A QUANTITATIVE ANALYSIS OF BREEDING BEHAVIOR IN THE AFRICAN VILLAGE WEAVERBIRD

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The quantitative analysis of behavior, from the viewpoint of work or energy requirements, attempts to answer the two questions—*how* and *why* animals distribute their time and efforts as they do among different activities. The data of this report are concerned mainly with the first question. How animals spend their time is a descriptive problem requiring ascertainment of the frequency, and measurement of the duration, of each activity in the species' repertoire during the day and at different seasons. An answer to this problem has further scientific importance primarily in relation to the second question. The question as to why animals spend the amount of time that they do on each activity often requires experimental study for its answer. Different acts vary widely in the amount or intensity of activity involved and therefore in their energy requirements. There is a need for some common basis of comparison. We suggest that a common basis of measurement and comparison is to be found in the increase of metabolism, as indicated by the amount of oxygen consumed, over a resting level, resulting from each of the activities in the behavioral repertoire of a species. Currently available methods of measuring energy requirements are unfortunately still too complex for the purposes of the student of animal behavior in the field. As a result, there are still no adequate studies of the energy requirements of the different acts in the behavior of any species in nature. One purpose of this report is to stimulate research in this regard and to emphasize the need for physiological techniques adapted to use in the field.

In this study we have generally been able to *determine* the proportions of various kinds of behaviors important to breeding in a bird, but only to *estimate* in a crude and relative way the probable energy requirements of some of those different kinds of behavior patterns. For these estimates we have relied on certain physiological measurements by other workers on various species of birds, as reported in the literature. We have attempted to determine the amounts of different activities involved in producing and fledging a brood successfully, and we have compared the division of labor between male and female. We have been especially interested in attempting to estimate the relative energy demands of nest building in a species of weaverbird in comparison with other aspects of its breeding behavior. In the term "nest building" we include and emphasize the effort of gathering nest materials by the bird.

This report deals with a Congo race of the African Village Weaverbird (*Textor cucullatus graueri*). The species, for which we are using Chapin's

(1954) nomenclature, belongs to the subfamily Ploceinae or true weaverbirds, of the family Ploceidae. Our study was carried out in the eastern Congo at the Institute for Scientific Research in Central Africa, located about 3° south of the equator near Lake Kivu. The particular colony we studied was located in cultivated country at the edge of mountain forest at an elevation of 6,400 feet.

We did not make a quantitative study of behavioral activities during the non-breeding season, nor of molting which overlaps but little with onset and cessation of breeding. In this race of Village Weaverbird the energy demands of non-breeding behavior would appear to be of far less importance than those of breeding behavior; first, because the breeding season of the bird at the site of study lasts some nine months; second, because of the equable tropical climate with small seasonal changes; and third, because in our area at least, the species does not appear to migrate but merely assembles into large feeding and roosting flocks in nearby fields after cessation of breeding. In contrast, the energy demands of migration or of a severe winter season are large in many birds that breed in the north temperate zone as has been shown by E. P. Odum, S. C. Kendeigh, D. S. Farner, J. R. King, and others in a series of many papers (for citations, see Salt and Zeuthen, 1960; King and Farner, 1961). Our report is restricted to the breeding behavior in an apparently non-migratory population of a tropical species.

Brief accounts of our qualitative observations of the general breeding behavior of the birds in this colony have been published elsewhere (Collias and Collias, 1957, 1959, 1964). The essence of the present quantitative study was given at the annual meetings in 1965 of the American Ornithologists' Union, the Animal Behavior Society, and the American Society of Zoologists (abstract; Collias and Collias, 1965).

