THE DEVELOPMENT OF NEST-BUILDING BEHAVIOR IN A WEAVERBIRD

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Nest building is often considered a prime example of instinctive behavior in birds, but few detailed and systematic studies of the development of this process in young birds seem to have been made. Our object was to make such a study. The observations and experiments to be described were carried out on a colony of captive Village Weaverbirds, *Textor cucullatus*, at Los Angeles, California. These birds belonged to the West African race of the species, *T. c. cucullatus*, and the original stock came from Senegal. The value of this species for the present study is that it makes a complex and highly organized nest. We have elsewhere published an account of the breeding behavior of the race *T. c. graueri* in the wild state in Central Africa (Collias and Collias, 1959), and a detailed analysis of the mechanisms of the nest-building behavior of the adult males, which do all of the weaving of the nests in this species (N. E. Collias and E. C. Collias, 1962). This latter project was extended into the present investigation of the development of the ability of young birds to make a nest, but only a brief abstract of this work (E. C. Collias and N. E. Collias, 1962) has been published. We report herewith some details of our experimental analysis of this problem.

The young birds used were all hatched in a large outdoor aviary on the campus of the University of California at Los Angeles. This aviary measured 16 × 30 × 16 (height) feet and contained a palm tree (*Phoenix canariensis*) and an African acacia tree of unknown species. The birds nested in both trees, but preferred the acacia. The colony was maintained on parakeet seed mixture, lettuce, and mealworms, with grit and cuttlebone continuously present. Mealworms proved inadequate as a diet for the young, but the latter were raised successfully when the mealworms were supplemented with crickets. Mr. Richard Burrows, Mr. Brian Kahn, Mr. Herbert Brown, and Mr. Edward Tarvyd each helped us rear the young brought up in the aviary during one of the three years of the study.

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Development of Ability to Manipulate Objects

The first use of the bill by young Village Weaverbirds, other than in gaping to receive food from the parent, is to preen disintegrating sheaths off the feathers. This preening action involves biting and nibbling at the feather sheaths, and we have observed it by the time the young bird is two weeks of age. Normally, the young Village Weaverbird spends almost three weeks in the nest, and the eyes open about a week after hatching. The mouthing of the feather sheaths would seem to be the precursor of the ability to mandibulate strips of nest materials, and thus to adjust the position of a strip in the bill.

The development of pecking activities introduces new motor elements needed for nest building. In the third week after hatching, the young bird begins to lunge toward and attempts to seize the food offered by the parent. But it is not before its first week out of the nest that the young bird becomes able to pick up food from the ground for itself. In part, the development of this ability is very likely facilitated by parental example. We have often seen young start to pick up food when next to the parent, shortly after the parent does so.

As it begins to feed itself the young bird develops a strong exploratory urge, i.e., it now picks up and manipulates all sorts of objects with its beak, and spends a good part of its day engaged in such activities. Mrs. Nice (1962) mentions exploratory pecking in young birds of more than a dozen different species, including both altricial and precocial types. Our general impression, after rearing and observing young birds of many species, was that few equalled and none exceeded our young weaverbirds in the frequency with which they manipulated various objects.

SELECTION OF APPROPRIATE NEST MATERIALS

A Village Weaverbird normally uses only fresh, green, flexible materials to weave the nest. The outer shell is woven by the male, of long strips torn from the leaves of elephant grass or palms, and he also adds a non-woven ceiling of short strips of grass or of dicot leaves. An inner lining of soft grass-heads and feathers is put in by the female. The key to the use of appropriate materials suitable for weaving is the green, or rather yellow-green, color of herbaceous flowering plants, and we have found that adults prefer green to other colors of artificial nest materials (N. E. Collias and E. C. Collias, 1962).

An experimental test was made of the color preferences of young weaverbirds upon initial exposure to nest materials. Some 30 young were hatched in outdoor aviaries. Half of them were left in the aviaries to be reared by their parents, and had access to the trees in the aviary and to the giant reed grass (*Arundo donax*) regularly placed in the aviary as a source of nest material. The rest of the young birds were removed from the nest before their eyes opened at the age of five to seven days, and

TABLE 1

SELECTION OF DIFFERENT COLORS OF NEST MATERIALS BY YOUNG WEAVERBIRDS REARED IN ABSENCE OF NEST MATERIALS*

	Number of birds	*Number of times color selected*					
		Green	*Yellow*	*Blue*	*Red*	*Black*	*White*
Controls	6	311	256	90	76	116	53
Deprived	7	488	79	55	62	58	129

