest was started 11 days after the single young left the second nest. We saw this independent young bird chased by the male on the territory the day the female commenced the third nest.

Each nest was composed principally of dry grasses and plant "down," mostly the pappus of a large thistle (*Cirsium*). The major structural supporting material was spider web. The female of pair 1 usually gathered this material while hovering, an energetically expensive technique. Nest-building trips were directly to and from the nest, even from distances of more than 100 m.

Summaries of the rate of nest-building are given in table 2. The general trend was for a slow rate of building at the beginning and end of the building cycle and a much faster rate in the middle stages. The slow rate of building at the end of the cycle was accompanied by an increase in time spent by the female foraging for insects, probably to accumulate nutrients for egg-laying. Normally several days passed between the end of the nest-

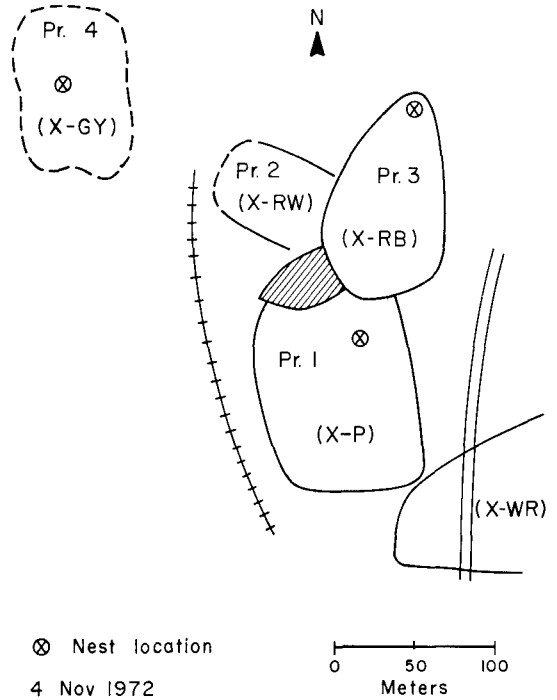


FIGURE 4. Territorial boundaries on 4 November, 1972. See legend of figure 3 for details of symbols. We did not follow the activities of the pair of which X-WR was the male.

building and egg-laying (van Someren 1956, Skead 1967; fig. 5) during which the female actively searched for insects, again probably to meet nutritional requirements of the developing ova.

TABLE 2. Rate of nest-building for females of three pairs of Malachite Sunbirds.

Date	Time	Number of visits	Visits per hr
Pair 1			
6 Sept.	10:36-12:00	12	10.7
	13:05-16:07	29	13.4
7 Sept.	08:00-09:15	17	13.6
	10:07-11:30	25	18.1
	12:58-14:30	51	33.3
11 Sept.	14:30-16:44	38	17.0
	08:35-09:35	20	20.0
	13:08-13:58	16	19.3
13 Sept.	14:55-15:31	24	40.0
	10:40-11:45	45	41.7
	13:03-13:47	34	46.6
	15:02-15:50	34	42.5
15 Sept.	08:45-09:25	12	17.9
17 Sept.	09:47-11:19	8	5.2
2 Nov.	10:35-12:05	0	0
8 Nov.	09:45-11:45	60	30.0
Pair 3			
31 Oct.	13:45-15:05	24	18.0
Pair 4			
28 Oct.	08:50-10:50	45	22.5

TABLE 3. Length of incubation periods and time off nest for two nesting female Malachite Sunbirds.

	Date	Time of day	Time on nest (min)			Time off nest (min)		
			Average	Range	N	Average	Range	N
Pair 1	23 Sept.	09:36-11:54	15.2	8.0-38.0	6	7.65	5.2-10.3	6
		13:21-16:02	8.6	3.5-17.9	10	5.8	3.4-8.7	11
	17 Nov.	09:00-11:00	8.8	5.0-15.0	8	7.0	5.0-10.0	7
Pair 4	8 Nov.	09:40-11:37	6.4	1.5-9.8	10	4.8	1.1-8.8	11
	16 Nov.	14:58-16:36	5.4	2.5-6.7	8	6.7	4.5-8.8	8

The nests were built in low bushes or annual plants. All nests were built within the boundaries of the feeding territories except for pair 3 which nested in a small, dense corn patch about 30 m from the nearest regularly visited and defended flowers and the first nest of pair 1, which was just beyond the perimeter of its flower area. The second and third nests of pair 1 were both within the foraging area. The nests were 1.0 to 1.7 m above the ground. All eight nests examined were domed and had side entrances that opened toward the NE quadrant. Most of the prevailing winds came from the southeast and the sun in the morning fell earliest on an entrance facing in this northeast direction. Verner (1965a) reported non-random nest entrance directions for the Long-billed Marsh Wren (*Telmatodytes palustris*). Ricklefs and Hainsworth (1969) noted the apparent relation between direction of nest entrance and prevailing winds for the Cactus Wren (*Campylorhynchus brunneicapillus*).

