AN EXPERIMENTAL STUDY OF THE MECHANISMS OF NEST BUILDING IN A WEAVERBIRD

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NEST building is a classic example of what has been called instinctive behavior. But such an explanation of the phenomenon is not sufficient. How does a bird build its nest? This question has intrigued many persons, and a partial answer, based upon a more or less close description of the process of nest building, has been furnished many times. But the basic question as to the nature of the forces that move and guide a bird at each stage in the act of building its nest has remained largely unanswered. This report is an attempt to answer this question for one species of bird, *Textor cucullatus* (Müller), the Common Village Weaverbird of Africa (also variously known as *Ploceus cucullatus* (Müller), the Hooded Weaver, or the Black-headed Weaver), which builds a highly organized and complex nest.

The results of some of our experiments were presented before the Ecological Society of America and before the American Ornithologists' Union in 1960, and an abstract has been published (Collias and Collias, 1959). We are here reporting the results of these and more extended investigations on the same problem in some detail.

METHODS AND MATERIALS

The methods used included a survey of the literature, detailed study of the breeding behavior and nest building of the Village Weaverbird in its native habitat in Africa, experimental modification of breeding behavior, study of nests and of nest building under controlled aviary conditions in California, attempts to duplicate the nest building mechanisms of weaverbirds by the authors, and study of abnormal nests and the conditions under which such nests are made.

Early studies of the general breeding biology of the Village Weaverbird are those by Benson (1945), von Grzimak (1952), and Chapin (1954). A more detailed study, making use of color-banded individuals and with emphasis on nest building, is one we made in the eastern Kivu District of the Congo on *Textor cucullatus graueri* (Collias and Collias, 1957a, 1957b, 1959). Crook (1960) has also recently described some of the details of nest building in the race *cucullatus* of Senegal, where he finds an essentially similar pattern of behavior to that we have found in the race *graueri*.

The birds that we used for our aviary studies in California belonged to the race *cucullatus* and came from Senegal. Each bird was marked with a distinctive combination of two colored leg bands, the same on each leg, so it could be immediately identified so long as one leg was visible. The birds were named from their colored leg bands; thus, male BW had a black over a white band on each leg. The birds were fed on the parakeet seed mixture readily available from pet shops. Fresh lettuce, cuttle bone, grit, and meal worms were regularly provided for the birds. Crickets were also furnished to birds rearing broods.

The outdoor aviary in which the birds were maintained during the breeding season (May–October) was 5.2 meters high, 5.2 meters wide, and 9.2 meters long, with a wooden shelter at the northwest side. A palm tree (*Phoenix canariensis*) approximately three meters high was planted at one end of the aviary, and an African acacia tree of unknown species, about three meters high, was planted near the other end. The latter tree eventually proved to be the more popular with the birds. Palm fronds and the giant Mexican reed grass (*Arundo donax*) were furnished to the birds as materials for weaving of the nest by the males, while blue grass (*Poa pratensis*) and chicken feathers were provided for the lining of the nest by the females.

The normalcy of the situation was attested to by the birds' fledging a number of broods and raising the young to independence successfully during the second and third years of the study.

In this species the male makes the outer shell of the nest. During the three years of the study, the 11 to 12 males in the aviary built over 250 nests, the great majority of which were normal nests, essentially no different in any detail from nests of the various races of the species built in Africa. During the coldest part of the year the birds were kept in small cages indoors.

When we were in the Congo, Dr. James P. Chapin suggested to us that we might try ourselves to make an artificial weaverbird's nest. Our field studies then left little time for the attempt, but we recently tried it. By carefully observing the basic techniques used by the males in making the outer shell of the nest and imitating the essential features of these techniques, we produced a reasonable facsimile of a normal nest, and this attainment provided a good check to our understanding of the basic mechanisms used by a weaverbird in making his nest. Figure 1 illustrates a nest built by a male weaverbird in our aviary, and Figure 2 illustrates the "weaverbird nest" built by the authors. As far as we know, no person has ever before successfully constructed a bird's nest of any real degree of complexity.

Another technique that we often used in attempting to gain some insight into the mechanisms whereby a weaverbird makes its nest was the study of the conditions under which abnormal nests were produced. Such nests were most common at the start and at the ending of the breeding season and in individuals presumed to have low motivation to build. For example, male BW, who built the bottomless or "canopy" type

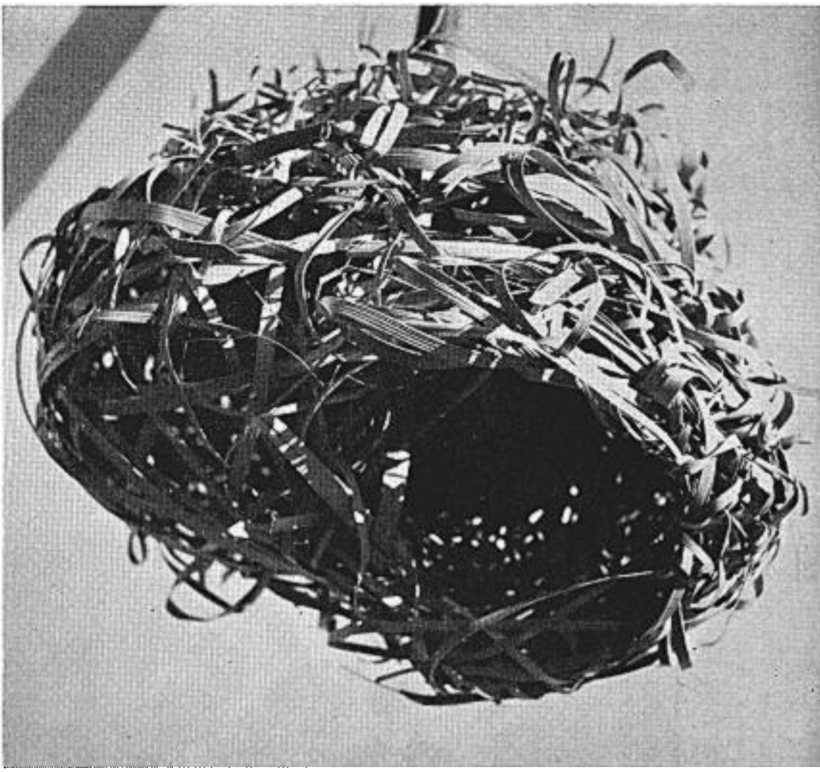

Figure 1. Nest built by a male weaverbird in an outdoor aviary at Los Angeles.

nest illustrated in Figure 3, was one of the more suppressed males in the aviary and built fewer nests by far than did most of the other males during the three years of the study. We found that the study of abnormal nests was an invaluable technique in giving new insights into the basic stimulus situations to which the birds were responding at the various stages of nest building. Such nests provided many natural experiments that helped guide the more systematic and deliberate planning of later experiments.