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METHODS

The Institute greatly facilitated our observations by constructing for us an observation tower, 10 m high and 2 m square. This tower was placed some 20 feet from the eucalyptus tree in which the main colony studied was situated. Over half the birds in the colony, including most of the males, were captured with Japanese mist nets, given colored leg bands in distinctive individual combinations, and then released. The colony was watched every day for the first few months. During the breeding season of 1956–1957 the birds were watched over a period of nine months, and for

TABLE 1

MEAN MONTHLY RAINFALL AND TEMPERATURE AT A WEATHER STATION NEAR THE AREA OF STUDY[1]

	Mean monthly rainfall (mm)	*Mean monthly temperature (°C)*	
		Maximum	*Minimum*
January	173	20.9	11.7
February	118	20.7	11.4
March	229	20.6	10.9
April	248	19.4	12.9
May	180	18.5	11.5
June	70	19.7	10.6
July	32	20.0	8.5
August	76	20.9	8.8
September	160	21.2	9.8
October	246	21.1	10.5
November	155	21.1	10.6
December	190	20.8	11.5
Annual	1883	20.4	10.7

[1] From Scaëtta (1934).

a total of over 355 hours. These observation hours were distributed as follows during different times of day: 0600–0900, 170 hours; 0900–1200, 115 hours; 1200–1500, 25 hours; and 1500–1800, 45 hours. We used 9 × 35 or 7 × 35 binoculars and a 30× telescope. The birds were not at all shy and it was not necessary to hide in a blind to insure their normal activity. Since every bird as a rule occupied a distinctive site or nest in the colony, it was easy to follow the history of the specific nests. Every nest in the colony was given a serial number, its place in the tree was mapped, and the male or pair owning it was designated. Distances the birds flew in gathering nest materials or food were estimated visually and by pacing.

BREEDING PHENOLOGY AND HISTORY OF NESTS

Our weaverbird colony was situated on the Tshibati Farm of the Institute. Table 1 shows the seasonal pattern of temperature and rainfall at the nearby Tshibinda weather station, located 10 km away and slightly higher than Tshibati, but with essentially the same climate. This table is based on four years' weather data, and illustrates the relatively small variations in temperature and the profound variations in rainfall typical of many tropical climates. July is the driest month, while October and April are generally the rainiest months, as based on these somewhat limited meteorological data.

In this species of weaverbird the male weaves the outer shell of the nest, and attracts the female to the nest by a special display. The female, if she accepts, lines the nest, does all of the incubating and most of the feeding of the young. Figure 1 shows the basic breeding phenology of the colony. During the breeding season the number of male birds that held territories in the colony tree gradually increased from 2 to 22 and of females with clutches or broods from 0 to about 30. There were generally

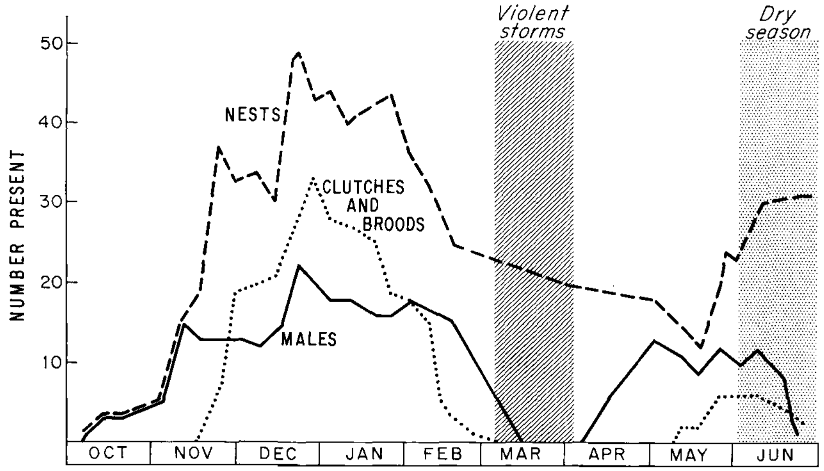

Figure 1. Basic breeding phenology in a colony of Village Weaverbirds situated in a eucalyptus tree in the eastern Congo in the breeding season of 1956–1957. Points are graphed at approximately weekly intervals (except for March and April when the colony was largely deserted and was observed less frequently), showing numbers of male birds or nests present on a given date, and numbers of clutches and broods present at least some time in the preceding week.

about 15 males and 30 to 40 nests in the tree. The birds normally cease to breed during the dry season from June to September, and during the year of study they also stopped breeding during a succession of especially violent storms in March and early April at the peak of the rainy season. The gradual cessation of breeding during late January and in February was in part a result of the fact that the natives at these times take the young for food, a tradition to which the Village Weaverbird is regularly subjected.