The females of pairs 1 and 3 very often went well beyond the boundary of the territory defended by the respective males to obtain nesting material. On many of these trips the male followed the female and occasionally chased other males from her vicinity. He sometimes followed the female as she went to the nest. Skead (1967) and Van Someren (1956) reported similar behavior.

The male often sat near the nest while the female was adding material and when she was not at the nest. He often sang from a perch close to the nest and sometimes he hovered at the nest or clung to the nest entrance.

**Incubation.** The female incubated the eggs unaided by the male. We have a total of 23.1 hours of incubation records for two females; the records are summarized in table 3. During observations of one or more consecutive hours the female of pair 1 spent from 52% to 70% of her time on the nest; the female of pair 4 spent 44% to 52% of her time on the nest. The female of pair 1 aver-

aged longer per session on the nest than did the pair 4 female ( $t = 2.75$ ;  $P < 0.01$ ). The two females showed similar differences in the average length of absences from the nest.

Two incubation periods for pair 1 were  $13 \pm 1$  day. Van Someren (1956) and Skead (1967) also reported incubation periods of 13-14 days.

The clutch sizes recorded during this study were 1, 1, 2, and 2 eggs. In addition, when first found the nest of pair 2 contained two young, and probably started with two eggs. The single-egg clutches were produced by the females of pair 1 and 3 near the end of the nesting season. For pair 1 this was probably the third nesting attempt (the first two were successful, at least to the fledgling stage), but for pair 3 this apparently was the first attempt of the season. The apparent third attempt by pair 4 produced a clutch of two eggs. Van Someren (1956) thought that around Nairobi one egg was the usual clutch with "very rarely two" egg clutches. Skead (1967) reported clutches of two and three eggs, mostly two, from southern Africa.

**Nestlings.** One verified nestling period was 15-16 days. Skead (1967) said that in southern Africa the nestling period is two to three weeks and van Someren (1956) gave 14-16 days as the nestling period around Nairobi. The young were fed by both adults, but the females made 83% (pair 1) and 76% (pair 4) of the feeding visits. The data on feeding rates are summarized in table 4. During some observation periods the male of pair 1 did not feed the young. For a one-hour period when the young were six days old, the male of pair 1 made slightly more than 60% of the feeding visits. This was the only case of more than 50% feeding by the male of either pair 1 or 4, the only two pairs for which we had nestling feeding data. Usually when the male fed the young the rate of delivery of food did not increase substantially over other observation periods when the male provided little or no food. Van Someren (1956) reported that only the female fed the nestlings

TABLE 4. Rate of feeding nestling(s) by two pairs of Malachite Sunbirds.

Date	Hours	Age of young (days)	No. young	No. feedings		Feedings per young per hr	Broodings per hr
				Female	Male		
Pair 1							
30 Nov. <sup>a</sup>	16:02-17:02	1	1	5	0	5.0	7.0
7 Oct. <sup>b</sup>	09:45-10:45	4	2	15	0	7.5	3.0
	11:05-11:59	4	2	9	0	5.0	3.3
8 Oct. <sup>b</sup>	08:56-10:45	5	2	16	4	5.5	1.0
4 Dec. <sup>a</sup>	09:00-11:15	5	1	12	1	5.8	5.3
8 Oct. <sup>b</sup>	10:52-11:35	5	2	5	1	4.2	0
	13:15-15:30	5	2	17	2	4.2	2.0
	08:15-09:15	6	2	7	0	3.5	1.0
9 Oct. <sup>b</sup>	09:15-10:15	6	2	5	9	7.0	0
	13:30-15:30	6	2	12	4	4.0	4.0
	09:20-10:50	8	1	10	6	10.7	0
11 Oct. <sup>b</sup>	11:00-12:00	8	1	5	1	6.0	0
	13:35-15:50	8	1	18	1	8.4	1.3
	10:00-12:00	10	1	15	8	11.5	1.0
13 Oct. <sup>b</sup>	12:58-13:28	10	1	4	0	8.0	0
	08:40-10:40	11	1	14	0	7.0	0.5
19 Oct. <sup>b</sup>	08:29-11:29	16	1	26	3	9.7	0
Pair 4							
29 Sept. <sup>b</sup>	08:25-11:45	?	2	35	12	7.0	4.2
	12:27-15:30	?	2	35	11	7.5	3.6
30 Sept. <sup>b</sup>	08:34-10:45	?	2	27	11	8.7	1.8
8 Oct. <sup>b</sup>	12:52-15:00	?	2	16	6	5.2	0
30 Nov. <sup>a</sup>	13:57-15:57	13±	2	36	7	10.8	0

