SOME OBSERVATIONS ON BEHAVIORAL ENERGETICS IN THE VILLAGE WEAVERBIRD. I. COMPARISON OF COLONIES FROM TWO SUBSPECIES IN NATURE

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BEHAVIORAL ENERGETICS deals with the relationship between animal behavior and energy income and expenditure. It is a relatively new and undeveloped field of study that attempts to account for the *amount* of time and effort that animals put into their various activities. The major objective of this and the following paper is to show how the quantitative aspects of behavior could eventually be expressed in terms of energetics using both behavioral and, where possible, caloric measures. This approach is relatively new, and we certainly do not claim to have attained anything like a final solution. The term "energy" is derived from a Greek word *energia,* which simply means activity, but even in modern usage the term *energy* in a broad sense is not synonymous with calories, as heat is only one form of energy. Nevertheless measurements of muscular activity and of energy budgets in terms of calories seem to be one of the most promising ways to quantify the different kinds of behavior on a comparable basis.

We need better and more accurate methods of measuring the energy demands of different behavioral patterns. Three basic methods are involved: (1) Counting the *frequency* of acts that can be easily counted, for example, the number of fights seen, number of pieces of nest material placed into a nest. (2) Taking the *time,* as with a stopwatch, devoted to acts of variable length that cannot easily be counted, such as time spent building a nest or displaying it, defending territory, or just resting. (3) Measuring or estimating the energy or *effort* required by different acts relative to each other. Thus in the male African Village Weaverbird (*Ploceus cucullatus*), fighting quite obviously takes more effort per unit of time than does flying to gather nest materials or displaying the nest to females, which in turn are more intense activities than building on the nest. In the female, flying to gather food for the nestlings evidently takes more work than does self-preening or resting. The best current studies of physiologists indicate that in flapping flight the oxygen consumption of a small bird increases from 5 to 20 times the standard or "resting" metabolism (cf. esp. Tucker, 1966, 1968).

Theoretically one could arrange all behavioral acts in order of their energy requirements by measuring the metabolic demand or oxygen consumed during and immediately following each act (Collias and Collias, 1967). But as yet no adequate method is available for measuring oxygen uptake *continually* in unrestrained, freely-moving animals engaging in

their normal behavioral repertoire. Therefore current studies of behavioral energetics, like this one, must be of an interim nature, and their prime function is to provide a point of view and to stimulate the development of better methods of measurement.

Details of breeding behavior for *Ploceus cucullatus* are given elsewhere (Collias and Collias, 1959, 1964, 1965, 1967; Crook, 1963). The birds are granivorous but also eat insects. In a previous quantitative analysis of breeding behavior in this species (Collias and Collias, 1967) we concluded that most of the male's energy above a resting level is expended in building nests and displaying these nests to unmated females, whereas most of the female's energy is expended in rearing the young. We found, for example, in a colony that was followed through the breeding season, that a male had to build 9 or 10 nests for every one from which a brood was fledged.

This previous study was on the race *graueri* of Central Africa, and involved over 355 hours of field observations. We now wish to compare these observations with somewhat similar ones we made on the West African race *cucullatus*, and to amplify a preliminary report (Collias and Collias, 1969). We have been especially interested in comparing the division of labor between male and female in reproductive behavior of the two subspecies. The taxonomy and geographic distribution of the various races of *Ploceus* (*Textor*) *cucullatus* are described by Chapin (1954).

Village Weaverbirds breed in conspicuous and noisy colonies with up to 200 or more birds nesting in a single tree. The species is polygynous, and each male builds a series of nests to each of which he attempts to attract unmated females by means of a stereotyped attraction display. If the female accepts the nest she lines it, lays eggs, incubates, and does most or all the feeding of the young. If no female accepts his nest the male tears it down and builds a new one in its place.

Procedure of the Study

The locality of study was in the rice culture region of Richard-Toll (16° 25′ N, 15° 42′ W) in northwestern Senegal, in savanna country near the south bank of the Senegal River just south of the Sahara Desert and at almost the periphery of the geographic range of the Village Weaver. For a detailed description of the various habitats of this part of Senegal in relation to avifauna, see Morel (1968). Irrigation for rice culture near Richard-Toll has produced quite good habitat conditions for the Village Weavers, which nest in colonies in the *Acacia nilotica* trees growing along the banks of the canals.