The number of nests present in the colony tree at any one time reflects the turnover rate between nests built and nests destroyed. After a week or two a male will usually tear down a nest that has been consistently ignored or rejected by inspecting females and build a fresh model in its place (Collias and Collias, 1959).

Figure 2 gives some of the details of the rate that nests were built or torn down by the males in relation to rate of inspection of nests by unmated females. The data are summarized for bi-weekly periods. The males start building nests more than a month prior to visits by any females, and after the peak of the breeding season, the males continue to build at a high rate for a few weeks despite a greatly diminished rate of nest visiting by the females. During the breeding season, the rate of nest building is greatly stimulated by any increase in the rate of visiting of

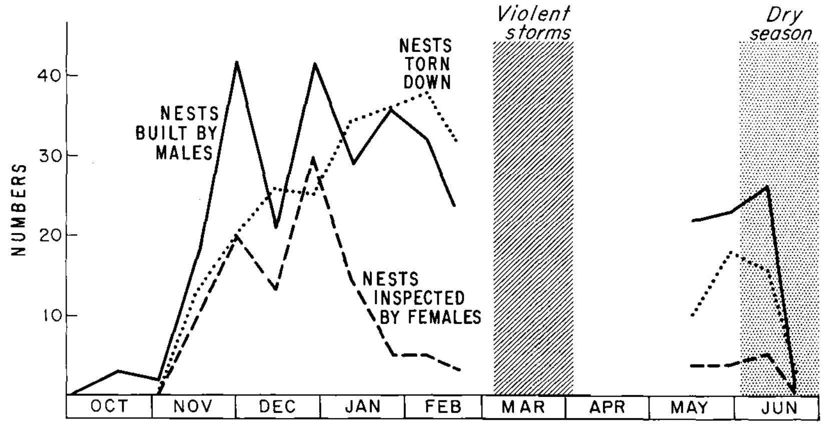

Figure 2. The rate at which males in the colony built and destroyed their own nests, in relationship to numbers of these nests that were inspected by prospecting females. Points are graphed at bi-weekly intervals, and represent the summation over the preceding two weeks.

nests by prospecting females, and a fall in rate of nest building generally parallels a fall in the rate of female visits to the colony to inspect nests. The inspecting females often arrive in small flocks, are courted, and stimulate vigorous outbursts of building activity by the males immediately following their departure. Similarly, with successive brood periods, each covering about a month from acceptance of a nest to fledging of the young, there occurs a succession of peaks in building activity by the males with successive peaks of building being about a month apart.

Figure 2 also shows that during the early part of the breeding season an increase in the rate of nest building exceeded the gradual increase in rate of nest destruction by the males. As the available and suitable twigs in the colony tree become crowded with brood nests, the rate at which nests are destroyed continues to increase because both old brood nests and non-brood nests which have been inspected and rejected by the females are torn down by the males. Near the end of the breeding season, the rates of nest building and of nest destruction by the males and of inspection visits by unmated females all become rather low. The whole intensity of breeding activity greatly diminishes and breeding ends with cessation of the rains and onset of the dry season.

A total of 342 nests was built during the entire season, including 51 that coincided so closely with the period of violent storms that there was virtually no chance of their having a brood. In fact, 47 of these 51 nests were never accepted by females. Table 2 shows the history of the remaining 291 nests that were built in the colony during the more favorable

TABLE 2
HISTORY OF NESTS IN THE COLONY DURING THE BREEDING SEASON[1]

Stage reached	*First 100 nests*	*Second 100 nests*	*Last 91 nests*	*Total 291 nests*
Never visited by female	44	55	67	166
Inspected and rejected	19	13	10	42
Accepted; eggs lost	10	8	10	28
Nestlings lost	13	10	0	23
Broods fledged	14	14[2]	4[3]	32

[1] Excluding 51 nests that had virtually no chance of success because of violent storms.
[2] Assuming last 4 broods fledged.
[3] Assuming last 3 broods fledged.

part of the breeding season. This table is subdivided to show the history of the first 100 nests, the second 100 (built during the peak of the season), and the last 91 nests. Our data are most complete and observation times greatest for the first 100 nests.

