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Department of Zoology, University of California at Los Angeles and Los Angeles County Museum of Natural History, Exposition Park, Los Angeles, California 90007. Accepted 28 January 1970.

SOME OBSERVATIONS ON BEHAVIORAL ENERGETICS IN THE VILLAGE WEAVERBIRD II. ALL-DAY WATCHES IN AN AVIARY

NICHOLAS E. COLLIAS, JANICE K. VICTORIA, ELLEN L. COUTLEE, AND MARTIN GRAHAM

IN this study we wished to find what a bird does with all its time each day, and, aided by the literature, to gain some idea as to how and why it distributes its energy as it does among the different activities in its behavioral repertoire. To this end we watched a specific individual Village Weaverbird *Ploceus* (*Textor*) *cucullatus cucullatus* (Müller) from dawn to dusk and counted or timed with a stopwatch the various things it did. In this fashion we watched one male and two females, all individually color-banded, on different days and in different phases of the breeding cycle.

The birds studied were captive in a large outdoor aviary in southern California. This situation of course has the disadvantage that the habitat is artificial. It has the advantage that in the confines of the aviary it is possible to watch what a bird does for every minute of the day. This gives a more complete picture than is as yet possible in the field, for example one can count all of the food items an adult bird eats during the entire day and in different phases of breeding. We do not deny that availability of food and nesting materials may have had some influence on activity schedules and rates, though in nature a source of nesting materials, such as tall grasses, often grows next and even directly beneath the colony tree and may sometimes be just about as available as in an aviary. As the food supply in the aviary was held constant, variations in the food situation cannot be held responsible for the great differences noted in certain behavior patterns in different phases of the breeding cycle. Besides being convenient and favoring close observation, aviary studies are at times useful in providing clues as to what to look for under the more difficult field conditions.

The artificiality of the aviary is to some degree negated by the fact that our captive birds bred well and the essential features of their breeding behavior differed in no apparent way from those Nicholas and Elsie Collias observed in the wild in the birds' native habitat in Senegal in the summer of 1967. We have attempted in this study of captive birds to limit our conclusions to the birds' breeding behavior, largely avoiding those aspects of behavior that might be more heavily dependent on the natural habitat, such as relations to enemies and distances to favorable places for gathering food or nest materials. The energetics of these latter aspects of behavior in a natural situation have already been considered (Collias and Collias, 1967). Enough information is available to suggest that the conclusions drawn from this aviary study in fact do apply to normal behavior in nature.

A description of the breeding behavior of this species of weaverbird in nature is available (Collias and Collias, 1959; Crook, 1963). The birds of this polygynous species breed in colonies in Africa south of the Sahara, particularly in savanna country along rivers and streams, in forest clearings, in cultivated lands, native villages, and towns. The male weaves the outer shell of the nest to which he attempts to attract a female by hanging inverted beneath the bottom entrance of the nest and flapping his wings in a nest advertisement display. The female, if she accepts the nest, adds a lining, does all the incubating of the eggs, and all or most of the feeding of the nestlings. If the female rejects his nest, the male, after a period that may vary from a day to a week or more, tears it down and builds another in its place.

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THE SETUP AND PROCEDURE

The three birds used in this study belonged to the race *cucullatus*. The male and one of the two females came from Senegal. The male, AW, had an azure over a white band on each leg, and one female, BA, had black over azure leg bands. The second female, WA (white over azure leg bands) had been raised in our aviaries and was mated to male AW. Other birds were breeding in the aviary, but they are ignored for purposes of this report, and on any given day we watched only one bird. This large outdoor aviary contained 8 males and 14 females in all, the equivalent of a small breeding colony in nature.