<sup>a</sup> Third nesting.  
<sup>b</sup> Second nesting.

in a nest near Nairobi. However, the male probably was reluctant to feed the young while the blind that van Someren had erected was present (see Skead 1967). Skead noted that in southern Africa both sexes fed the nestlings, with one male feeding about 60% of the total recorded visits for the pair.

The feeding rate per young at the second nest of pair 1 averaged higher after one of the two original young disappeared. However, this same pair fed their young at a similar rate per young during the first five days of the second and third nestings (table 4). During their second nesting, pair 4 maintained a high rate of delivery to two young, a rate per young not different from pair 1 feeding one young. Some of the higher rate for pair 4 results both from the added feeding rate of the male and the faster delivery rate of the female.

Food for the nestlings seemed to be mostly insects, although van Someren (1956) reported "plenty of nectar" fed to a nestling. We frequently watched adults go immediately to the nest following a bout of insect-catching. Most often we could not see anything in the bill of the adult, but occasionally we saw an adult lepidopteran, several times a beetle, and once a caterpillar. Upon arriving at the nest the adult pushed its bill

down the throat of the young and delivered the food. Contrary to van Someren (1956), we had no evidence of regurgitative feeding.

When foraging for insects, both sexes behaved differently than when foraging for nectar. Insect catching was almost entirely by hovering around or just above the ground vegetation, either weeds or grasses and plucking insects from the vegetation. The female of pair 1 regularly hovered just above the grasses and weeds picking principally at the flowering heads of both plant types. The male performed identical movements just before he went to the nest and fed the young; this was almost the only time we saw him hovering in this fashion. The male occasionally caught a passing insect and immediately flew to the nest, but he generally moved to specific areas to collect food for the young. What stimulated these deliberate feeding trips was not clear, but it was not always related to a decline in the rate of delivery by the female (table 4).

When female 1 was actively feeding her young she usually fed on *Aloe* nectar just after visiting the nest and then went off to collect insects. At times, more than 50% of her insect collecting was well away from the territory of the pair; sometimes she flew an estimated 500 m (flights lasting 60 to 70 sec).

TABLE 5. Time budget for nesting female Malachite Sunbird.

Nesting activity	Date	Number seconds spent in:						Total
		Sit	Forage	Fly	Chase	On or at nest	Gone	
Incubation								
	24 Nov.	3455	820	705	0	5985	—	10965
	27 Nov.	1815	1035	430	50	7505	355	11190
	28 Nov.	1780	845	410	50	7545	170	10800
	29 Nov.	1815	1220	735	15	6250	105	10140
Feeding nestling								
	11 Oct.	2695	2295	2295	35	530	(2385)	7850
	13 Oct.	290	650	495	15	350	(330)	1800
	14 Oct.	2385	1170	3215	45	470	(2800)	7285
	19 Oct.	4215	2225	4190	85	295	(4390)	11010

On such flights when we could see her activities the female almost immediately began hovering through the grass, occasionally sitting, and then flew directly back to the territory and to the nest. Usually the male did not follow on these long flights, but remained in the territory.

Both sexes carried fecal sacs away from the nest. Sacs were removed only after a feeding visit and were carried away at the rate of 0.5 to 1.7 sacs per young per hour.

Brooding, performed only by the female, occurred frequently during the first six days of the nestling period then continued on a limited basis until young were 10–11 days old (table 4). After the young were about six days old the female brooded most often when the ambient temperature was 22°C or less.