Table 2 reveals that the male Village Weaverbird has to do a tremendous amount of nest building for every brood fledged. (Throughout, we use "brood fledged" to imply that at least one young fledged.) Thus, early in the season almost half and, late in the season three-fourths, of the nests built were never seen to be entered by a female. About 10 to 20 per cent were inspected internally and rejected. Of those nests that were accepted, the eggs or nestlings were lost in a majority of instances. In fact, of the first 100 nests built only 14 ultimately contained broods that fledged, this during what seemed to be the most favorable part of the breeding season. Success was poorest in the latter part of the breeding season, coinciding with the onset of the dry season.

We attempted to obtain some idea of the proportion of the birds' energy required for nest building relative to other breeding activities. It is, of course, necessary to take into account the effort expended in failure for every brood successfully fledged. From the data presented in Table 2, together with other observations, we were able to calculate for the first 100 nests built, corresponding to the first 14 broods fledged, some relevant measures. To help raise these 14 successful broods, it was necessary for the *males* of the colony to: (1) establish and maintain individual territories, (2) build and display 100 nests, (3) copulate for 37 clutches of eggs, (4) reinforce 37 nests accepted, and (5) help feed 27 broods, including 13 failures. Correspondingly, to help raise these 14 broods it was necessary for the *females* to: (1) inspect the interior of 56 nests, (2) copulate for 37 clutches of eggs, (3) lay eggs in 37 nests, (4) line those 37 nests (only partially in 10 of them in which the eggs were lost) and (5) help feed 27 broods, including 13 failures.

TABLE 3
AVERAGE DISTANCE A MALE WEAVER OF THE COLONY FLEW IN GATHERING MATERIALS FOR A NEST

Materials gathered	*Number of pieces*	*Round trip (meters)*	*Number of trips*	*Kilometers flown*
For outer woven shell				
Brood nest	325	80	325	26.0
Non-brood nest	275	80	275	22.0
For ceiling				
Elephant grass	60	80	45	3.6
Dicot leaves	140	0–30	100	3.0
Grass-heads	25	80	13	1.0
Totals				
Brood nest	550		483	33.6
Non-brood nest	500		433	29.6

NESTS

Table 3 gives an estimate of the average amount of flying required by a male weaver of the colony in order to gather materials to build a nest. To weave the outer shell, he uses about 275 long, narrow strips torn from the leaves of elephant grass (*Pennisetum purpureum*). Prior to acceptance of the nest by a female, the male puts in a more or less rain-proof ceiling that is thatched, but not woven, of short pieces of nest material (from *Pennisetum*, plus whole leaves of *Eucalyptus* or leaflets of *Grevillea*, and some grass heads). The male reinforces a brood nest by adding an average of about 50 long strips to its outside, but he is no longer permitted by the female to enter to work on the inside. We estimated the male has to fly a total distance of about 30 to 34 km in building a brood nest. Since frequent take-offs and landings are involved, the energy required is doubtless greater than for merely flying this distance non-stop.