Among the experiments carried out, the details and results of which are described below, were experiments on selection of nest materials of different colors, modification of substrates for analysis of factors determining site of nest attachment, defect experiments relating to the importance of sequences in building and repair, covering of artificial holes in the nest with wire frames of differing mesh size in order to determine the significance of the pre-existing framework to weaving, hooding of parts of incomplete nests as an aid to the elucidation of factors terminating certain

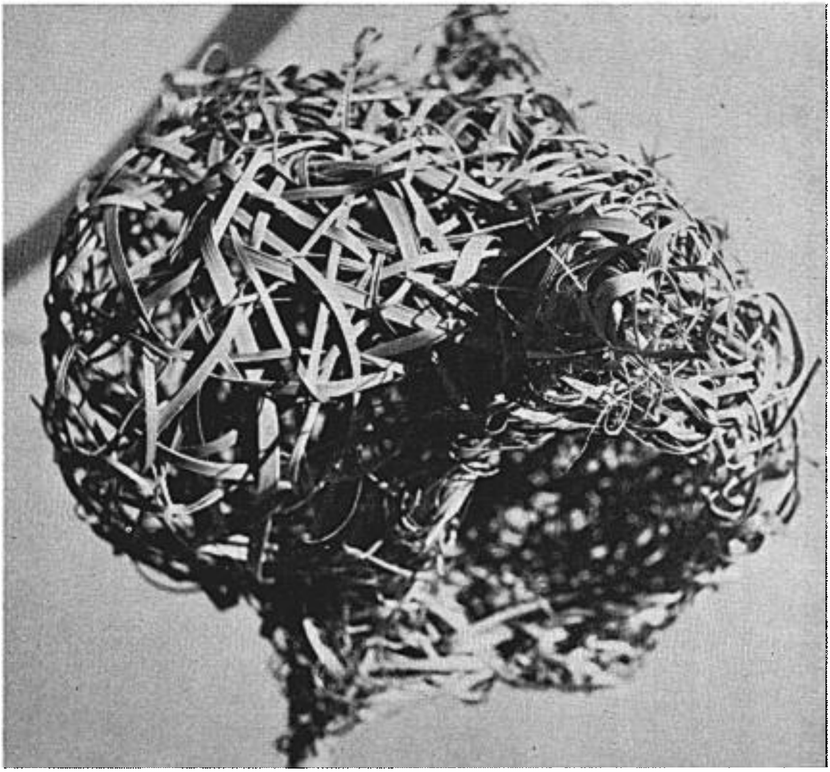

Figure 2. A "weaverbird nest" built by the authors of this article.

stages, and experimental shifts in orientation of nests in an attempt to ascertain factors governing the normal polarity and orientation of the nest.

DESCRIPTION OF NEST BUILDING AND THE GENERAL MECHANISMS OF WEAVING

The following description and illustrations of the nest and nest building apply equally well to nests we observed built in nature (Collias and Collias, 1957b, 1959), or in our aviaries. All drawings were made by N. E. Collias.

The outer shell of the nest is woven by the male of long strips torn by him from the leaves of giant grasses or palms. The general external appearance of the nest, which is ovoidal or kidney-shaped in form with a bottom entrance, is illustrated in Figure 1. Just within the roof of the external shell the male thatches a special ceiling of short, broad strips of grass leaves (Figure 4). The ceiling is not woven, and in some parts of Africa may be thatched of dicot leaves in addition to the use of strips of grass leaf. However, the birds in our aviary generally restricted themselves to

Figure 3. An abnormal, canopylike nest built by a male weaverbird while perching on the bare twig below the canopy.

Figure 4. A normal nest from below, having the bottom half of the nest removed in order to reveal the thatched ceiling of short, broad strips of grass lining the inside of the roof. Antechamber to the right.

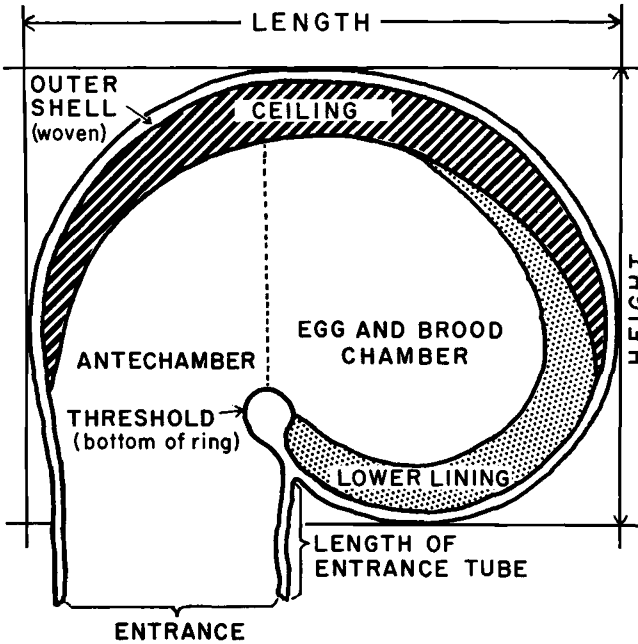

Figure 5. Longitudinal section of a weaverbird nest to show the inner construction. The lining of the lower half of the nest is put in by the female.

grass leaf strips for their ceiling, rarely adding an acacia leaf or a *Poa* grass head. Figure 5 represents a longitudinal section through a nest and shows the normal extent of the ceiling, as well as that of the lining of the floor of the nest that is put in by the female. This bottom lining is thatched of short strips of palm or grass leaf, grass heads, and feathers. A nest of the Village Weaver is usually about 14–17 cm long by 11–13 cm high. About the entrance in brood nests the male often weaves a short tube, 4–8 cm long.

There are five stages to the building of the outer shell of the nest by the male (Figures 6 and 7): (1) initial attachment, (2) roof and egg or brood chamber, (3) antechamber, (4) entrance, and (5) entrance tube. The ceiling is often started long before the egg chamber or the antechamber has been completed. Figure 7 illustrates the principal stitches used by a Village Weaver in the attachment and outer shell of the nest. In actually weaving his nest the male uses certain basic general mechanisms. He tends: (1) to seize a strip of nest material near one end, or mandibulates it along his beak until he has shifted his hold to one end; (2) to double back a strip on itself, especially if the strip is long; (3) to poke one end of the strip with a vibratory motion into the nest mass or alongside some object such

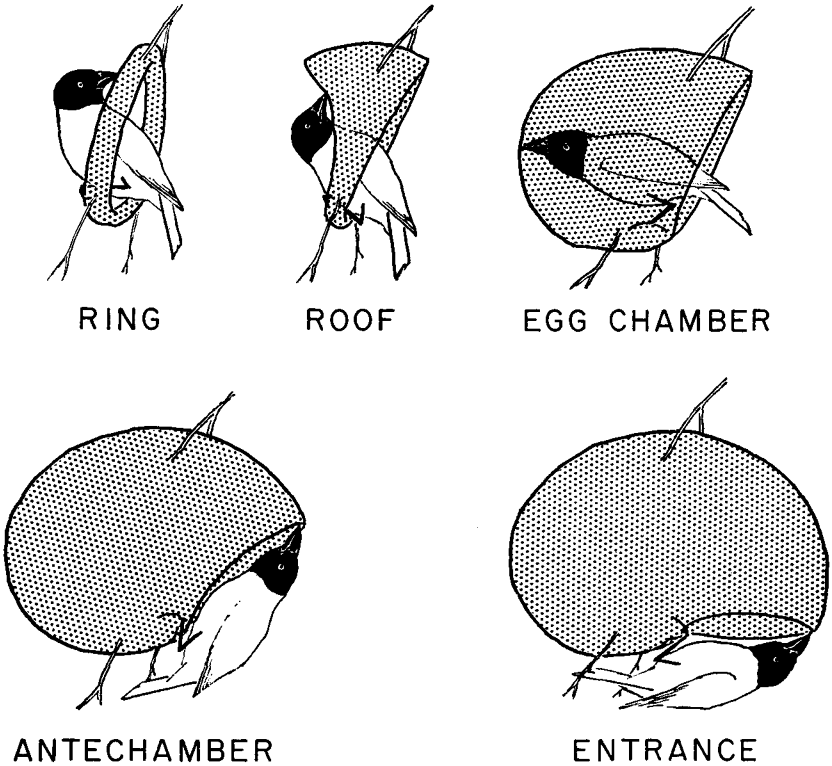

Figure 6. Normal sequences in nest building by a male Village Weaverbird include: (1) ring, (2) roof, (3) egg or brood chamber, (4) antechamber, and (5) entrance.

as a twig; (4) if the strip sticks, to release it, to move his head around to the other side of the twig or nest mass and again seize the strip; (5) to bend or wind a strip about objects such as a twig, ring, or about another piece of nest material; (6) to reverse and alternate the direction in which he winds a strip; and (7) to poke and pull a strip through holes, normally the interstices of the nest.