The aviary was subjected to natural daylight only. It was 5.2 m high $\times$ 5.2 wide $\times$ 9.2 long, with a wooden and roofed shelter at one (northwest) end. An African acacia tree about 3 m high, planted near the shelter, provided nesting sites for the

TABLE 1
AMOUNT OF SOME ACTIVITIES DURING THE DAY OF A MALE VILLAGE WEAVERBIRD IN AN AVIARY

	Building nest (min)	Territorial defense (min)	Resting time (min)	Bouts of nest display	Mealworms eaten
Built on old nests only					
15 July (15 hours)	90	12	386	69	110
21 July (15 hours)	159	10	262	101	107
Built new nest					
5 August (12 hours)[1]	409	2	17	555	84

[1] On this day observations began 2½ hours after dawn.

birds. The giant Mexican reed grass (*Arundo donax*) was furnished in pails of water as a source of materials for weaving by the males, while grass heads of various species and chicken feathers provided additional materials the females used to line their nests.

The birds were supplied with fresh water daily, parakeet seed mixture, fresh lettuce, mealworms, and crickets. Cuttlebone and grit were constantly present. During their breeding season (May–October in southern California) the birds ate a heavy proportion of insects and often neglected the grain.

Observations were made from a hiding place within a cloth blind at one end of the aviary and were aided by binoculars. We worked in relay fashion, one observer taking the place of another at regular intervals, our usual routine being 05:00–08:00 (M.G.), 08:00–10:00 (N.C.), 10:00–14:00 (J.V.), 14:00–15:00 (N.C.), 15:00–18:00 (E.C.), 18:00–20:30 (N.C.). Each observer counted various specific acts such as trips for nest material, bouts of display by the male, numbers of insects and other food items eaten, etc. Each observer used a stopwatch to record the time the birds spent resting, building the nest, or in territorial defense by the male, or inside the nest by the female. The temperature was read from a thermometer within the blind at the shady side at the start of every hour. The whole study was coordinated by Collias who also prepared the final report.

RESULTS

Amount of different activities in one day.—Table 1 shows that a male Village Weaver may have active and inactive days when the relative amounts of time spent resting and time spent in other activities differ radically. On his two inactive days AW spent 4½ and 6½ hours just resting, but on the day he built a new nest he rested only 17 minutes out of 12 hours and spent about 7 hours gathering materials and building a nest that he essentially completed in one day. He also engaged in nest advertisement 5 to 8 times more frequently on his active than on his inactive days.

There were only 12 rather than 15 hours of observation for AW's active day because of the difficulty of predicting just when AW was going to start a new nest. This nest had not been started by the time AW went to roost the preceding evening, and when observations began at

TABLE 2
AMOUNT OF SOME ACTIVITIES DURING THE DAY OF A FEMALE VILLAGE WEAVERBIRD AT DIFFERENT PHASES OF HER BREEDING CYCLE IN AN AVIARY

	Copulations	Time in nest (min)	Resting time[1] (min)	Insects eaten	Insects fed or shared
Pre-egg stage	10	86	86	70	—
Incubating	0	607	4	85	—
Feeding 3 newly-hatched young	0	425	5	57	62
Feeding week-old young	0	166	62	77	170

[1] Outside the nest.

08:00 it was just at the end of the ring stage, a very early stage in nest construction. In subsequent observations by Janice Victoria, AW took 69 minutes from start of another nest to the completion of the ring stage. Adding this to the preceding figure, we found that AW, one of our best builders, could construct a well-completed nest from start to finish within 8 hours of nest building time, including the gathering of materials within the aviary. In this time he made 404 round trips for nest material.

Territories were stabilized in the aviary and AW had occupied the same place in the tree for several years. As Table 1 shows, AW had to spend very little time in defense of his territory on either inactive days or on his active day. He apparently had little time for singing on his active day, (34 songs) while on his inactive days (116 and 168 songs) he gave three to 5 times as many songs.

During the 3 days when we watched him all day AW subsisted almost entirely on mealworms, taking only a few crickets, some lettuce, and very little or no grain on any one day. Furthermore, his food intake was very similar on inactive and active days, averaging about seven mealworms per hour.