Having built a nest, the male must also "display it," in order to attract visiting females to it. The display used for this purpose involves much excited hopping and flying back and forth in the tree and much vocalizing, all on the part of the male. The peak of his display comes when he hangs beneath the nest from the entrance (which opens downward), flutters his outstretched wings vigorously, and utters special call-notes. The female is often stimulated by this display to enter and inspect the nest. The hanging display of the male must require a fair amount of his energy, but we could not measure this precisely in the field. Often each bout of such display lasts only a few seconds but it may last much longer. From measurements with a stop watch taken in an aviary colony of this species we calculated that the male may spend as much as an hour a day in hanging display when females are actively visiting the colony. Until a method can be devised to measure the energy demands of this display

TABLE 4
AVERAGE DISTANCE A FEMALE WEAVER OF THE COLONY FLEW IN LINING THE BOTTOM OF A BROOD NEST

Materials gathered	*Number of pieces*	*Round trip (meters)*	*Number of trips*	*Kilometers flown*
Elephant grass[1]	35	80	35	2.8
Grass-heads[2]	565	80	280	22.4
Feathers[2]	35	100	35	3.5
Plant pappus[2]	⅓ cup	80	40?	3.2
Totals	635+		390	31.9

[1] Average of 10 nests.
[2] Average of 2 nests.

accurately, we can only state that most of the male's total activity goes into building *and displaying* nests. We shall elaborate this conclusion after considering the demands of other aspects of breeding behavior.

Females as a rule accept only fresh nests and if a nest fails to be accepted in a week or two, the male ceases to display it, tears it down and puts up a fresh one in its place. Whereas it takes him one or two days to build a nest, he can tear one down in only 15 to 30 minutes, tearing away especially at the attachment of the nest to the twigs. Nest destruction, therefore, in contrast to nest construction, requires only a relatively slight amount of the male's time and energy.

Only 56 of the first 100 nests built were seen to be entered by a female (Table 2). With an average of about 12 internal inspections per nest per day, some 672 such inspections were required before 14 successful broods were fledged, or an average of 48 internal inspections for every brood fledged. But inspection of nests would not seem to be very demanding of energy since it consists largely of the female's sitting in one spot in the territory and looking at the nests and the displaying males, plus entering by a very short flight and sitting in, or poking and pulling at, the inner materials of the nest once she has entered.

Table 4 gives an estimate of the amount of flying a female has to do in order to line the interior of the nest, and this amount turns out to be surprisingly great, being some 32 km and almost equalling the amount involved in the much more conspicuous work of the male insofar as the brood nest is concerned. One reason for this is that the female continues to bring soft lining materials, especially feathery grass-heads (*Eragrostis*) to the nest throughout the incubation period of 12 days as well as before laying eggs and even to some degree after the young hatch.

FIGHTING AND TERRITORIAL DEFENSE

With regard to fighting and territorial defense by males, although a grappling fight would seem to expend more energy than does any other single activity, such vigorous fights are rare. Only 10 were observed in the period when the first 100 nests were built and the first 14 broods fledged, or about 5 fights for every 7 broods fledged. Actually, no other fights were witnessed in this colony during the remainder of the season despite many hours of observation. Furthermore, each fight generally lasted only a few minutes or less. The total demand of grappling fights on the over-all energy budget of the birds would, therefore, appear to be relatively minor. Similarly, although the male may actually spend most of his time on certain days guarding his territory, such guarding as a rule consists mostly of resting in the territory. Even border display contests by posturing, singing, and pecking back and forth, ordinarily take only a very small fraction of his time each day. After the early breeding season, territorial intrusions and thefts of material from nests are not very frequent, and the intruder often promptly leaves when the resident male merely approaches.

COPULATION, EGG LAYING, AND INCUBATION

A moderate amount of activity during the breeding season results from copulations, which, however, are normally restricted to an average of only about three days just before and during the period of egg laying. One female was seen to copulate 26 times during 9½ hours of observation over three days; another copulated 11 times during 23 hours of observation over four days. Estimating a total of some 40 copulations per clutch and allowing for 23 broods and clutches that failed, males and females of this colony engaged in something like 100 copulations for each brood fledged. Unfortunately, we do not know the physiological demands of copulation in birds in terms of energetics, but the time factor involved in copulation is so short in birds (generally being of momentary duration in the Village Weaverbird), that we may perhaps be justified in considering that such mating activities would be of secondary importance with regard to the over-all energy budget involved in raising a brood.