The unit movements used in nest building are quite stereotyped. All of the weaving is done with the bill, although the bird often uses one or both feet to help hold a strip. When a piece of nest material fails to stick on the initial push, the male often shifts to some other spot and tries again, and this exploratory pattern confers flexibility and adaptability to weaving. If the movements of No. 4 (see above) are repeated more than once in the same direction, the strip is coiled about the twig, as seen in Figure 7 (upper right). Alternately reversed winding (Figure 7, upper), when done repeat-

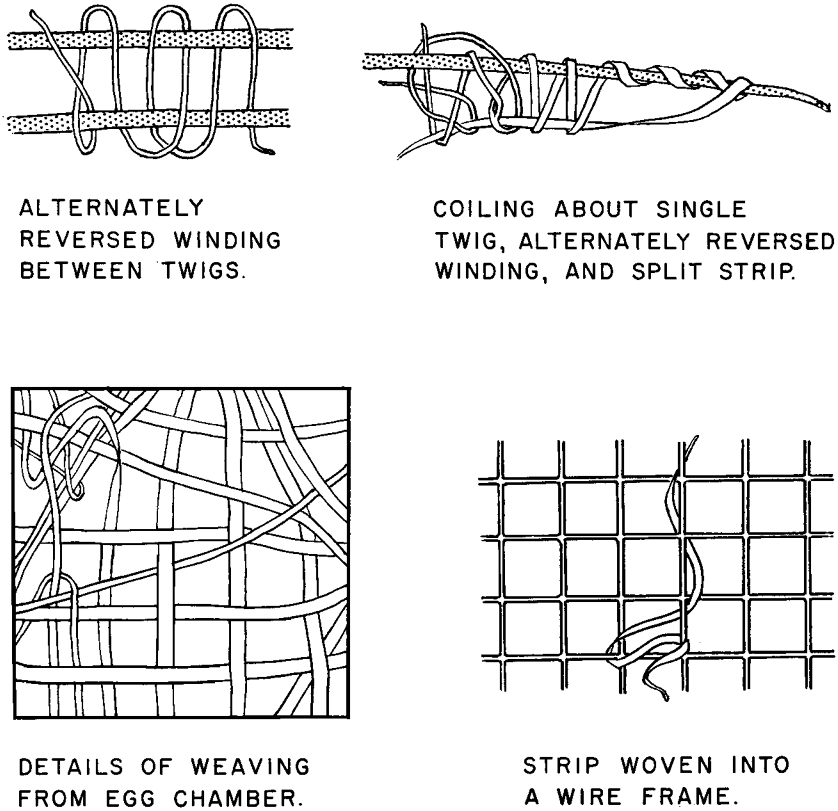

Figure 7. Details of weaving of the initial strips in a nest (above), and nature of stitches in later stages of weaving (below).

edly and closely between two twigs, two grasses, or a twig and a grass strip, binds them firmly together and gives a strong suspension for the nest, as well as being important in helping to hold the rest of the nest together. In the egg or brood chamber many of the constituent strips are continued and threaded over and under other grass strips, at times approaching the classic conception of human weaving, as in some simple forms of basketry or cloth (Figure 7). But at times, especially when strips are long, the ends may apparently be lost sight of, and the bird pokes and tucks loops of the strip in as such. Knots of other types than "hitch-knots" are quite rare in the nest of the Village Weaver, but the end of a strip is frequently looped back on itself or on other strips in such a way that pulling on the strip tightens its attachment, *i.e.*, a typical hitch-knot. A hitch is also a type of knot that is characteristically easy to untie or tear loose and conceivably the prevalence of hitchlike stitches in the nest of a weaverbird is related to the habit of the male of tearing down his nest when no female accepts it, and of building a fresh nest in its place (Collias and Collias, 1957a, 1959).

Every nest is unique in the details of its fine pattern. But the repeated use of the same basic mechanisms in weaving by the male results in nests that look extremely similar to each other, whether built by the same or different males, and readily recognizable as belonging to the same species. This is a statistical concept of nest form and structure.

EXPERIMENTAL ANALYSIS OF THE STIMULUS SITUATION AT EACH STAGE OF NEST BUILDING

The different stages of nest building that will be analyzed, omitting the nonwoven lining of the floor put in by the female, refer to the work of the male, and include: (1) gathering of nest materials; (2) the initial attachment; (3) ring; (4) egg or brood chamber; (5) antechamber and entrance; (6) ceiling; and (7) entrance tube. To a large extent these different stages represent a chain of specific stimulus situations and response tendencies. Each stage automatically provides the stimuli for its own termination and for the start of the next stage in construction. This conclusion was reached only after asking and answering, at least tentatively, the question: "What starts and what ends each stage of nest building?" The evidence will next be considered.

Gathering of nest material. For weaving the outer shell the male requires some 300 long strips of grass or palm leaf, and tears and transports each strip individually. For weaving it is important that flexible materials be used. In nature, the most common flexible materials are, of course, the leaves of green plants. That the color green serves as a clue or signal to which the birds are responding can be shown by giving them materials of different colors. Thus, the birds selected green in an overwhelming number of choices when allowed to select between an equal number (10) of toothpicks of each color (Table 1). In fact, green was selected far more frequently than were the other five colors combined. The preference for green was so strong that statistical tests of significance here seem superfluous.

The toothpicks were colored by Tintex Fabric dyes, and the green selected (known as "jungle-green") was one that matched the green of land plants; in other words, it contained some yellow. The stiffness of the toothpicks also indicates the importance of color as a signal, and rules out small differences in flexibility that might have provided cues for the birds had flexible materials of different colors been used.

In this experiment two or three males were kept together in small cages (40 cm wide by 40 cm high by 90 cm long). When colored toothpicks were placed into the cage, an attempt was made to intermix them uniformly,

TABLE 1
WEAVERBIRDS SELECTED GREEN NEST MATERIALS WHEN PRESENTED WITH VARIOUS COLORS SIMULTANEOUSLY
(Half-hour test periods of five males for a total of 7½ hours of observation)

	Number of times chosen
Green	686
Black	146
Yellow	105
Red	80
White	70
Blue	33

and toothpicks damaged during the test were replaced by fresh toothpicks for the next test.

An interesting point that developed in the course of the experiment was that young adults showed a gradually increasing preference for green, as if mere selection of "green" had more of a self-reinforcing effect than did selection of any other color. During the tests 1,120 choices were made by the five males, and when these tests are divided into four successive and equal periods, selection of green over all other colors for each period was, respectively: 46 per cent of 178 choices, 60 per cent of 289, 63 per cent of 312, and 69 per cent of 341 choices. Table 1 also shows that yellow was selected three times as often as was blue, and this preference accords with the fact that the greens of natural terrestrial vegetation are generally yellow-greens and not blue-greens.

The possibility that birds were reacting to differences in intensity rather than in color was checked by testing preference for a given color from among various shades of gray (Table 2). Green toothpicks were easily selected when mixed with toothpicks of eight different groups of gray of various intensities. Gray toothpicks were grouped in four sets of 10 toothpicks each because the two intensities within each set were too similar for the human observer to determine accurately in the course of testing. It is assumed therefore that some of these grays must have been very close in intensity to the green color tested. Certainly, the weaverbirds virtually

TABLE 2
WEAVERBIRDS SELECTED GREEN NEST MATERIALS WHEN ALSO PRESENTED WITH VARIOUS GRAYS SIMULTANEOUSLY
(Half-hour test periods of five males for a total of 2½ hours of observation)

	Number of times chosen
Green	299
White or whitish	45
Pale grays	18
Dark grays	12
Black or blackish	41

ignored the achromatic toothpicks in contrast to their strong predilection for green. It is of interest that, although the toothpicks were unsuited for weaving activities, the birds consistently treated them as nest materials, attempting to poke them into place along the perch or into the wire meshwork of their cage.

We concluded that green or yellow-green is definitely the preferred color by Village Weaverbirds interested in nest materials, and that this color functions as an index of flexible materials suitable for weaving.