This locality has a 3-month rainy season (July–October) when the Village Weaverbirds breed and a 9-month dry season (Morel and Morel, 1959). We made our field observations during the rainy season of 1967 while based at the Station d'Ornithologie at Richard-Toll. Some 238 hours were spent observing weaverbird colonies here, but this report is largely based on 140 hours spent watching one colony in which most of

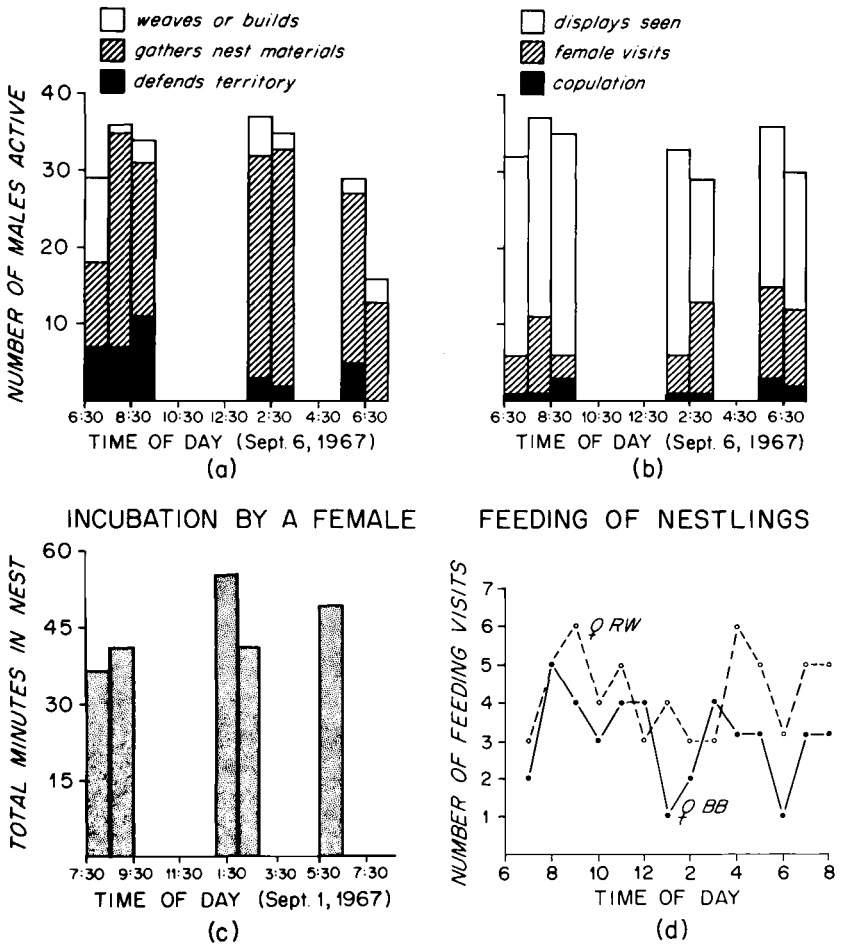

Figure 1. Relationship to time of day of some important activities of the Village Weaverbird in Senegal.

the males and almost one-third of the females were captured with mist nets and given colored leg bands for individual identification. This colony contained about a dozen males and twice that number of females. We counted the number of occurrences of specific behavioral acts and timed the duration of the more variable acts with a stopwatch, as described in the section on results.

Results of Field Observations

Daily routine.—Figure 1 depicts some important activities during different times of day, and shows that the breeding behavior of both male and female *P. c. cucullatus* in this locality was quite generally distributed

TABLE 1
COMPOSITION OF NESTS FROM TWO SUBSPECIES OF *PLOCEUS CUCULLATUS*[1]

	P. c. graueri	*P. c. cucullatus*
Outer shell (long strips)		
Nonbrood nest	275	212
Brood nest	325	258
Ceiling		
Pieces of grass leaf	60	226
Grass heads	25	5
Dicot leaves	140	31
Bottom lining		
Grass strips	35	72
Grass heads	565	307
Feathers	35	0
Plant down	⅓ cup	⅛ cup

[1] Data for *graueri* from Collias and Collias (1967). For *cucullatus*, counts of strips in outer shells based on one nest each, the rest of figures on an average of four nests.

throughout the day with no very pronounced rise or fall in activity at particular times except for the first and last half-hour of the day. We had earlier found similar relations to time of day for the race *graueri*, which suggests that our observations should be comparable for the two races, largely irrespective of time of day. In each case the great bulk of observations came during the morning hours. Nest building or nest advertisement took more of the male's day than did any other activities.