The metabolic demands on the female of forming and laying the two eggs of the average clutch may be considerable, but are unknown for this species. Incubation of the eggs allows the female to sit quietly most of the day, and therefore, the drain on her energy for this behavioral pattern would appear to be relatively small; however, some energy is, of course, expended to keep the eggs warm and to bring them back up to temperature whenever the female returns to her eggs after having left them to feed, drink, bathe, etc. Kendeigh (1963) has calculated for the House Wren (*Troglodytes aedon*) that the energy expended for incubation may be considerable on cold days, but is probably slight on moderately warm days. Comparable figures are not available for the Village Weaver; the

TABLE 5
FEEDING RATES OF NESTLINGS BY VILLAGE WEAVERBIRDS OF THE RACE *GRAUERI*

Time of day	*Number of nests*	*Hours observed*	*Feeding rate/hour/brood*	
			Male	*Female*
0600–0900	9	12.5	1.8	6.0
0900–1200	6	8.5	2.2	3.4
1200–1500	7	4.5	2.0	4.4
1500–1800	11	8.0	1.8	3.2

female conserves her energy by sitting steadily at night and by not leaving her nest until long after dawn. Also she has only to face generally equable temperatures during the day (in much of its geographic range this tropical species inhabits lower and warmer elevations than at Tshibati, the study area).

FEEDING OF THE YOUNG

We took a considerable number of samples of feeding rates for various broods at different times of day and at different ages of nestlings. The results are summarized in Table 5. On the whole, except for heavy feeding by the female in early morning, there are no very pronounced differences in feeding rates at different times of day. The total feeding rate per brood per hour is shown in Table 6 for both sexes. This table shows that in this colony the female, on the average, fed the nestlings more than twice as often as did the male, and that she had to fly more than twice as much as the male in so doing.

The reason for the emphasis on the role of amount of flying in the breeding behavior of this species is that flying, at least in the case of flapping flight, probably requires much more energy expenditure by a bird than almost any other activity it engages in (see p. 407). Table 7 provides a summary of the demands for flying activity in fledging a brood by the weaverbirds in the colony we studied. This table takes into account the broods that failed as well as those that succeeded and covers the entire season, during which 342 nests were built. It is evident that for every

TABLE 6
AVERAGE DISTANCE FLOWN BY PARENT BIRDS TO FEED EACH OF THE FIRST 14 BROODS IN THE COLONY TO FLEDGING

Activity	*Male*	*Female*
Feeding rate/brood/hour	1.9	4.4
Total feedings/day	22.8	52.8
Feedings/nestling period of 20 days	456	1056
Kilometers flown (based on 300 meters/trip)	137	317

TABLE 7
AVERAGE FLYING TIME REQUIRED FOR VILLAGE WEAVERBIRDS TO FLEDGE A BROOD

Activity	*Number of nests*[1]	*Flying required (km)*	
		Male	*Female*
Gathering nest materials			
Non-brood nests	8.0	237	0
Nests where brood failed	1.7	54	27
Nests where brood fledged	1.0	34	32
Totals		325	59
Feeding of nestlings			
Nest where nestlings lost	0.7	48	111
Nests where brood fledged	1.0	137	317
Totals		185	428

[1] Expressed as the average number of nests of each type per each successful nest. Based on a total of 342 nests.

brood that fledged, the males had to build 9 or 10 unsuccessful nests. They also had to do almost 10 times as much flying to build nests that failed or had no brood as for the successful nests. The females are spared much of this wasted effort in nest building, since they have only to line the brood nests. On the other hand a female's energy is channeled more into the feeding of nestlings. Whereas, about two-thirds (64 per cent) of the flying done by the male was for gathering nest materials, almost nine-tenths (88 per cent) of that done by the female went for feeding nestlings. After the young leave the nest, her burden in this regard actually increases, since she takes complete charge of the fledglings and may feed them daily for a few weeks. Meanwhile, the male stays in the colony tree to build more nests and attempts to attract new females to them.