The identification of appropriate nest materials in nature undoubtedly depends on the bird's previous experience with such materials, the example and attractive influence of other birds, and the traditional location of colony trees close to good patches of elephant grass (*Pennisetum purpureum*), palm trees, or other good sources of nest material. As we have found out in observations to be published in detail later, a good deal of practice is probably involved before a bird can skillfully bite and tear off long strips of nest material. Once a bird has a piece of nest material in its beak, it seems to be subject to a strong tendency to fly back to its territory and nest site or prospective nest site. Although a weaverbird gathering materials may sometimes tear and drop a few strips before making its final selection, there is probably a self-satiating factor also at work tending to make it return to its nest site. In our tests with colored toothpicks by far most of the active interest of the birds in these substitute "nest materials" took place within the first 15 minutes of the half-hour observation periods.

Initial attachment of the nest. In the initial stages of building the male seems subject to some indecision as to where to attach his nest within the bounds of his small (on the order of one-half to one cubic meter) territory in the colony tree. This uncertainty is reflected in the frequency of two or more false starts, in which one or two strips will be attached to a twig and then abandoned, and is particularly evident where a particular substrate pattern is closely replicated several times. One weaver, for example, made five false starts, each along one of five large identically appearing spines along the rachis of a palm frond. Twigs, 0.3–0.6 cm in diameter, seem to be preferred. A series of perches ranging from 0.6 to 1.8 cm in diameter were placed in the aviary, and only rarely did any bird attempt to attach a strip to the thickest perch. Forked twigs are preferred to single twigs for attachment of the nest.

With the attachment of the very first strip of a prospective nest, we at once confront most of the problems involved in analyzing the basic act of weaving itself. The fundemental mechanisms in the stitching or weaving of individual strips have been described above and are illustrated in Figure 7. It remains to give some of the experimental evidence related to these mechanisms. When a male arrives with an initial strip at the twig or fork where he intends to make a nest, he may hold the strip with one or both feet against the twig, seize one end and double back the strip. If a male in a cage with no normal nest materials is given a toothpick, he will often seize it and attempt repeatedly to double back one end until he succeeds in bending back and breaking the tip. In our color preference tests with toothpicks, the usual damage done by the birds was to bite the tips of the toothpicks in trying to bend them back. The tendency of the weavers to poke one end of a strip with a vibratory motion alongside a twig or other strip was observed with especial clarity in the toothpick tests. Repeatedly, the birds would poke and vibrate the tip of a toothpick against the smooth, round, wooden perch in their cage, although there was no chance of fastening this very artificial bit of "nest material" in place. Consequently, the next step in the chain reaction of weaving did not occur, *i.e.*, releasing the material with the bill and moving the head around the perch to the opposite side to seize the material anew.

Analogy with human knots and stitches can be considered part of the experimental approach to the problem of weaving by weaverbirds. In the attachment of initial strips in starting a new nest, the technique of alternately reversed winding, combined with loop-backs (Figure 7), as described above, is frequently used by a male weaver, and it is of interest that "nippering" (a knot used to lash together two parallel ropes—cf. Hasluck, 1942) is a very similar type of fastening.

In fastening the initial strip, not only may the male double back a strip and alternately reverse his winding of one end of the strip between twigs or between a twig and the rest of the strip (Figure 7), but he may also pass the leading end of the strip back through the self-made loops of the strip produced by the act of looping and winding itself. This tendency to poke the strip through any available hole can be demonstrated experimentally by providing the birds in an aviary with smooth, wooden perches through which many small holes have been drilled. Some of our birds then poked and wove strips through these holes. This observation suggests that the bird may respond to any small hole when weaving and not specifically to the normal interstices of the developing nest or to a criss-cross framework as in the weaving that commonly occurs in the sides of the wire cages.

After attaching the initial strip, others are soon added at the same spot, and a small pad of woven material is quickly formed. The reason that strips subsequent to the first one are not diffused over a wide area is probably due to two different response tendencies of the bird: the stronger attraction of the loops and interstices and color of the initial strip as compared with its substrate, and the tendency of the bird to become quickly fixated on one particular site from which to weave. The importance of a fixed point from which to weave was emphasized by the case of a male kept with five other males in a small indoor aviary. This male was strongly subordinate to the others, and he was not allowed to remain long on any one perch, but spread his weaving over an area of some 900 cm^2 on the wire side of the aviary near one corner. A male prefers to attach his strips in forks or at the site of minor irregularities. We have seen a nest start on a perfectly smooth, round, wooden perch prolonged for 30 cm along the length of the perch as if, in the absence of any irregularities on the perch, the male could not decide where to stop.

Construction of the ring. Building by the male continues, leading to growth of the initial nest mass into the form of a ring that in turn will provide the basic supporting framework for the whole nest. The main force in formation of a ring rather than some other shape is the tendency of the male to keep his feet in much the same place as he weaves in all directions. He also tends to follow the substrate pattern and so weaves first along the twig; or, if the nest is in a palm tree, he tends to follow the support afforded by palm leaflets and spines. Occasionally, slavish adherence to the substrate pattern leads to such abnormalities as incomplete rings, lacking perhaps one entire side (Figure 8).

Saddled rings and nests seem to be built more commonly by young than by adult males, while the latter usually make pensile rings and nests slung within and below a forked twig. Presumably the pensile nest is safer from predation.

Saddled rings are frequently placed in the upright fork of twigs, being built up along the twigs on either side; closing of the upper part of the ring results from the strong tendency of the male weaver to weave over his head. Whether a twig forks up or down, the male weaverbird customarily straddles between the two sides of the fork with one foot grasping a twig on either side. Even in the complete absence of nest materials, Village Weavers will straddle between objects such as the fork of a twig or the side and roof of a small cage with legs and feet spread quite widely.

In the case of pensile rings, closing of the ring beneath the male involves a few special problems. Because of the general tendency to weave over his head and along the substrate, the top and sides of the ring are often completed first. The fixation of the male at a particular site for straddling where the spread required is not too great keeps the male from moving down with his work. A series of dangling ends of strips gradually accumulates on either side. But the tendency of the male to seize the ends of loose strips leads him to reach down and pick up these danglers one by one and then either to weave them up on the same side or to cross them over and attach them to the other side, bridging the gap beneath himself and gradually completing the ring. It is important that the strips be of