Copulations (10 by female WA with male AW) on one of his two "inactive" days were restricted to the pre-egg stage; the female concerned laid her first egg the following day. Table 2 shows how the relative amounts of time spent in her nest by a female Village Weaver varies with her phase in the breeding cycle. When incubating eggs (female WA) or brooding small nestlings (female BA) that need to be brooded often, the amount of time the female spent resting outside the nest during the day virtually vanished. The incubating female spent 10 hours of her 13½-hour-day in her nest, counting from the time she first left her nest in the early morning until she returned to her nest at dusk and remained the night. Her first egg hatched the following morning. The same female, when in the pre-egg stage, spent only 1½ hours in her nest during the day. Female BA with newly hatched nestlings spent considerable time

—7 hours out of the day—in the nest with them, presumably brooding them. But when her same young were a week older she spent fewer than 3 hours in the nest with them, and she rested much more frequently outside the nest. Much of her time was spent getting food to meet their enlarged appetites. The food intake of the female and her young combined doubled within 1 week.

The nestlings are fed largely on insects. Before feeding a cricket to her nestlings the female Village Weaver often eats part of the insect herself. This sharing helps the female to solve part of her own food problem. Probably when working hard to feed nestlings the female has an increased need for food for herself, and the habit of eating part of the food taken to the nestlings helps meet this need.

Table 2 shows the numbers of insects a female was seen to eat on any one day during different phases of her breeding cycle. We did not do an all-day watch on a female weaverbird that was in a nonbreeding or resting state. El-Wailly (1966) found in laboratory studies of the Zebra Finch (*Taeniopygia castanotis*) that the caloric intake of a nonbreeding pair is significantly less than it is when the same birds are in the egg-laying and nest-building phase, or when they are incubating, but there was no significant difference in caloric intake between these two phases of breeding. Our Village Weaver female ate slightly more mealworms when incubating than she did on the day before she laid her first egg when she copulated.

During incubation El-Wailly's Zebra Finches increased their caloric intake with lowered ambient temperatures. During our all-day watch of a Village Weaver female, the temperature was mild and its range (17°C–27°C) was not great (Figure 2), and probably caused the bird little stress. According to Kendeigh's (1963) calculations for the House Wren (*Troglodytes aedon*) the female expends considerable energy for incubating on cold days, but rather little on moderately warm days.

When a female Village Weaver was feeding nestlings we were unable to separate her own food intake from that of her nestlings, because she often ate part of the insect herself before giving the remainder to her young. In captive Ring Doves (*Streptopelia risoria*), Brisbin (1969) describes a significant rise in caloric intake of breeding pairs with nestlings to feed compared with the same pairs' caloric intake when incubating or in the courtship phase.

The female Village Weaver usually weighs 30 to 40 g, 20 to 25 per cent less than the male which usually weighs 40 to 50 g. The females ate fewer insects than did the male, but they ate lettuce twice as often and drank water more frequently. During her pre-egg phase, female WA often ate cuttlebone, which served the birds as a source of lime. Like the male,