It is evident that economy of energy expenditure in this species must require an adequate source of suitable nest materials as well as an abundant food supply near the breeding colony. Almost every breeding colony of the scores that we observed in the Congo and in East Africa was within 50 yards of suitable nesting material, generally a patch of elephant grass (*Pennisetum purpureum*) or of palm trees. In traveling eastward from the Congo to Kenya in March we noticed that with increasing dryness the elephant grass disappeared and as it did so there was an abrupt disappearance also of colonies of the Village Weaver. Thus such colonies were abundant west of Entebbe in Uganda, but became relatively scarce east of Entebbe along the route we traveled.

DISCUSSION

As mentioned earlier, a number of authors have investigated the energetics of bird migration by estimating the caloric intake and outgo during migration. Studies of the energetics of other aspects of bird behavior have attracted less attention. Orians (1961) and Kale (1965) have made stimulating attempts to assess the bioenergetics of breeding behavior of certain blackbirds (Icteridae) and of Long-billed Marsh Wrens (*Telmatodytes palustris*), respectively, and have dealt with problems somewhat similar to the main objectives of our own report. However, present techniques do not permit exact determinations of the energy involved in most activities as they occur in nature. Fortunately, there are some physiological data available for the energy demands of flapping flight, and some of these studies enable us to conclude that the demands of flying, on the energy resources of a male Village Weaverbird, in gathering materials for nest building are probably greater than the demands of other breeding activities. Studies by Zeuthen (1942), Pearson (1950, 1954), Lasiewski (1963), LeFebvre (1964), and Tucker (1966) on various birds indicate that oxygen consumption and metabolism during flapping flight are from five to more than eight times the resting values. The measurements of pulmonary ventilation in pigeons by Hart and Roy (1966) indicate increases of 7 times over the resting value when walking and some 20 times when flying. The oxygen consumption of Long-billed Marsh Wrens moving about in a respirometer was only 26 to 46 per cent greater than that of inactive birds (Kale, 1965: 51–53).

We paid little attention to the amount of time spent by the weaverbirds in foraging for themselves. There are two reasons for this lack of attention to what would seem to be a highly important thing to measure. Village Weaverbirds feeding young in nature were seen to eat part of the insect, especially of large insects, themselves before feeding the nestlings; in close observation of these birds in our aviaries, we found such behavior to be regular, when crickets were given as insect food for nestlings. Therefore, our tables of feeding visits to the nestlings in nature cover a good part of the time and effort spent by the parent in feeding itself. In the second place, during most of the breeding season, male birds without nestlings to feed were only rarely seen foraging, although more than 12 specimens of both sexes collected generally had seeds or insects or both in their stomachs. In our all-day watches of captive Village Weaverbirds in aviaries, we and our assistants (Janice Krutak Victoria, Martin Graham, and Ellen Coutlee) have observed that a male bird can eat enough food (mainly meal worms) in less than 10 minutes, spread throughout the day, to maintain itself for a whole day. Insects and grain were plentiful at Tshibati Farm. Our general impression was that with very little time and effort the males were able to garner enough food for themselves, incidental to their excursions for gathering nest material. They obviously devoted much more time to the latter activity than to foraging, except when feeding nestlings.

Where males are more numerous in a particular colony than are breeding females, less effort in feeding nestlings by each male would be expected per brood than in colonies where males are fewer. However, we did not measure the sex ratio throughout the season in different colonies. In our colony, taking the breeding season as a whole, each banded male averaged almost three different mates, while each banded female had on the average only one or two different mates. Unlike the females, male birds very often had more than one mate simultaneously. It is possible there is an element of economy in polygyny for the colony. Since the female weighs about 20 per cent less than the male, it is conceivable that flying is less work for her. It would therefore place less of a demand on the energy resources of the colony as a whole for the females to do most of the flying involved in obtaining food for the young.