Demands of nest building and nest advertisement.—We have been unable to decide whether more of the male's energy is expended for building or for displaying his nests, largely because the relative metabolic requirements of these two activities are unknown. In the present study of *P. c. cucullatus* we timed with a stopwatch the variable acts of gathering nest materials, actual building, and the displaying of nests in a natural and presumably typical situation. Four different male birds were watched for a total of 15 hours. Although more total time was devoted to gathering of nest materials (80 minutes) and to nest building (213 minutes) than to display of the nest (61 minutes), a good deal of time (one hour out of 15) was devoted to the latter. In this display the male hangs inverted at the bottom entrance of the nest, flaps his wings widely and vigorously, and vocalizes continuously. This display attracts unmated females to the nest. The gathering of nest materials and the advertisement display are both demanding activities and both take a substantial portion of the male bird's time each day. It should be noted that the time spent gathering nest materials includes both actual gathering and the time required to fly to and from the gathering site some 20 m from the colony. Our observations on *cucullatus* lead to the same conclusion made previously

TABLE 2
COMPARISON OF NEST BUILDING IN TWO RACES OF *PLOCEUS CUCULLATUS* IN A 13-DAY PERIOD AT THE PEAK OF THE BREEDING SEASON

	cucullatus	*graueri*	Probability[1]
Number of resident males	9	18	
Nests per male at start	5.1	2.4	<0.005
Nests built per male	3.3	1.4	<0.005
Nests destroyed per male	3.1	1.6	<0.005
Resident females per male	3.1	1.8	<0.05

[1] Probabilities of no difference based on *t*-test with square root transformation (Dixon and Massey, 1969: 116, 324).

for a colony of *graueri*, that a major part of the male's total energy is expended in building and displaying his nests.

Composition of the nest.—Table 1 gives sample counts of the number of pieces of different kinds of materials in nests from birds of each subspecies in the localities of special study. The outer shell of the nest was woven by the male of long strips torn from leaves of elephant grass (*Pennisetum purpureum*) by *graueri* and from leaves of a sedge (*Carex*) and from leaves of a tall grass (*Andropogan gayanus*) by *cucullatus*. The colony of *graueri* was in a clearing in montane forest and the outer shell of the nests contained more strips and probably gave a little better insulation against the cooler climate. Furthermore the lining put in by the female *graueri* was much thicker, containing feathers and many more grassheads, than the lining put in by the female *cucullatus*. The total pieces of lining material in the Central African nests averaged 635, but only 379 in the West African nests. The Central African nest may provide better insulation to the female and her young.

There was little difference in the amount of ceiling material put in by the male, since this averaged 225 pieces in the *graueri* nests and 262 in the *cucullatus* nests. The ceiling in the former contained chiefly dicot leaves, in the latter mainly pieces of grass leaf. The ceiling helps furnish protection from the strong sun and rain in breeding localities of both populations. The difference in kind of materials used may largely reflect differences in availability.

Nest building and extent of polygyny.—Comparisons were made over a 2-week period taken during the peak of the breeding season for each race. Table 2 shows that on the average the male of the race *cucullatus* (1) had more than twice as many nests an any one time, (2) built and destroyed his nests at twice the rate the *graueri* male did, and (3) had over half again as many mates. These differences were all found statistically significant.

TABLE 3
FEEDING RATES OF NESTLINGS IN TWO RACES OF *PLOCEUS CUCULLATUS*

	Number of birds	Number of nests	Nest hours observed	Feedings per nest per hour	Prob.[1]
Males					
cucullatus	12	15	52	0.14	
					<0.005
graueri	6	11	95	2.28	
Females					
cucullatus	15	15	52	4.08	Diff. not
graueri	11	11	95	4.66	signif.

[1] Probabilities based on *t*-test with logarithmic transformation (Dixon and Massey, 1969: 116, 324).

Division of labor in feeding of nestlings.—Before going to West Africa we had observed during some years in aviary-housed birds of the race *cucullatus* that the male almost never fed the young, in marked contrast to what we had observed in *graueri* males in nature. We found the same characteristic among *cucullatus* males in a natural colony (Table 3). The nestlings are fed mainly insects. We counted as one feeding each time a parent bird visited the nest and fed. On the average the *cucullatus* male scarcely fed the nestlings at all, whereas the *graueri* male made a substantial share of the feedings.

The *cucullatus* female fed somewhat less often than did the *graueri* female, but took a much greater proportionate share than did her mate, apparently helping to make up for his deficiencies in this respect.