*Fledgling.* The single fledgling for which we have data stayed around the nest for 10 days and was fed by the adults approximately two times per hour when it was from two to four days out of the nest. By the fourth day the young was feeding itself by extracting nectar from the *Aloe* flowers within the pair territory. By the sixth day the fledgling seemed to be nearly as expert as the adults at nectar feeding. By the 11th day the young bird was feeding independently. We saw it in the territory of the pair on that day.

#### TIME AND ENERGY BUDGETS

*Males.* The time and energy budgets of male Malachite Sunbirds during the breeding season have been discussed elsewhere (Wolf 1975b) but are summarized here for clarity. The data are only for the males of pair 1 and pair 3. The males averaged about 64% (range = 38–83) of their time sitting during the time budget observation periods, 22% (range 10–42%) of their time foraging, 7%

(range 2–13) of their time in miscellaneous flying (flying not associated with chases of intruders or foraging for nectar); 6.8% (range 2–15%) of their time in chasing intruders, either conspecific or interspecific; and less than 0.2% (range 0–1.6%) of their time out of sight of the observer. Male 3 had significantly higher foraging time and chase time during nest-building than while the female was incubating, although he did not directly participate in either of these activities. During the nestling period, the only time when the males directly participated in the nesting effort, the male of pair 1 foraged and chased significantly more than during the incubation and fledgling period.

*Female.* All the time budget data are for the female of pair 1 (table 5). We estimated her time budgeting during incubation and during feeding of nestlings. During the nestling stage we had to estimate total foraging time when the female flew more than 100 m, often out of sight. On some of these occasions we watched the female throughout her absence from the territory and measured the proportion of the time the female spent sitting (46%) and flying (54%) once she arrived at the foraging area. These values, to which we added the time of flying to and from the foraging site, were used to calculate time and energy expenditures on all long trips.

During incubation the female spent most of her time on the nest and little of her time actively foraging at *Aloe* flowers. In fact, she spent remarkably long periods of time sitting in the territory away from the nest. Flying, which included some insect catching as well as miscellaneous flying comprised 4–7% of her time. As expected, chasing of other birds by the female was very limited during incubation and was almost entirely the province of the male, even though he also chased less

TABLE 6. Energy budgets for nesting female Malachite Sunbird.

Stage of nesting	Date	Calories spent in: <sup>a</sup>					Nectar intake <sup>c</sup> (cal.)
		Sit <sup>b</sup>	Forage	Fly	Chase	Total	
Incubating							
	24 Nov.	440	205	530	0	1435	1350
	27 Nov.	230	260	325	40	1180	1850
	28 Nov.	225	210	310	40	1115	1390
	29 Nov.	230	305	550	10	1365	1945
Feeding nestlings							
	11 Oct.	410	575	1720	25	2730	815
	13 Oct.	80	165	370	10	625	415
	14 Oct.	365	295	2410	35	3105	1510
	19 Oct.	575	555	3145	65	4340	3240

<sup>a</sup> Caloric expenditures calculated from following values: Thermal conductance equals 1.24 (Herreid and Kessel 1967); body temperature equals 41.0°C; daytime ambient temperature equals 22°C; sitting costs equal 460 cal/hr; incubating female assumed to be at standard metabolic rate at  $T_A$  of 30°C; flying costs equal 2700 cal/hr; foraging costs equal 900 cal/hr.

<sup>b</sup> Sitting costs include the short periods female spent at nest feeding young.

<sup>c</sup> Nectar intake calculated from equations given in Wolf 1975b and are identical to those for male Malachite sunbirds feeding at *Aloe graminicola*.

during incubation than during other phases of nesting (Wolf 1975b).

When the female was feeding young, her foraging and flying time increased dramatically, but time sitting away from the nest stayed about equal to that spent during incubation. Thus, most of the increased time expenditure associated with feeding herself and nestlings was taken from the time the female earlier spent on the nest incubating eggs. A small proportion of her time was still spent at the nest, feeding and brooding young. Unfortunately we do not have similar data for this or another female when caring for two young. Since the feeding rates with two young were somewhat higher than those for a single young it is expected that foraging and flying time would be increased somewhat with two young and that sitting time would probably be decreased. The differences in feeding rate were not offset by the aid of the male (see earlier).

Using techniques already described in detail (Wolf 1975b) we calculated the approximate intake of energy by the female while she fed at *Aloe* flowers during the time budget observations. We assumed that females were not different from males in the determinants of foraging efficiency at *Aloe graminicola* (Wolf, unpubl.). The estimated intake and expenditures of energy during the nesting cycle for this single female sunbird are presented in table 6. During incubation the intake of energy normally somewhat exceeded expenditures. However, this situation was reversed when the female began feeding the young. Interestingly, the estimated intake

of nectar per flower visited shows a similar trend to that found in the males (Wolf 1975b), suggesting that the quality of the territory does vary with stage of the nesting cycle.