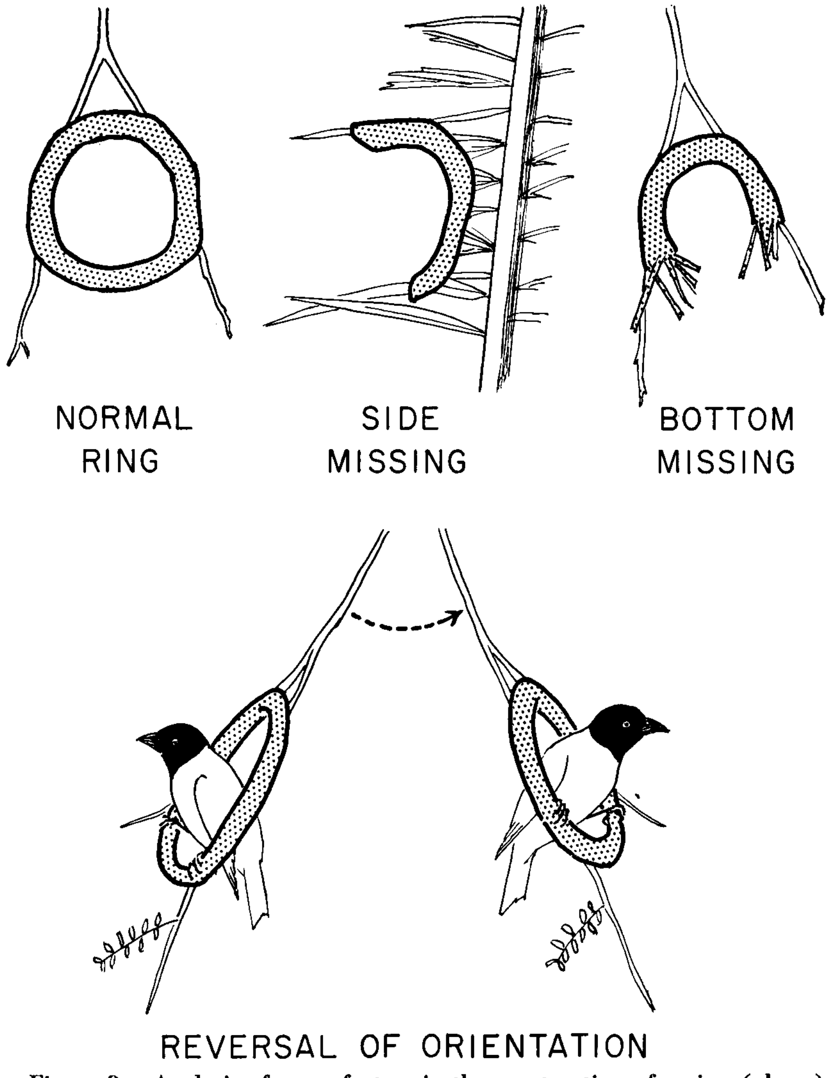

Figure 8. Analysis of some factors in the construction of a ring (above), and in the determination of nest polarity (below). Details in text.

sufficient length. When we supplied only strips 12–15 cm long to our colony, only one male succeeded in bridging the bottom of his ring, and the rest of the rings attempted by the birds remained without a bottom (Figure 8), although the top and sides gradually thickened. The one male that succeeded in closing his ring was able to do so because the twigs on either side converged at the point where the bottom of the ring had to be closed.

In thickening the ring (Figure 9) the male enters the ring with one end of a strip in his bill and the rest of the strip crossing his breast and trailing behind. He pokes the strip into the opposite side from the dangling and trailing end, often first inserting one end through one side of the bottom half of the ring. He then reaches around to the other side of the ring and seizes this same end, bending it back and weaving it in. He next shifts to the other end of the strip and weaves in this end. He tends to shift the place in which he weaves successive strips, so the ring becomes thickened rather uniformly.

One of the most striking and significant features of the orientation of the male in his ring is that he almost always enters it from one side and almost always faces the same way, keeping one foot on each side of the bottom of the ring. We made some investigation of the factors determining the orientation of the male. On observing the plane of the ring, we discovered that vertical rings are rare. Generally, the ring tilts backward from a few degrees to a nearly horizontal level, with 10 to 40° being the most frequent tilt. When in his ring the male faces in such a way that invariably the ring tilts toward him. But if a twig containing a ring is swung back so that the tilt is reversed, the male upon his first subsequent visit will immediately reverse the direction in which he faces. Thus the male keeps the same general relationship to the plane of tilt of the ring, *i.e.*, the ring still tilts back toward him (Figure 8). This experiment was done in five cases with similar results.

The significance of this orientation is that it determines the longitudinal polarity of the nest. The male invariably builds the egg or brood chamber out in front of himself from the ring, while he leans over backward to build the antechamber and entrance on the opposite side of the ring, all the while keeping his feet on the threshold of the nest (Figure 6).

Egg chamber and roof. There are several problems in attempting to determine the factors involved in construction of the egg chamber and antechamber: the start, size, shape, details of woven pattern, and ending of these parts of the nest.

What stimuli cause the male to stop building the ring and begin the roof and brood chamber? One possibility is that once the male has done a certain amount of work on the ring, purely internal changes are set up leading him to begin the next stage of building, *i.e.*, the egg chamber, and continuing through each successive stage of the nest building in a gradual unfolding of internal processes. The alternative hypothesis would be that each successive stage of the nest itself provides the necessary stimuli for its own termination and for the beginning of the next stage. An argument against the first supposition is the fact that destruction of one stage of the nest in most instances leads to prompt repair of that defect (Figure 10),

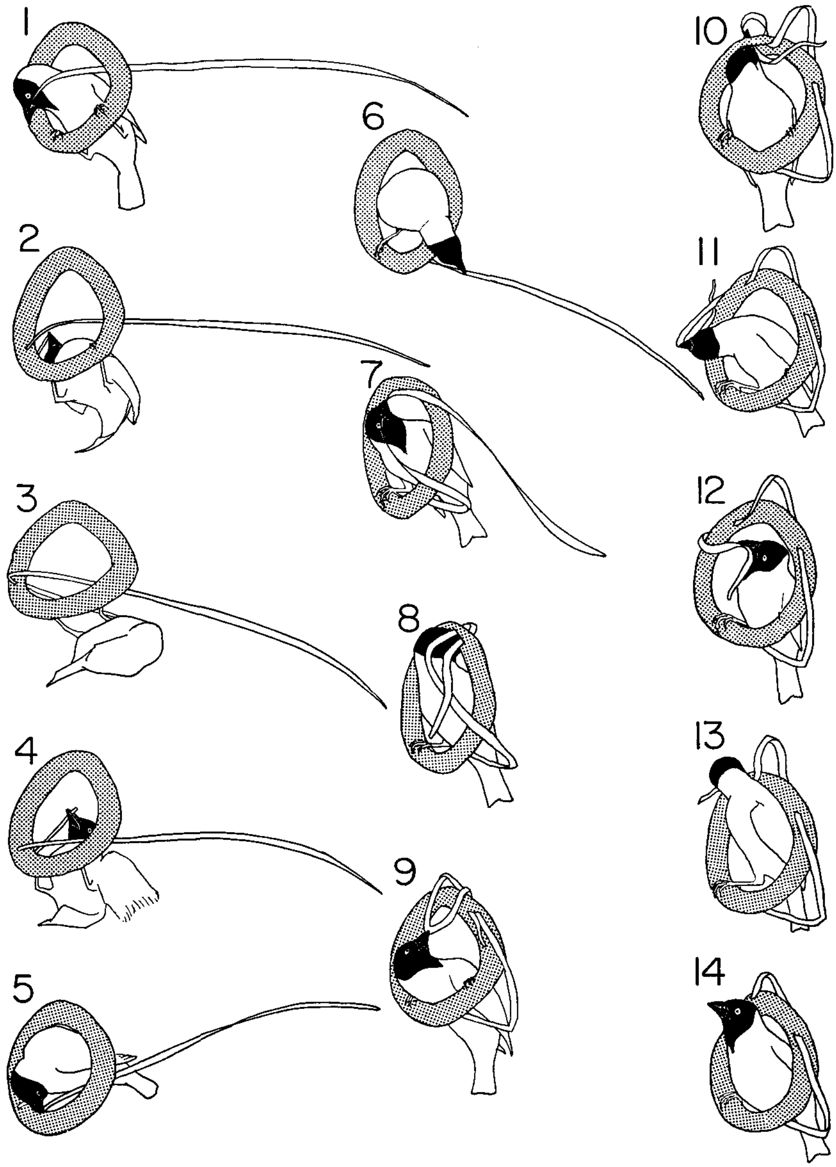

Figure 9. A typical sequence of movements by a male Village Weaverbird as he weaves a single strip, torn from a leaf blade of elephant grass, into his ring. Selected from motion-picture frames.

regardless of its place in the normal sequence of building. Each type of defect experiment was carried out on at least five fresh nests, with similar results in each case. Thus, if the egg chamber is removed from a fresh nest, the bird does not ignore the defect, as if he had exhausted all of his building potential for that particular stage, nor does he continue merely building at the entrance side. Instead, he promptly builds a new egg chamber on the same nest. The one exception to this procedure is the base of the ring. Whereas all other defects are repaired, a nest with the lower part of the ring cut out (Figure 10) is usually abandoned. When a bird attempts to perch in such a nest, the two sides spread apart to such a degree that the bird finds it difficult to maintain position. The main function of the bottom of the ring seems to be to provide a footrest from which to work. Mr. Richard Burrows and we observed that a nest with the bottom of the ring built around a twig was not abandoned when the strips around the twig were removed. Rarely, we have seen nests built that have only a bare twig as the threshold and footrest.