CONCLUSIONS AND DISCUSSION

Comparing racial differences in nest building and feeding rates, as indicated by these two small population samples, one may conclude that a relatively greater proportion of the male's energy in the West African race *cucullatus* is channeled to building of nests and less to feeding of young than in the race *graueri* of Central Africa.

The ecological basis of this difference is still rather conjectural. The somewhat greater total feeding rate of male and female *graueri* combined when compared with that of *cucullatus* suggests more difficult feeding conditions for *graueri* in the mountain clearing where we studied it. Our *graueri* colony, although only about 3° south of the equator, was at 6,400 feet elevation and the climate was relatively cool with an average maximum of 21°C and a minimum of 12°C at the peak of the breeding season. The corresponding maximum at the Senegal study area was 34°C and the

minimum 24°C. The lower temperature probably made a greater metabolic demand on both adult and nestlings of *graueri*.

Another possible factor, related to the greater rate of nest building and nest destruction in the West African subspecies, is the greater rate of fading of *cucullatus* nests with more total hours of sunshine in the drier Senegalese climate. The Kivu district of the eastern Congo where we studied *graueri* has a 9-month rainy season in contrast to the 3-month rainy season of northwestern Senegal.

In northern Senegal we were at the periphery of this species range. Compared with Central Africa trees available in suitable sites for colonies were often smaller and fewer in number, consequently suitable nest sites were at a premium. It was our impression that the territories of the males in the colony trees of *cucullatus* were smaller and more crowded than those of *graueri*. In turn, more females were accommodated within the suitable parts of the colony in the more polygynous *cucullatus*. One would expect this concentration of females in the colony tree to increase the total reproductive effort of the colony, thus helping to compensate for the very short breeding season in northern Senegal.

Other writers have developed the topic of food availability as related to polygynous or monogamous habits in birds. Armstrong (1955) and Lack (1968) have written general reviews of the subject, and Crook (1962) discusses the matter with special reference to the Ploceinae or true weaverbirds. The general idea is that monogamy is favored by selection under conditions of limited food availability, polygyny where the female is capable of raising the young alone. These concepts are now well-known and in harmony with what we have found in comparing two races of one species of weaverbird. Verner and Willson (1966) discuss some of the complexities involved in the evolution of polygynous and monogamous mating systems in passerine birds with special reference to the habitat situation.

Populations belonging to different subspecies of the Long-billed Marsh Wren (*Telmatodytes palustris*) have been studied from a somewhat similar viewpoint to the one presented here but with some differences. Verner (1965a, 1965b) emphasizes time-budgets of behavior without relating them to possible differences in metabolic needs of different behavioral patterns, while Kale (1965) emphasizes bioenergetics and metabolism as related to population turnover without attempting to fractionate the behavior into a time budget. Some of their comparative results are of interest here. The main difference in behavior seems to be that the marsh wrens secure their food in the male's territory, whereas our weaverbirds foraged away from the colony tree and the nesting territories. Verner compared the behavior of three populations of a resident race of marsh wrens near Seattle with that of two populations of a migratory

race near Spokane, and he found the males of the resident race had a lower percentage of polygyny, larger territories, helped the female much more in the task of feeding the young, and appeared to be under conditions of greater food scarcity. In contrast Kale's wrens, belonging to a third race of the same species in Georgia, had only 3 to 5 per cent polygyny over a 4-year period, but the males only rarely fed the nestlings. They were under a high population density, had territories of a peculiar linear shape and appeared to spend much more of their time in territorial defense than did Verner's wrens in Washington.

ACKNOWLEDGMENTS

The field observations of *Ploceus cucullatus cucullatus* were made near Richard-Toll, Senegal, where we based on the Station d'Ornithologie, Office de la Recherche Scientifique et Technique Outre-Mer. The officers and other personnel of O.R.S.T.O.M., both in France and in Senegal, gave us every encouragement and aid. We are particularly indebted to the director of the station, Dr. Gérard Morel and to Madame Morel. Monsieur Abdoul Salim N'Diaye, Director General of the Societe de Developpement Rizicole du Sénégal, kindly made it possible for us to do our research in the rice culture area at Richard-Toll. We received helpful information from H. Friedmann and K. Stager. The field study was made possible by grants from the National Science Foundation to the University of California at Los Angeles and to the Los Angeles County Museum of Natural History. W. J. Dixon kindly advised us on statistical procedure. We thank all these organizations and individuals for their generous assistance.