At least under the conditions of this study the female probably was operating on a positive, or certainly neutral, energy budget while incubating eggs. While feeding nestlings she probably was operating on a negative energy budget although the contributions of insects to her diet must have been higher than during incubation. During incubation the female probably stored energy from her positive energy budget for use during the nestling period.

## DISCUSSION

### BREEDING SEASON

The timing of the breeding season of Malachite Sunbirds, in Kenya and southern Africa (Skead 1967), probably is determined mostly by the requirements of the adults for a rich, easily accessible energy source in the form of nectar, coupled with sufficient insect abundance to allow the female to sequester nutrients for eggs and to feed the offspring. The correlation of the end of breeding at the study site and the decline in flower availability is obvious in figures 2 and 5. One of the banded males reappeared in the study area during the slight resurgence of blooming in May and June (fig. 2) and seemed to be attempting to pair with one of several females in the area. The rains were very light during the first half of 1973, leading to the



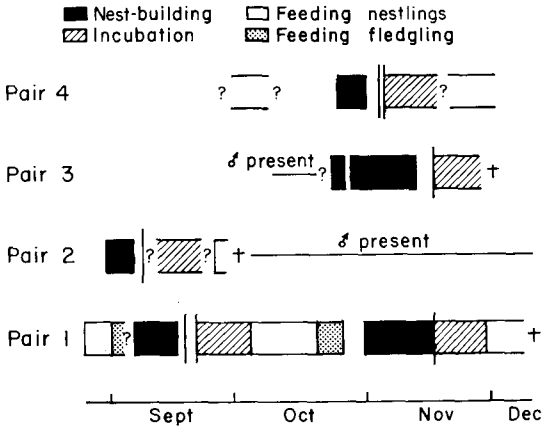


FIGURE 5. Summary of reproductive activities of 4 pairs of Malachite Sunbirds in the study area. Crosses indicate mortality of young. Question marks indicate uncertainty about precise timing of start or end of a phase of nesting.

reduced flowering. In years of heavier rainfall, as could be expected during the first half of the year in "normal" years (see fig. 6) these sunbirds should have abundant *Aloe graminicola* flowers in the vicinity of the study area and undoubtedly would breed.

Van Someren (1956) noted that the breeding season of Malachite Sunbirds in the vicinity of Nairobi, Kenya was during the long, heaviest rains (see fig. 6). He said that the birds would breed as early as March if the short rains in November and December ran into long rains. However, he noted that in his study areas the sunbirds probably did not breed in August or later as many of the males were in eclipse plumage at this time of minimal rains. Van Someren suggested that the breeding season in his area was timed to the blooming of certain flower species, of which he mentioned *Leonotis* (Labiatae).

Breeding during long, rainy periods has two potential advantages over the other rainy seasons of the year. First, these rains are more predictable, at least in general timing and minimum levels of rainfall. Second, the length of the rainy periods means that on average, the birds will have sufficient time to raise at least one and often more than one brood successfully. The *Aloe* flowers around which this sunbird species was breeding continued to produce flower stalks throughout the periods of rains so that single plants may produce as many as three or four consecutive flower spikes if the rains last long enough. Similarly, smaller *Aloe* individuals, probably younger plants, have a greater chance of pro-

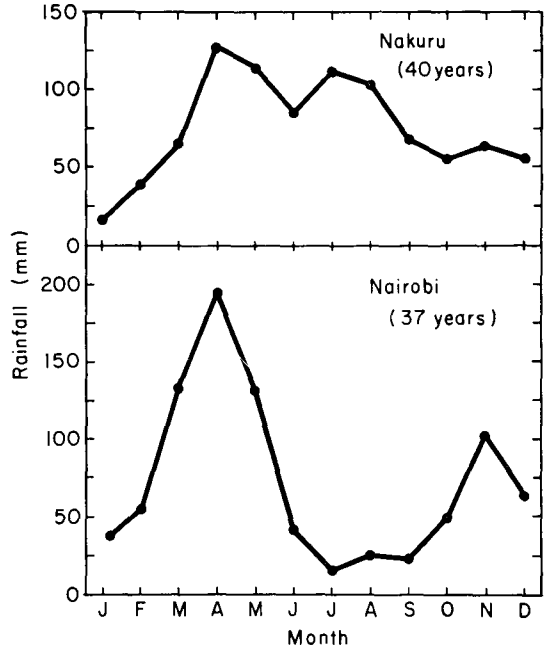


FIGURE 6. Summary of average monthly rainfall for Nairobi and Nakuru, Kenya. Nakuru is approximately 30 km NW of the study area.