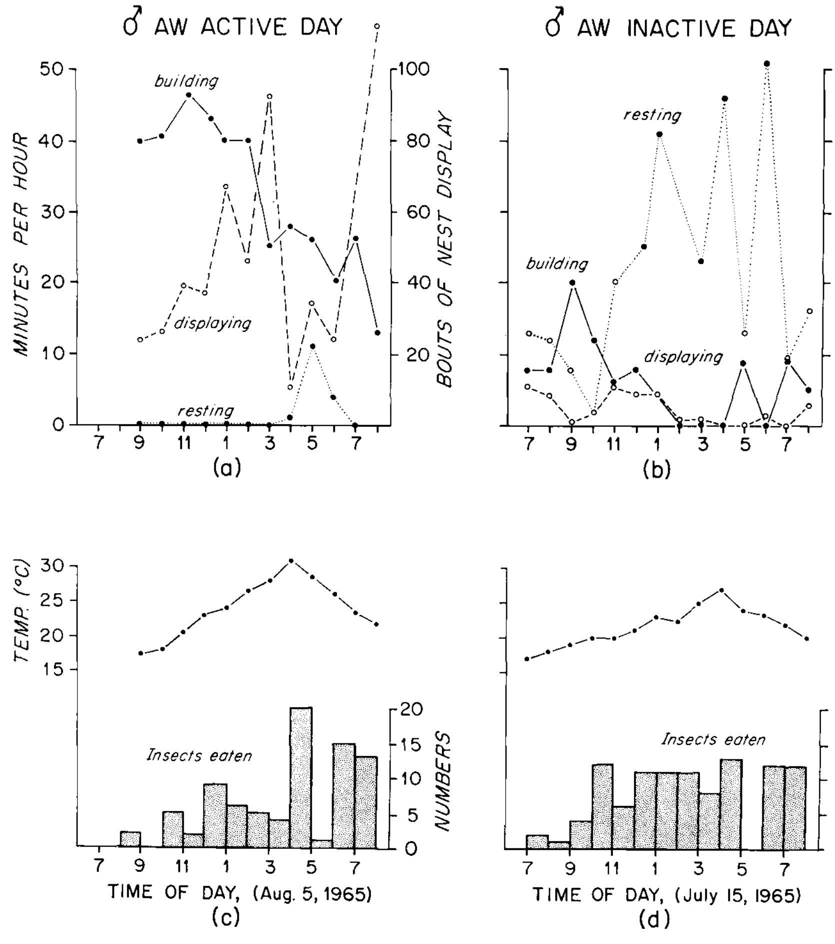

Figure 1. Distribution of some activities throughout the day of a male weaverbird in an aviary.

the females bathed three to five times a day, mostly in the afternoon and evening, and preened themselves at irregular intervals throughout the day, especially during the warmer hours and in the evening before retiring.

Distribution of activities during the day.—Figure 1a shows the distribution of certain important activities by male AW during the day on which he was most active and built a new nest. The time he spent building tended to fall off in the latter part of the day, and correspondingly, as the nest became more nearly completed he spent a greater amount of time in display, advertising the nest to visiting females. Not until late afternoon did he spend any time resting, and then only briefly. At this time the frequency of his nest displays fell off markedly, but rose greatly again toward evening when the females again began to visit the territories and nests of males in the colony.

Figure 1b records the same activities of male AW on one of his inactive days, when he spent most of his time resting. Peak periods of rest tended to alternate with minor peaks of activity during which AW refurbished some of his old nests. He started no new nests that day. He did a little building during the morning and most of his resting in the afternoon. He displayed his nests very little in the morning and almost not at all in the afternoon.

Figure 1c refers to the active day and has the same abscissa as Figure 1a directly above it, so activities during the same hours of the day can be compared directly. During the warmest hours of this day male AW rested more and built less than at other times, but there was no close association between temperature changes and either resting or building time. He ate insects (mealworms) during brief visits to the food bowl throughout the day, eating most in the late afternoon and evening. There was no correspondence between variations of air temperature and insects eaten. Relatively few mealworms were eaten in the morning compared with afternoon and evening, probably because AW then spent practically all his time either building or displaying his nest.

Figure 1d refers to the same inactive day as Figure 1b directly above it, and has the same abscissa. On this day male AW rested much more during the warm hours of the afternoon and early evening than he did in the cooler hours of the morning. He did most of his work on his various old nests in the morning. As on his active day, there was little or no correspondence between variations in air temperature and the times he took his meals. Male AW ate rather little during the first 4 hours of the day. He ate fewer insects (mealworms) in the morning than in the afternoon, and as during his active day, ate many mealworms in the 2 hours of evening prior to roosting time.