With each successive strip the ring tends to become thicker and more compact, and it may become more and more difficult for the male to push and pull a strip through the mass of the ring. It would seem that increasing resistance may lead him to weave in less of each end of the strip, resulting in establishment of a system of loose loops extending out from the ring and providing a framework from which to weave out farther. When the male has woven in both ends of a strip and can see only the body of the strip, his pushing-out reaction seems to be activated, *i.e.,* instead of tucking in the loose ends he tends to push the body of the strip away from himself with his beak.

The brood chamber is often started from the roof of the ring, and this tendency is related to the stronger tendency of the male to weave over his head than to one side or beneath himself. A male Village Weaver placed in a small, wire cage often weaves strips of nest material into the roof; less often he weaves into the sides of the cage, and almost never into the wire mesh of the floor.

The male continues to enter from the same side of the ring and to face into the developing egg chamber, perching on the floor of his ring as he works. Each strip he brings is held in his bill, and as he lands, he often pokes that end into the ring to one side. If, as he arrives with a strip, the latter extends backward along his right side, he tends first to weave to the left. But, if the strip extends backward along his left side, he tends first to turn to the right for the initial poke. The far end of a long (30–37 cm) strip is not readily visible to him since it extends across his breast and far behind him. Not being able to see the ends of the strip, he pushes the main body of the strip out in front of him as far as he can,

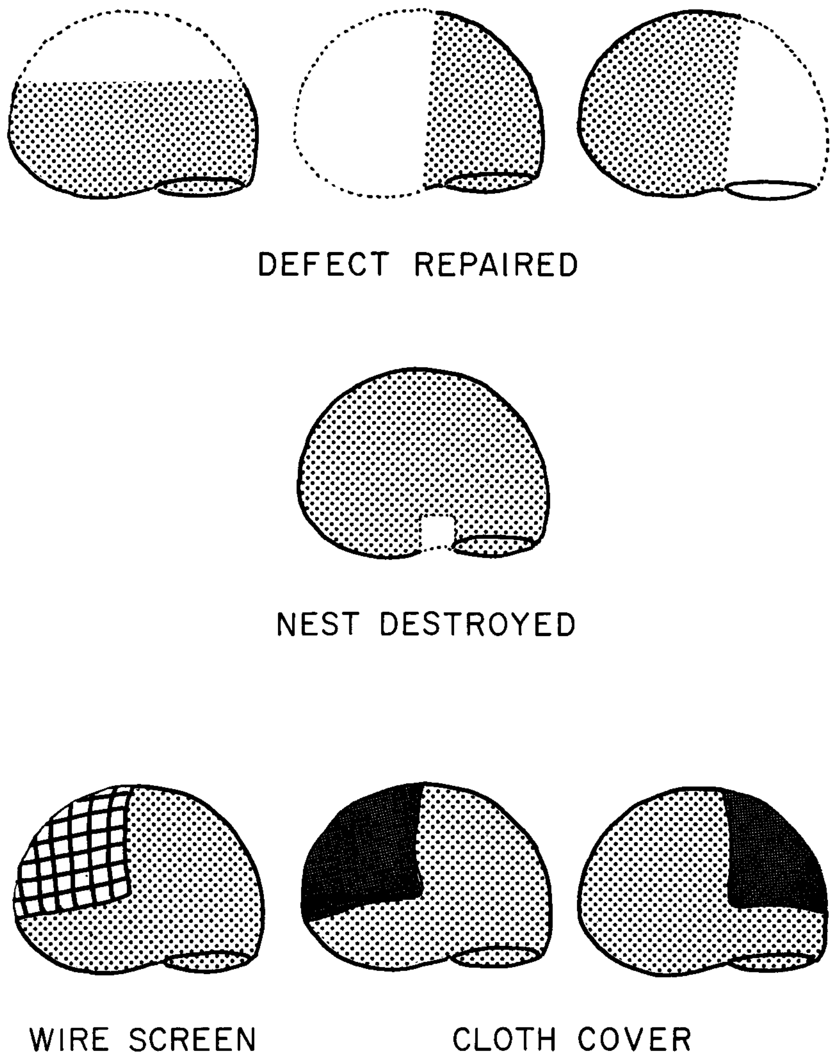

Figure 10. The male weaver replaces various parts of the nest, with the exception of the lower half of the ring, when the experimenter cuts away these parts (above). Nature and location of various artificial covers fastened over the nest to analyze factors involved in building of the egg chamber (below). Details in text.

the strip crossing the ring from one side to the other. He then leans over backward and weaves in the second end of the strip. The tendency of the bird to shift his point of weaving with successive strips, combined with the pushing-out reaction when he can no longer see the ends of each woven or tucked-in strip, gradually results in outlining the form of the brood chamber.

The size and globular shape of the egg chamber depend on the size of the bird, combined with his tendency to keep his feet on the bottom of the ring as he pushes out with his beak in all directions as far as he can reach. If a particularly resilient strip springs back to its original position after being pushed out, the male often pushes it out or up repeatedly until it stays in place. We have often seen cases where a male without access to a tree or bush in a cage or aviary becomes fixated on weaving from the perch where the latter adjoins the wire side of the cage or aviary. In such instances, the bird often weaves a round disc of woven materials into the wire frame of the cage, neatly outlining the extent of his reach from the one spot on the perch where he persists in standing as he works. At the same time, his tendency to weave above the level of his belly rather than below it often results in a shallow, bare notch in the bottom part of his disc or mat of nest materials.

The pattern of weaving in the egg chamber depends on the male's tendency to (1) cross preexisting lines of the developing framework at right angles as he weaves in subsequent strips, and (2) to alternate the direction of his winding with each stitch, resulting in an in-and-out threading of the strip as he moves it along by pushing and pulling it with his beak through the loose meshwork of the early stages of the egg chamber.

The tendency to cross strips at right angles is well shown by giving different colored strips of raffia to a male in a cage having parallel vertical wires but not horizontal cross wires on the side. The bird tends to weave each strip in a horizontal plane doubling back and forth and weaving in and out between the vertical wires, the basic pattern being readily revealed by the different colors of each strip. If the bird weaves on a wire meshwork consisting of a pattern of squares or rectangles, there is the same tendency to weave each strip at right angles across preexisting lines. But as more and more strips are added, the pattern soon degenerates into a helter-skelter and kaleidoscopic pattern of variously colored raffia strips interweaving with each other in an apparently irregular and complex pattern.

The tendency of the male weaver to alternate the direction of his winding through the nest interstices is the essence of what we normally think of as "weaving." If the basic framework is very regular, as in a wire meshwork of squares, such threading in and out of strips of nest material may often proceed in perfect alternation (Figure 7). Apparently the weaverbird learns much of this tendency to progressive alternation, the reinforcing stimulus being firmness or resistance to being pulled farther by each successive stitch combined with an early-developed tendency to alternate pushing and pulling or forward and backward movements of the head. Not infrequently, loops are woven in as such in the nest. When palm strips 37–42 cm in length were the only nest materials provided to the birds, loops were more frequent than when only strips of 12–15 cm were given, and the many loose loops projecting from the external surface gave the long-strip nests a rather crude and scraggly appearance.

The stronger tendency of the male to weave above rather than beneath himself is reflected by the much finer meshwork of the roof of the nest compared with the floor of the nest at any given instant (Figure 1).

As the meshwork of the nest becomes filled in, the male tends to do less weaving. This tendency was indicated by an experiment in which a large hole was cut in the roof of the egg chamber and then covered over with a green wire mesh frame (Figure 10). In experiments on different nests, four frames, each with different-sized mesh, were used, and the bird did more weaving in those cases where the meshes were larger. Apparently, the male tended to some degree to accept the meshwork of the wire frame as if it were his own work.

When the bird can no longer see daylight through the egg chamber, he stops building. An initial conjecture that this was the case was based on an abnormal nest in which the egg chamber abutted the rachis of a palm frond that actually furnished the back of the egg chamber. The egg chamber at this point was incomplete, with a large hole in its back.