* Based on 14 hours and 40 minutes' observation of controls (37 days) and 8 hours and 20 minutes' observation of deprived birds (11 days). Birds tested at age of 7 to 10 months.

these young were hand-reared while deprived of any normal nest materials. However, it seems impossible completely to separate a young bird from at least some analogue of nest material, for these hand-reared young, in contrast to the controls, often manipulated their own feathers or those of cage-mates. It was not uncommon to see such a bird hold a protesting cage-mate's wing under one foot and attempt to "weave" its wing feathers. Similarly, at times, one of these birds would reach down and try to weave its own tail feathers. Since many of the feathers of young weavers are yellow, yellow-green, or olive-green in color it is evident that we are far from having a perfect control in this experiment. However, it is true that, relative to the controls, the hand-reared young had far less experience with anything that much resembled normal nest materials. Prior to the experiment now to be described, the aviary-reared young had often manipulated normal nest materials, but had not yet built nests.

For a test of color preferences the birds were exposed to equal numbers of colored toothpicks, 10 of each color: green, yellow, blue, red, black, and white. The green was chosen to imitate the color of natural vegetation and contained some yellow, the commercial dye ("Tintex") used being known as "jungle-green." The toothpicks were mixed completely at random on presentation to the birds for standard observation periods, generally half an hour in length. The birds were not given more than two such observation periods a day. A bird would pick up a toothpick and treat it as nest material, attempting to poke it into or alongside the perch with a typical vibratory motion. As the table of results (Table 1) shows, young male weaverbirds, whether or not they had been reared in the absence of nest materials, selected green over other colors. The controls, however, also showed a strong predilection for yellow. Most of the tests with the aviary-reared young were done under fluorescent lighting; some, as in the case of all the tests with the hand-reared young, were done under ordinary incandescent light or else natural daylight.

It is of interest that in the case of the relatively naive, deprived young,

TABLE 2

SELECTION OF DIFFERENT COLORS OF NEST MATERIALS BY FOUR MALE WEAVERBIRDS, REARED IN ABSENCE OF NEST MATERIALS*

	Number of times each color selected						*Per cent green*
	Green	*Yellow*	*Blue*	*Red*	*Black*	*White*	
First two days	51	42	0	11	2	28	38
Second two days	163	16	6	13	1	29	71
Third two days	147	4	6	4	7	18	79

* Based on a total observation time of 5 hours and 50 minutes, over six successive days, when the birds were approximately seven months old.

the degree of preference for green on initial exposure to the artificial nest materials quickly increased with experience (Table 2). Thus, a Chi Square test, comparing the relative preference of green over all other colors combined for the first two days with the second two days of testing showed a significant difference well beyond the 1 per cent level (Chi Square > 50). As seen in the table, only 38 per cent of the selections in the first two days were of the green toothpicks, whereas 71 per cent were selected in the second two days of testing, and 79 per cent in the third two days. Five control weaverbirds, toward the end of their first year, under similar conditions of testing, showed an immediate and sustained preference for green, selecting 54 per cent green toothpicks in the first two days of testing, 48 per cent in the second two days, and 66 per cent in the third two-day period.

As Table 3 shows, the young male birds that were reared in the absence of normal nest materials, also had the normal preference for flexible over rigid nest materials (Collias and Collias, 1959) when tested at approximately eight months of age. These tests were conducted with green vinyl plastic strips of identical shape and weight, but differing in flexibility. Two thickness classes were used; a greater differential between "flexible" and "stiff" in the thicker strips was reflected in a greater difference in the frequency of strips selected (Table 3).

TABLE 3

SELECTION OF NEST MATERIALS DIFFERING IN FLEXIBILITY, BY FOUR YOUNG MALE WEAVERBIRDS REARED WITHOUT NEST MATERIALS*

Thickness	*Picked up*		*Wove*	
	Flexible	*Stiff*	*Flexible*	*Stiff*
0.02 inch	258	160	8	0
0.01 inch	169	127	1	0
Totals	427	287	9	0

*Tested at approximately eight months of age. Observed 13 hours and 20 minutes.

These young males also preferred long over short strips, and when offered equal numbers of one-, two-, and four-inch strips, took the four-inch ones in 44 out of 69 choices. When eight-inch strips were added they chose these in 15 of 17 choices.

Weaverbirds develop an increasing discrimination in the selection and use of nest materials with normal experience, and will come to reject such things as toothpicks, string, and even raffia, when normal materials are available, and sometimes they may reject the artificial materials, even when normal materials are not available. Artificial nest materials are ignored by experienced adults when normal nest materials are available.