Figure 2a shows the distribution during the day of time a female weaverbird spent in the nest during different phases of her breeding cycle. An incubating female, or one brooding small nestlings, spends much more time in her nest at all hours of the day than does a female in the pre-egg stage or one with older nestlings. Female WA, when in the pre-egg phase, spent most time in her nest in the cool of early morning and almost no time there during the hot afternoon hours. In the first hour after leaving her nest in early morning she copulated four times, more than in any other hour of the day. She copulated with male AW 10 times that day, 8 times in the morning and twice in the afternoon. As Figure 2a shows, female WA ate a relatively heavy meal of insects (meal-

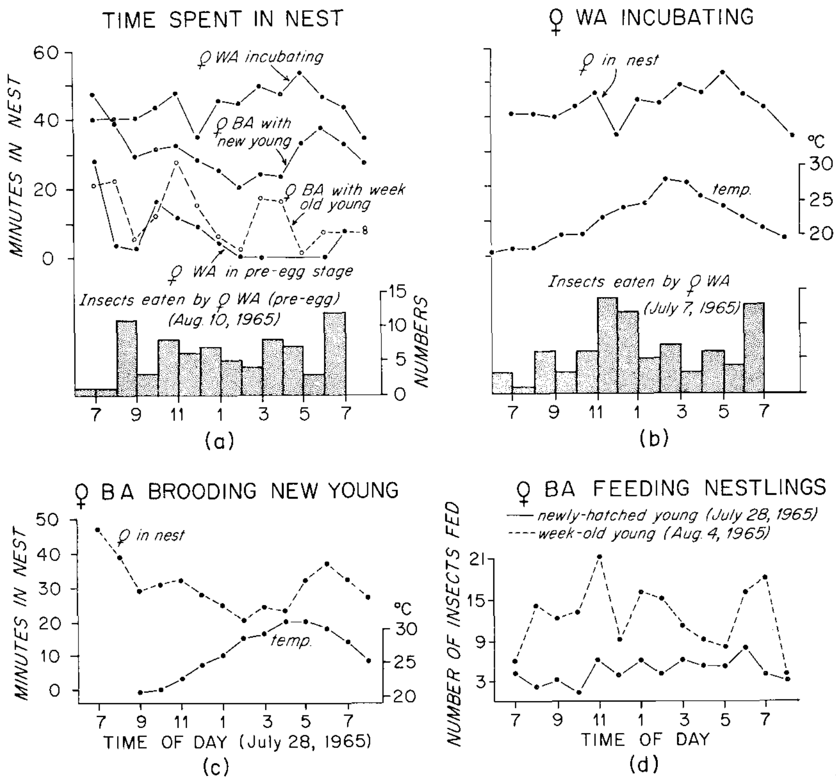

Figure 2. Distribution of some activities throughout the day of female weaverbirds at various phases of their reproductive cycle.

worms and crickets) fairly early in the morning and continued to eat insects at all hours of the day for lighter meals. In late evening toward roosting time, she again ate a rather heavy meal.

Figure 2b shows that when incubating, female WA spent most of each hour in her nest throughout the day. During the hottest hours she was rarely out, possibly resting in the shade furnished by the roofed nest as well as actually incubating for an undetermined proportion of the time she was in the nest. The length of time she stayed in her nest varied considerably, usually ranging from 5 to 15 minutes. She ate insects and little else, except some lettuce, at all hours of the day, having her heaviest meals at midday and again in late evening before retiring to her nest for the night. During the day she spent virtually no time resting outside her nest.

Figure 2c shows that female BA brooded her three newly-hatched nestlings most often in the cool hours of early morning and least often during part of the hot afternoon. She apparently resumed brooding the young in late afternoon long before the heat of the day had really begun to decline. Two of these young had hatched the day before, and the third by 08:00 on the day of observation.

As is evident from Figure 2a, female BA brooded her newly-hatched young much more consistently during the first day than she did when they were a week old. Furthermore, as Figure 2d shows, the young ones, when one day old or less, were fed small but frequent meals consistently throughout the day, whereas when they were a week old they were given much more food but were fed more erratically during the day. Irrespective of the age of the young a peak of feeding came in the evening just before dusk.

Awakening and roosting times.—The male consistently emerged from his sleeping nest in the early morning before the female left hers and consistently reentered it for the night well after the female had entered her sleeping nest at dusk. For example, on 28 July male RA emerged from his sleeping nest 5 minutes before sunrise, his mate, female BA, with small nestlings to feed, not until 5 minutes after sunrise. The discrepancy was greater between a male and an incubating female. On 7 July male AW emerged from his sleeping nest 33 minutes before his mate WA first came off her eggs.