Ceiling. As the meshes of the nest become smaller and smaller, particularly in the roof, the male shifts quite abruptly from weaving in long, narrow strips to thatching in short, wide strips just under the roof. We believe that this significant shift from weaving to thatching can be explained by the fact that after the meshwork of the roof becomes very fine, the male finds it increasingly difficult to locate or pull through the ends of a strip that he has just poked into place. His tendency to push the main body of the strip away from himself is then automatically stimulated, since he can no longer see the ends or pull them into place. One can actually see this process in operation each time the male puts in a ceiling strip, poking in first one end to one side, then the other end into the roof, followed by pushing the center of the strip well up into the arch of the roof.

A partial experimental test of this theory was made by tying a piece of green fly screen over a hole cut in the roof of the egg chamber. The meshes in the screen were too fine for the weaverbird to thread through any strips readily, and the male put many ceiling strips just inside the screen, but did very little weaving. It seems possible that as a male gathers experience he attains a measure of what we would call "judgment," *i.e.*, he realizes at a glance whether or not he can easily weave another strip through the mesh.

When a male starts to put in a ceiling, a spectacular shift takes place. Instead of gathering long strips adapted to weaving, he gathers short, broad strips needed for thatching. Evidently, the male is able to carry a picture or "set" in his brain of the best type of material for a given stage of the nest. Probably a certain amount of learning is involved in this process, since the ceiling of young males is characteristically sparse, relatively irregular, and composed of strips quite variable in length.

Work on the ceiling is greatly slowed or discontinued by the male when the roof and ceiling become thoroughly opaque. We described above the abnormal nest that was backed against a palm rachis, which replaced the wall of the egg chamber at the place of contact. We made an experimental test by sewing a piece of green cloth over the roof at an early stage of the egg chamber (Figure 10), removing the few ceiling strips present. The male continued to work on the nest at places other than those covered by the cloth, putting in an abundance of ceiling strips under the roof on the entrance side, but almost none beneath the cloth. We also did the reciprocal experiment, hooding the entrance side (Figure 10), and this time the many ceiling strips subsequently put in by the male were almost entirely confined to the egg chamber. The developed ceiling itself provides the stimulus for its own termination, for if one repeatedly removes the ceiling from a reasonably fresh nest, the male repeatedly replaces it.

In conclusion, we believe the ceiling is started at the roof when the roof first reaches the requisite smallness of mesh size, and, secondly, that the work on the ceiling slows or stops as the roof plus ceiling becomes thoroughly opaque.

Antechamber and entrance. In general, little work is done on the antechamber, aside from its roof, before the egg chamber is well-nigh complete. The greater tendency of the male to weave over rather than under himself helps lead to a gradual building down of the roof and sides of the antechamber until it reaches the horizontal at a level approximately with the bottom of the nest (Figure 6). Throughout the process, the male as usual keeps his feet on the bottom of the ring or threshold, leaning over backward as he works. As the antechamber reaches the horizontal, it is gradually narrowed to make the bottom entrance, the narrowing probably being due to the lesser reach of the male as he hangs beneath the threshold. If a nest is rotated backward about its transverse axis, bringing the entrance upward with its margins now vertical instead of horizontal, the male promptly weaves the entrance back down to the horizontal level, and in doing so, builds from top to bottom an extra, abnormal hood on the nest (Figure 11).

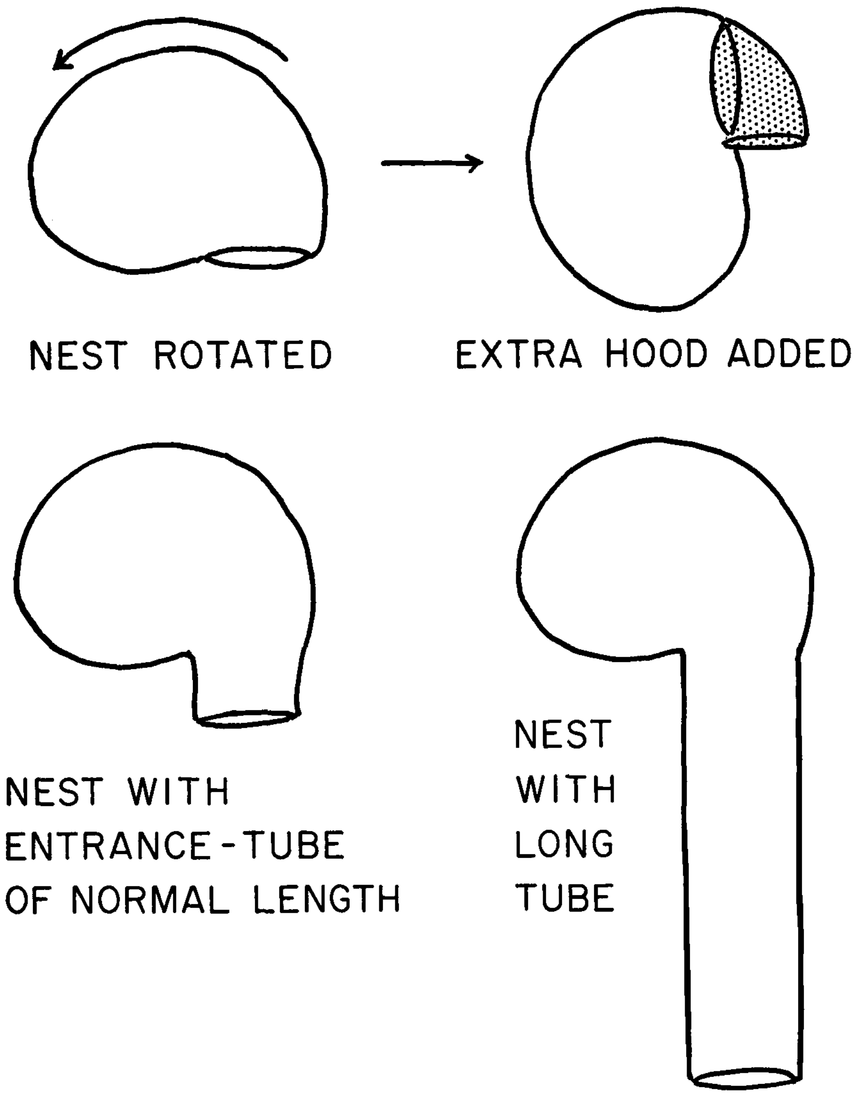

Figure 11. When a nest is rotated back 90°, the male weaver again builds the entrance down to the horizontal, adding an extra hood to the antechamber (above). A male weaver was experimentally induced to build a nest with an abnormally long entrance tube (below). See text.

Therefore, work on the antechamber generally can be said to end only when its opening has reached the horizontal. At this stage the male may continue to thicken the nest and ceiling somewhat, but the primary shift in his behavior is toward greatly increased efforts, by means of various displays and vocalizations, to induce visiting females to enter and inspect his nest. If a female accepts the nest and settles down in it, she thenceforth tends to exclude the male from the inside of the nest, although he often looks up into the entrance and sings to her.

The male now generally adds a short tube about the entrance, whereas nests not accepted by a female are likely to be torn down without ever having had an entrance tube (Collias and Collias, 1959). Possibly the stimulation leading to the addition of an entrance tube on brood nests is the added motivation to build afforded the male by having his nest occupied by a female, combined with his exclusion from the interior of the nest that up to that time had furnished the main site for his building activities. If a female disappears or deserts a nest, the male owner soon tears it down.

In weaving the entrance tube, the male for the first time during the construction of his nest begins to work not while his feet rest on the threshold or bottom half of the ring, which provides the supporting framework of the nest, but clings with his feet at almost any place on the rim of the entrance tube as he adds to its length. The entrance tube is not thick—only about one layer of woven material being involved. The abrupt shifting of the male from his normal orientation point of weaving on the bottom part of the ring is perhaps due primarily to the mechanical impossibility of his weaving an entrance tube from that position. The diameter of the entrance tube usually varies little, but occasionally we have noted abnormally narrow or wide tubes, the former being correlated with working positions of the male in which the longitudinal body axis was almost upright, the latter in which it was nearly horizontal.