ducing a flower spike if the rains continue. Thus, both the total number of flowering plants and the number of stalks per plant are enhanced by prolonged rains. This longer period of flower availability extends the period during which territories will support breeding adults and their offspring.

Another important aspect of timing of breeding for Malachite Sunbirds is their position in the interspecific dominance hierarchy of sunbirds at potential feeding sites. The nesting pairs were in the only area of concentrations we saw in which males were able to hold territories for any length of time. In all other high density areas these sunbirds were dominated by larger sunbird species, probably precluding any territoriality, and hence, any nesting attempt. At Hell's Gate (near Naivasha, Kenya) in an area of flowering *Leonotis* in July, 1971, and also in March, 1972, and July, 1973, male Malachite Sunbirds were mostly nonterritorial wanderers throughout the study areas while being continually chased from *Leonotis*-based territories defended by the larger, more dominant Golden-winged Sunbird (*Nectarinia reichenowi*) (see Gill and Wolf 1975) and the Bronzy Sunbird. In the study area in August and September, 1972, the appearance of the male of pair 3 as a territorial and later as a paired, individual followed the disap-

pearance of several Bronzy Sunbirds that had been feeding regularly and sometimes were territorial for short periods in the area later occupied by male 3. This area became a viable nesting territory for the Malachite Sunbirds only after these dominant individuals departed. During the nesting attempt of pair 3, a young male Golden-winged Sunbird took over a portion of the territory and excluded the pair from the area. This young bird left after 3–4 days, but while present he reduced the energy base for the nesting pair.

This suggests that suitable nesting sites for Malachite Sunbirds should be in areas of high flower availability in plant species that are not effectively used and/or defended by more dominant species. These sunbirds should have lower energy requirements than larger sunbirds and could use energetically poorer resources. Additionally, an energy-rich source could be less efficiently extracted by more dominant species because of differences in body size and bill morphology (see Wolf et al. 1972). Male Malachite Sunbirds have the highest rate of nectar extraction among males of four species of sunbirds that regularly forage at *Aloe* flowers, but their rate is not significantly higher than that of *N. kilimensis* (fig. 7). The higher foraging costs for the larger species make the Malachite Sunbird the most efficient of the three species at exploiting the *Aloe* nectar. Males of the Variable Sunbird (*N. venusta*) are smaller than *famosa*, and extract nectar much more slowly than either *famosa* or *killimensis*, a reflection of the short bill of *venusta*, which makes it nearly impossible for these birds to reach nectar at the base of the corolla of *Aloe* flowers. The smaller size of *venusta* and hence lower foraging costs per unit time would make them about as efficient as *famosa* at extracting energy from *Aloe*, but *famosa* is able easily to dominate the smaller *venusta*.

#### TERRITORIALITY

In view of the numerous trips for food and nesting material that the female made beyond the boundaries of the regularly used and defended area of the male, it appears that the nesting territory of these birds was restricted to defense of the flowers as a nectar source and defense of nests. The males also chased other males from the vicinity of their female before and during egg-laying, but the spatial location of this behavior was wherever the female happened to be, behavior similar to the Brewer's Blackbird (*Euphagus cyanocephalus*; Williams 1952).

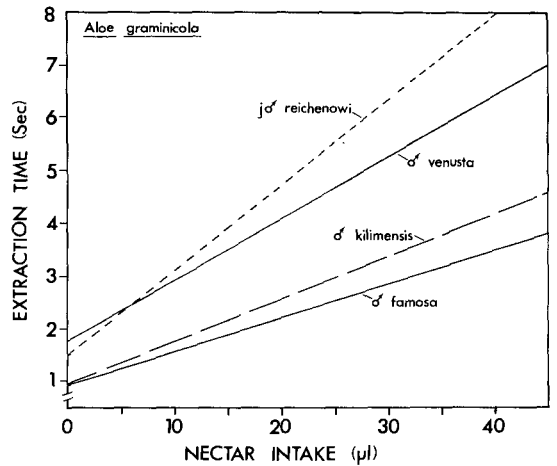


FIGURE 7. Rate of extraction of nectar from flowers of *Aloe graminicola* by males of four species of sunbirds. The data for *N. reichenowi* are for a juvenal male. The slopes of the lines for *N. famosa* and *N. kilimensis* are different from the slopes for *N. reichenowi* and *N. venusta* ( $P < 0.05$ ), but the slopes are not different within the pairs. The intercept for *N. venusta* is significantly higher than for *N. famosa* and *N. kilimensis* ( $P < 0.05$ ). None of the other intercepts are different.