SUMMARY

This report compares the behavior, from the viewpoint of work expenditure, of two subspecies of *Ploceus* (*Textor*) *cucullatus* (Müller), the African Village Weaverbird. We had earlier studied the behavior of *P. c. graueri* in Central Africa and we now add and compare a study of *P. c. cucullatus* in West Africa. In both studies we utilized color-banded individuals.

In the birds' daily routine we found in neither race any very marked peak or depression in the frequency of various activities engaged in. The total time spent in resting was not measured.

In both races the male weaves the outer shell of the nest, advertises it to unmated females with a stereotyped wing-flapping display at the entrance, and the female, if she accepts the nest, adds the lining, incubates, and does most or all of the work of raising the young. In both races, if a nest is repeatedly rejected, the male tears it down and builds a fresh nest in its place.

Most of the work expended by the breeding females of both subspecies goes into the task of feeding the young.

In the colonies studied the male of *P. c. cucullatus*, during the main

part of the breeding season, had more than twice as many nests at any one time on the average as the male of *P. c. graueri*, built and destroyed his nests at twice the rate, and had more than half again as many mates. These differences were all statistically significant.

In contrast to the male *graueri*, the male *cucullatus* took almost no part in the feeding of the young.

Various factors that might account for the differences in behavior of the two subspecies are discussed, including the marked differences in the general habit and breeding season of the birds.

LITERATURE CITED

ARMSTRONG, E. A. 1955. The Wren. London, Collins.

CHAPIN, J. P. 1954. The birds of the Belgian Congo, part 4. Bull. Amer. Mus. Nat. Hist., 75B.

COLLIAS, N. E., AND E. C. COLLIAS. 1959. Breeding behavior of the Black-headed Weaverbird, *Textor cucullatus graueri* (Hartert), in the Belgian Congo. Ostrich, Suppl. No. 3: 233–241.

COLLIAS, N. E., AND E. C. COLLIAS. 1964. The evolution of nest-building in weaverbirds (Ploceidae). Univ. California Publ. Zool., 73: 1–239.

COLLIAS, N. E., AND E. C. COLLIAS. 1965. Nest-building and the bioenergetics of breeding behavior in a weaverbird. Amer. Zool., 5: 196 (Abstract 27).

COLLIAS, N. E., AND E. C. COLLIAS. 1967. A quantitative analysis of breeding behavior in the African Village Weaverbird. Auk, 84: 396–411.

COLLIAS, N. E., AND E. C. COLLIAS. 1969. Some observations on behavioral energetics of two related subspecies of birds. Amer. Zool., 9: 1064 (Abstr. 22).

CROOK, J. H. 1962. The adaptive significance of pair formation types in weaver birds. Symp. Zool. Soc. London, No. 8: 57–70.

CROOK, J. H. 1963. Comparative studies on the reproductive behavior of two closely related weaverbird species (*Ploceus cucullatus* and *Ploceus nigerrimus*) and their races. Behaviour, 21: 177–232.

DIXON, W. J., AND F. J. MASSEY, JR. 1969. Introduction to statistical analysis, third Ed. New York, McGraw-Hill.

KALE, H. W., II. 1965. Ecology and bioenergetics of the Long-billed Marsh Wren *Telmatodytes palustris griseus* (Brewster) in Georgia salt marshes. Publ. Nuttall Ornithol. Club, No. 5.

LACK, D. 1968. Ecological adaptations for breeding in birds. London, Methuen and Co.

MOREL, G. 1968. Contribution a la synecologie des oiseaux du Sahel Sénégalais. Memoires O.R.S.T.O.M., No. 29: 1–179, planches 1–8. Paris, Office de la Recherch Scientifique et Technique Outre-Mer.

MOREL, G., AND MOREL, M. 1959. Dates de reproduction de quelques oiseaux du Sahel Sénégalais. Ostrich, Suppl. No. 3: 260–263.

TUCKER, V. 1966. Oxygen consumption of a flying bird. Science, 154: 150–151.

TUCKER, V. 1968. Respiratory exchange and evaporative water loss in the flying Budgerigar. J. Exp. Biol., 48: 67–87.

VERNER, J. 1965a. Breeding biology of the Long-billed Marsh Wren. Condor, 67: 6–30.

VERNER, J. 1965b. Time budget of the male Long-billed Marsh Wren during the breeding season. Condor, 67: 125–139.

VERNER, J., AND M. F. WILLSON. 1966. The influence of habitats on mating systems of North American passerine birds. Ecology, 47: 143–147.

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

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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