The male can be caused experimentally to extend the entrance tube to several times the normal length (Figure 11). As he smooths off the rim, tucking loose ends in back from the rim, the male tends normally to terminate work on the entrance tube with attainment of a finished rim. But if the experimenter loosely threads in a strip of nest material by one end into the entrance tube, leaving the main part dangling, the male promptly weaves in the whole strip, instead of merely pulling it out and discarding it. By means of this experimental technique, we have induced a Village Weaver to add a tube 30 cm long to his nest, instead of the normal length of only 5–10 cm.

Finishing of brood nests. While the female incubates, the male quite often works on the outside of the nest. He strengthens the attachment of the nest, weaving in fresh green strips, their bright-green color contrasting with the faded green or brown of the rest of the nest. He also tucks in loose ends here and there over the surface of the nest so that egg or brood nests come to have a smooth, compact, and relatively neat appearance.

Much of the interior work is, of course, done by the female, who adds a thick but nonwoven lining.

Nest destruction. As a rule, the male usually destroys his own nests, including those never accepted by a female and brood nests shortly after the young have departed. In our experiments concerning the repair of various nest mutilations, we found that it was important to use fresh nests. If defects were made in nests that were starting to age, to fade, and to become a little brittle, the male was far more likely to tear these nests down than he was to repair them. But if the nest were fresh, large parts of it could be removed and would be repaired. These results suggest that there is a balance between the tendency to tear a nest down and to build it up. Factors that stimulate building on a nest include not only freshness of materials in the nest, but also position of the male inside the nest in the bottom half of the ring, and a recent visit by inspecting females to the colony tree. Factors that favor destruction of his own nest by a male, on the other hand, include not only the brittleness of aging materials in the nest, but also position of the male outside the nest and failure of a female to accept his nest, or abandonment of the nest by the female, as is normally done when the brood leaves.

DISCUSSION

It is evident in the preceding pages that while we have attempted to analyze the basic mechanisms or causes at each stage of nest building by a Village Weaverbird, we have avoided any detailed discussion of endocrine motivation or of the role of experience. This is because each of these problems is a large and separate topic and will be considered in subsequent articles. We and our colleagues have worked on these problems, and have found that breeding behavior, including nest building by the male of this species, is stimulated by male hormone (Collias, *et al.,* 1961), and that practice plays a not inconsiderable role in nest building by weaverbirds (Collias and Collias, 1962). This article attempts primarily to make a precise and detailed specification and analysis, based on experimental studies, of the significant stimulus situation at each stage of nest building.

Comparable studies in the literature from this point of view are rare and fragmentary. In fact, a detailed, experimental analysis of nest building in any bird seems to have scarcely been attempted before the pioneer studies of Herbert Friedmann on the nest building of the Red-billed Weaverbird (*Quelea quelea*) at the United States Zoological Park in 1922, which appears to have been the first really detailed description of nest building in a bird. But although he carried out some experiments with regard to nest materials, the emphasis of his paper was necessarily on the descriptive aspects of nest building. In India, Ali and Ambedkar (1956) made some interesting observations on the effects of cutting differently shaped holes in completed nests of Baya Weaverbirds, and they found that the birds generally repaired the damage. Crook (1960b) removed different parts of the nest in *Quelea quelea.* But in all but one case this was done subsequent to egg laying, and the nest was soon abandoned and not repaired, except in the case of one male in an aviary who repeatedly replaced the cut-out back of a nest when this was removed.

Two other authors, who have recently analyzed nest building, did not work with weaverbirds. Robert Hinde (1958) has dealt with a much less highly organized nest—the simple cup nest of the canary, which is built in a very different way from the complex woven nest typical of ploceine weaverbirds. Tinbergen (*in* Thorpe, 1956) has suggested a possible causal scheme for the building of the domed and nonwoven nest of the Long-tailed Titmouse in Europe. His scheme is apparently deduced from close observation of the process of nest building in this species, but his causal analysis seems to be entirely theoretical and little or no experimental verification seems to have been published. Our own analysis has proceeded not so much from a theoretical preconception as to the possible mechanisms, but rather by attempting to formulate the problems involved in the construction of each stage of nest building, guided particularly by observation of the building of abnormal nests.

Apart from the developmental aspects, which will be dealt with elsewhere, our conclusions as to some of the more general mechanisms operating in nest construction do not differ greatly from the general conception of instinctive behavior adopted by many authors since the times of Darwin and of Fabre. Stereotyped action patterns are evident in the fixation by the male weaverbird on the lower half of the ring from which to weave, or in such movements as mandibulation and of poking a strip into the nest walls and then moving the head in a deliberate manner to the opposite side before again seizing the end of the strip. Key stimuli guiding the movements of nest building are illustrated by the tendency of the bird to weave or tuck in loose ends of strips, but to push the body of a strip away when its ends are no longer visible. The principle of the chain reaction is illustrated by the regular manner in which each stage of nest building succeeds the other, and by the fact that to a large degree each stage of the developing nest automatically provides the stimuli for its own termination and the starting of the next stage.

Other general mechanisms of species-typical behavior that do not appear to have been so widely recognized include gradients of action tendencies, and exploration tendencies. Thus, the male weaverbird weaves much more readily over his head than beneath himself. If in attempting to place a strip in one place the bird encounters some difficulty, he readily shifts his attempts to some other spot, and this exploratory behavior helps confer some flexibility and adaptability to the weaving of the nest.

The principal contribution of this report is to offer some experimental evidence for the nature of the key external stimuli and conditions that govern the causal sequences of nest building, and an explanation of the basic mechanisms of nest building in a bird as based on this evidence, combined with observation of the details of nest building.

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SUMMARY

Study of abnormal nests and experimentally altered nests gives clues to the nature of factors operating in the course of construction of normal nests. Experimental evidence is presented for the following causal factors at each stage of nest building by the male Village Weaverbird, *Textor cucullatus* (Müller).

1. Weaving requires the use of flexible materials. The selection of yellow-green materials, the usual color of fresh, herbaceous vegetation, helps insure this needed flexibility.

2. Initial attachment results from the tendency of the male to poke and vibrate ends of strips into or alongside twigs, to wind such strips about twigs, to reverse his direction of winding between adjacent twigs or strips, and, finally, to poke and pull ends of strips in through holes made by the act of looping back strips.

3. Construction of a ring results from the tendency of the bird to weave in all directions along the immediately adjacent substrata while keeping the

feet in a fixed orientation in the bottom half of the ring. Strips longer than 15 cm are important to the closing of the ring that results from the tendency of the bird to shift its weaving from one end of a strip to the other and from one side of the ring to the other.

4. The polarity of the nest, with the brood chamber on one side and the antechamber on the other, is a consequence of the plane of tilt of the basic ring frame, since the weaver faces so that the ring tilts toward him, and then builds the brood chamber out from the ring before himself. The globular form of the brood chamber results from the fact that the male always stands in much the same place on the ring as he weaves, and then pushes the developing brood chamber out with his bill in all directions as far as he can reach.

5. A ceiling is thatched within the roof when the meshwork of the roof becomes too fine to permit more weaving easily, and the ceiling is terminated as it becomes opaque and blocks off the entrance of light through the roof.

6. The antechamber and entrance are built out from the ring, as the male, keeping his feet in the standard position on the base of the ring, weaves over his head, gradually leaning over backward more and more until he has built the entrance down to a more or less horizontal level.

7. An entrance tube is generally added after a female has accepted the nest. She prevents the male from entering the nest, and he satisfies part of his building drive by adding to the rim of the entrance. One factor tending to terminate growth of the entrance tube is the smoothing of the rim as the male works in loose ends.

8. It is evident that each stage of the developing nest automatically provides the external stimuli for its own termination and for the starting of the next stage.

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