**Territory Size.** The number of flowers in the territory of a breeding pair of Malachite Sunbirds will depend on a variety of factors. An individual requires about 17,000 calories per day (Wolf 1975b) so that the total requirement for a pair should equal approximately 34,000 calories per day. For short periods the requirements will be somewhat higher than 34,000 calories, especially when one or two fledged young are still feeding in the territory. Then energetic requirements for the pair and young could reach 50,000 calories per day or more. Since the caloric output is 45 cal per flower per day, the pair would require 800 or more flowers to meet the requirements of the two adults, and perhaps up to 1500 flowers to meet the requirements of the adults plus two young. These values, however, depend on exclusive access to the total nectar production.

The defensive behavior was not wholly effective in keeping other individuals from exploiting the *Aloe* nectar. In part this reflected the size of the territories which meant that individuals intruding at one periphery could feed before the arrival of the resident male. Foraging intruders often went undetected for some time. Additionally, intruders of dominant species of sunbirds, while often flown at, rarely were displaced from the territory.

Flower abundance on a territory changed seasonally. To maintain even the minimum

number of flowers on any given day required that the bird control an area that on other days very often contained more flowers than it required.

Finally, the initial starting volumes on a given day will depend on flower use the previous day plus the number of flowers that wilted overnight and the number of new flowers that opened in the morning. Nectar production starts as the new flower opens so there is no accumulation of nectar in a recently opened flower. If the average nectar volume is low the efficiency of foraging also will be low (fig. 7) and the total foraging time will increase (Wolf et al. 1975). The combined effect will increase total costs and the foraging efficiency required to maintain the pair. Low nectar volumes will become progressively lower during the course of the day unless sufficient flowers are controlled so that production rate exceeds utilization rate and nectar can accumulate.

All these variables should influence the number of flowers a bird attempts to control. In general the number should either exceed by some margin the minimum energetic requirements of the pair or be modifiable seasonally. Males 1 and 3 regularly defended areas that at peak abundance contained more than 2000 flowers (an excess of 100,000 cal) and generally more than 1500 flowers (67,000 cal). Male 2 abandoned his territory when flower abundance declined below 1000 flowers (45,000 cal). Each male had potential access to more than the minimum number of flowers, but male 1 because of different intruder pressures was better able to control use of these flowers than male 2.

#### PAIR BOND AND SEX ROLES

In common with the South African species of sunbirds for which data are available (Skead 1967), the Malachite Sunbird in Kenya has a pair bond that lasted only for the nesting season. During the nonbreeding season there was no evidence of pairing, and females were subordinate to males.

The female made a larger direct contribution to the nesting effort than the male. She did all nest-building, incubation, and brooding of the nestlings. Both sexes fed the nestlings and fledglings. However, at the nests studied the female made most of the feeding trips. Skead (1967) noted that a male Malachite Sunbird that lost its female successfully fed the young alone.

The male's major contribution to the nesting effort is defending the flower nectar used

as a food supply by the adults and fledglings. The male spent much more time during the nesting period in chasing intruders from the territory than did the female (Wolf 1975b, table 5). At the onset of nesting he also spent some time following the female while she collected nesting material. While following her, he chased other male Malachite Sunbirds that approached the female, behavior that protected his potential genetic and energetic investment in offspring. During the nestling stage the male did not follow the female when she left the territory to collect insects. The male no longer had to protect this ability to fertilize the female and it probably was important that one parent help protect the young from potential predators, such as Fiscal Shrikes (*Lanius collaris*) that were regularly present and mobbed by the sunbirds.