The incubating female first left her nest in the morning 22 minutes later than she did when in the pre-egg phase of another brood one month later. When incubating, female WA entered her nest for the night (7 July) 2 minutes before sunset, but when in the pre-egg phase (10 August) not until 17 minutes after sundown. Female BA with newly-hatched young entered her nest for the night 15 minutes after sundown. It appears therefore that the strong attachment of an incubating female to her nest and eggs is also reflected in definitely later times of arising and earlier times of retiring.

Discussion

Time-motion studies of behavior are of limited significance unless they can be related to behavioral energetics in terms of metabolic measures. The ultimate goal is to be able to obtain a time and energy budget for a bird as one way to evaluate the relative importance of different behavioral activities in the life of the species. Because of measurement difficulties this goal is not yet fully attainable, but nevertheless some analysis of this problem will be profitable to indicate the general approach and also possible directions for future research. We use the male Village Weaverbird to illustrate, as our data for the more complicated case of the female are less adequate.

The problem of an energy budget can be divided into subsidiary problems of estimating energy income and energy expenditure. The energy income for male AW on the day he spent some 8 hours in building a new nest and in gathering nest materials can be calculated at about 19.6 kcal. This calculation was made as follows. As AW ate about 100 mealworms (Table 1) on this day, his caloric intake can be estimated by using Kale's (1965) measurement of 6.569 kcal/g of mealworms. We found 100 of our mealworms to weigh 12 g, equivalent to 4.26 g ash-free dry weight. If we assume 70 per cent assimilation, the same figure Kale found for his Long-billed Marsh Wrens, we reach an estimate of 19.6 kcal energy received by a weaverbird from 100 mealworms.

Energy expenditure estimates are more difficult, mainly because it is not yet possible to make direct, accurate measurements of the energy requirements in terms of calories or of oxygen consumed for nest building and for the nest advertisement display. The precise fractionation of available energy among the different behavioral acts of a species is a problem largely for the future. Some further discussion of this problem is given elsewhere (Collias and Collias, 1967). The standard metabolic rate for a bird of this weight (about 40 g) is approximately 12 kcal/day (King and Farner, 1961; Lasiewski and Dawson, 1967), leaving at the most only about 8 kcal for everything else that male AW did, to be provided from his daily food intake or his stores of body fat.

On each of his two inactive days when AW was watched all day, he rested a great deal, and since he ate about the same amount as on his active day (Table 1), these quiet days very probably served to restore his energy balance.

SUMMARY

Single individuals of the Village Weaverbird *Ploceus* (*Textor*) *cucullatus cucullatus* (Müller) were watched all day in a large outdoor aviary and the time or frequencies of various activities engaged in was recorded. The breeding behavior of the birds in the aviary was essentially similar to that seen in nature.

The male observed and a female in the pre-egg stage showed some tendency to rest more during the warmest hours. A female with small nestlings brooded them most during the cool hours of early morning. Both male and females took meals at practically all hours of day, with least food being eaten in the first two morning hours and most during the hour or two before the birds entered their sleeping nests for the night. Females retired before males, and males appeared before females in the morning.

The male built a nest on only one of the three days he was watched, and there was a radical difference in the proportions of activity and rest on his active and inactive days. As his food intake was about the same each day, it is suggested that his work expenditure on a day when he spent

some 8 hours building a new nest could have exceeded his caloric intake, and that his energy balance was restored on days of relative rest.

The activity pattern of the female varies greatly with her reproductive phase. The amount of time she spends in her nest is least in the pre-egg stage and greatest during days of incubation, while she consistently spends much more time in the nest with newly-hatched than with week-old nestlings. The female has to work much harder to feed the older nestlings that need more food. The female feeds mainly insects and solves part of her own energy needs more efficiently by eating part of large insects herself before giving the remainder to her young.

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