We did not measure the influence of predation pressure on the total activity of the colony, although during the height of the breeding season, the colony was attacked or threatened almost every day by certain species of hawks, especially the African Goshawk (*Accipiter tachiro*). Generally, only a few such attacks or threatened attacks were seen on any one day, despite our many hours of observation. When attacked by a hawk the birds would abruptly dive into the corner of elephant grass beneath the colony tree or take evasive action, flying low and swiftly to the dense shelter of a thorny tree about 75 yards away. However, usually fewer than 15 minutes would elapse before the weavers returned to their colony and resumed normal activities. One day an accipitrine hawk actually captured a weaverbird and more than 45 minutes after this occurrence, a rare one relative to unsuccessful attacks, not a weaver had returned to the colony tree.

The quantitative requirements for the various activities of a bird will, of course, vary with the nature of the life of the species concerned. As yet, investigations in this relatively new area of research are too few to make comparisons possible between many different races or species. Among Village Weaverbirds of the west African race *T. c. cucullatus* the males, as we found in aviary observations over some seven years, almost never fed the nestlings, in strong contrast to our field observations of males of the Congo race *T. c. graueri.*

Orians (1961), reasoning by analogy from Brody's (1954) summaries of the bioenergetics of farm animals and Pearson's (1950, 1954) studies of the metabolic demands of flight in hummingbirds, made some rough estimates of the percentage of energy above the resting level required for various breeding activities by a pair of Red-winged Blackbirds (*Agelaius phoeniceus*) and of Tricolored Blackbirds (*Agelaius tricolor*) in California. The male Red-wing, Orians found, does not help feed the young and apparently spends most of his energy during the breeding season in territorial defense, while the female searches for food on foot. In Tricolors, the feeding grounds are much more distant from the nest sites and most of the energy of both male and female goes into flying to and from these feeding areas. In neither species does nest building appear to require more than a small share of the energy resources of the birds.

In Washington, Verner (1950*a, b*) made an interesting and detailed study of the amount of time spent in various breeding activities by male Long-billed Marsh Wrens. Like the weaverbirds, wrens are a predominantly tropical family. The Long-billed Marsh Wren, while of course not itself a tropical species, resembles the Village Weaverbird in that, in the course of the breeding season, the male builds many roofed nests to which he attempts to attract unmated females. Verner based his numerical data particularly upon five marked males of a resident population, and these males built an average of 14 nests each. This study is of special interest in that here we have a small bird from a family of tropical origin maintaining itself in the north temperate zone. In contrast to the equatorial weaverbirds we studied, Verner's wrens spent about 10 times as much of their time foraging (usually within the territory) as in nest building. But this wren is only half the weight of the weaverbird species, lives in a cooler climate, and has twice as many nestlings to feed. Thus, a male marsh wren in the north temperate zone must meet much greater metabolic demands and needs to forage much more than do equatorial Village Weaverbirds. Second, nest building appears to be more economical in the Long-billed Marsh Wren, as the nest is built in the midst of a plentiful source of nest material and only very short trips (averaging 10 to 30 feet) are needed to gather the material.

SUMMARY

The quantitative analysis of animal behavior, including the behavior and life history of birds, is a large and relatively new field for investigation. An approach is illustrated in terms of the amount of different types of activity required to produce and fledge a brood in a species of weaverbird.

It is suggested that the amount of oxygen consumed during a given activity provides a common basis for comparing the energy requirements of different kinds of behavior patterns. There is definite need for more adequate techniques in this regard to aid the quantitative analysis of behavior in the field. Current studies of physiologists indicate that flapping flight in a bird takes vastly more energy than does sitting or walking. But there are no measurements available at present for comparing the relative metabolic requirements of flying, display, and mating activities as they occur in the field. However, there are great differences in frequency of occurrence of these activities in the species of bird studied.

In the African Village Weaverbird (*Textor cucullatus graueri*) the male weaves the nest, the female lines its lower part and incubates. About 9 or 10 nests were woven for every 1 from which a brood was fledged in the course of the nine-month breeding season. Both sexes feed nestlings, the female taking much the greater share. When the amounts of flying (considered as one of the activities demanding the most energy) required to build nests and to feed nestlings were compared, it became evident that most of the male's energy over a resting level must go into building and "displaying" nests, that of the female into rearing young. In turn, these energy demands may influence the habitat requirements and distribution of the species.

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