The male's main contributions to nesting were his genes and time and energy spent in defense of a high quality food source that enabled the female to maintain herself energetically while carrying out the nesting effort nearly unaided. The male's contribution in maintaining a high level food source must be balanced against ways that he more directly could aid the nesting effort. The more time and energy spent by the male in feeding young, the less time available for defense of the territory. Even sitting time, if spent watching for or calling at intruders, can be an important component of defense. A male's levels of direct and indirect contribution should depend on the quality of the territory, both number and density of open flowers, and the probability of intruders feeding at the accumulated nectar.

Another possible explanation for the limited aid at the nest by the male bird is the potentially higher predation rate on nests that might occur if the brightly colored male made regular trips to the nest (Skutch 1967). This explanation probably does not hold for Malachite Sunbirds. The nest is not placed in a noticeably inconspicuous or hidden location; during the course of building the female makes trips with nesting material directly to the nest and does not attempt to "sneak" to the nest. Additionally, the male regularly sings by the nest and often hovers at or near the nest during the building phase. Finally, the male does help feed the young. We conclude that the lack of male aid at the nest is not an important anti-predator device, but that the male is doing something else, in this case defending the nectar resources of the

territory, as his major contribution to the nesting effort.

If this suggestion is correct, then the fact that the male provides limited direct aid in rearing the young may have more important implications on the maximum reproductive output of the pair than workers such as Skutch (1967) would allow. One must understand what, in fact, the male of a pair is contributing to the nesting effort, before the conclusion is drawn that the clutch size is not set by the maximum number of offspring the pair normally can raise. In many bird species, especially in the tropics (Cody 1966), the male may play an important role in competitive interactions for the food supply for either the adults as in the case of these sunbirds, and/or the young or perhaps for nesting sites or nesting material (Lack 1968, Morse 1968, Verner and Willson 1969, Williamson 1971, Selander 1972, B. Snow 1973).

These reproductive contributions by the male are remarkably similar to those reported for the Fiery-throated Hummingbird (*Panterpe insignis*) of the high mountains of Costa Rica (Wolf and Stiles 1970). In the case of the hummingbird no direct male aid was observed. The reported observations were limited to the incubation and nest-building periods, but subsequent observations in the same area revealed that the males did not help feed the young (Stiles, pers. comm.). It should be noted that the male of pair 1 of the sunbirds also did not contribute to the feeding effort during about 35% of the observation periods. It is possible that the male *Panterpe* would contribute to feeding the young under conditions of high energy availability and low intruder pressure.

The evolution of pair bonding for the breeding season in sunbirds paralleled the case for *Panterpe*. In both situations essentially a single flower species was available that was sufficiently abundant and dense to provide a rich energy source for the nesting female. However, the spatial and temporal distribution of the flowers made territorial defense economical (Brown 1964), restricting the availability of flowers not defended by conspecific males. In this situation there was strong selection for the females to mate only with those males that allowed regular access to the flowers on their territory. Males that did not allow such females use, and perhaps provide some help in feeding the young, on the average should leave fewer offspring, making pair formation an advantage for the males also. This contrasts strongly with the mating system of most hummingbirds in

which the males are promiscuous and provide no aid, even resource defense, for the breeding females (see Orians 1969, Wolf and Wolf 1971, Wolf and Stiles unpubl. data).

## SUMMARY

This paper describes the breeding biology of Malachite Sunbirds (*Nectarinia famosa*) in the central Rift Valley area of Kenya. Nest-building and incubation are performed solely by the female while the male, to a variable extent, helps to feed the nestlings and fledglings. One female for which we had good time budget data probably operated on negative energy budgets during the nestling period, but positive energy budgets during incubation. The principal activity of the male during reproduction, in addition to mating with the female, seems to be the defense of the nectar supply used by the female and the young.

Monogamy, the usual mating system in sunbirds, seems to result from a combination of breeding season territoriality in single flower species, the nectar of which is all or mostly defensible by available males, and relatively high intraspecific and interspecific competitive pressures resulting in limited alternative nectar sources for nesting females. Under these circumstances a female pairing with a male holding a "good" territory ensures herself access to the food; efficient defense of the food by the male requires sufficient time to preclude as active a part in rearing of the young as taken by the female. A female not so paired probably is unable to feed herself and her young, thus wasting her reproductive effort as well as that of the male with whom she mated. Anti-predator behavior does not seem to be important in reducing direct participation in nesting of the brightly colored male.

Evolution of monogamy and pair bonds throughout the breeding season in sunbirds parallels the one well-documented example of nonpromiscuity in hummingbirds, the New World ecological equivalents of sunbirds.

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