GATHERING OF NEST MATERIAL

When a weaverbird obtains a strip from a leaf of elephant grass (*Pennisetum purpureum*) in Africa or, in our aviaries, from 5 to 15-foot tall Mexican reed grass (*Arundo donax*) as a suitable substitute, it perches on the stalk or firm base of the leaf, bites through one edge of the leaf, tearing off part of the strip, and then tears the rest of the strip loose by flying away with it in the general direction of the tip of the leaf. In watching young weaverbirds, whether these birds were reared by hand or in the aviary, it seemed to us that they had to learn many things in carrying out the process of tearing a strip of reed grass properly. While experienced adult males generally fly off, finishing the tearing in one smooth action, the young often made such mistakes as perching in an unstable place, starting the tear too close to the tip of the leaf, or at the very base, or taking too broad or too narrow a bite, or tearing in the wrong direction, or tearing part way and repeatedly starting partly detached strips, or tearing strips that were too short to be woven.

Comparable and systematic observations on other species, in regard to the handling of nest materials, have been made by Dilger (1962), who finds that hybrid parrots of the genus *Agapornis* gradually improve their ability to cut and transport suitable nest materials.

DEVELOPMENT OF THE ACT OF WEAVING

In nature, the first-year males build very crude nests, with relatively sparse ceilings and with many loose loops projecting from the outer surface of the nests, in contrast to the compact, neat nests with thick, well-organized ceilings of the fully adult males (Figure 1). The latter are easily distinguished from the yearling males by their black heads. In India Sálim Ali (1931) had similarly observed, in the case of the Baya Weaver (*Ploceus philippinus*), that the nest of the young male is relatively crude compared with that of the adult male. This age-correlated difference in ability to construct a nest may turn out to be a quite general phenomenon among weaverbirds.

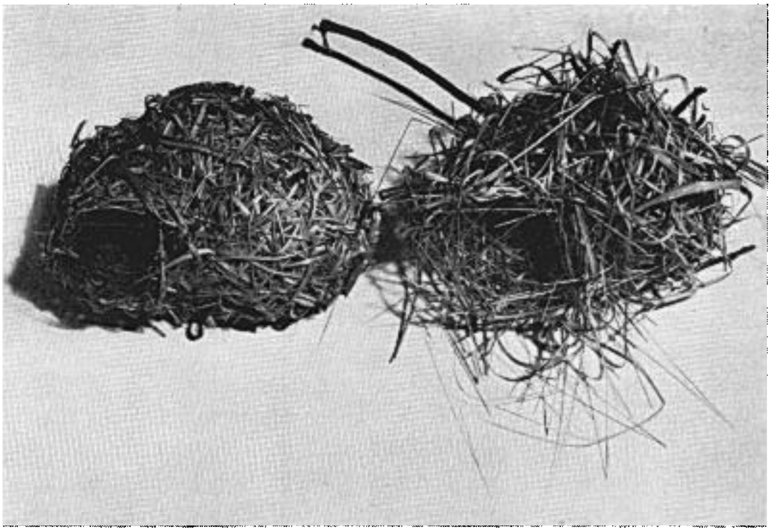

Figure 1. The first nests built by young males (right) are more loosely and crudely constructed than are nests built by adult, experienced males. Photographed by us at Entebbe, Uganda, 1957.

We have gathered experimental evidence that, in the Village Weaver-bird, the ability to build improves with practice. We used the same males employed in earlier experiments on color preference with artificial nest materials. When these birds were almost a year old, three control and three deprived males still survived, and these two groups were placed side by side in two identical indoor aviaries, each with a guava bush of the same size. Normal nest materials in the form of palm strips or reed grass were supplied during standard observation periods of one-half hour or one hour. In the interim between this experiment and the earlier one on color preference, only the controls were given any access to normal nest materials. An opaque cloth partition between the two aviaries precluded the possibility of observational learning by the hand-reared young from the more experienced, aviary-reared young.

The initial observations were made in early August, 1961. In the first week the birds were given palm strips, and the hand-reared males wove not a single stitch onto the bush or onto the wire meshwork of the cage, in contrast to all the control males, which wove well in both places. In the second week, with reed grass, the hand-reared young wove a few stitches on the wire only. In the third week, the experiments summarized in Table 4 were started. As shown in the table, the deprived males succeeded only in weaving a very small percentage of strips compared with

TABLE 4

ABILITY TO WEAVE OF YOUNG MALE WEAVERBIRDS REARED IN ABSENCE OF NORMAL NEST MATERIALS TO ALMOST ONE YEAR OF AGE

	Number of birds	*Dates*	*Hours observed*	*Strips carried*	*Per cent woven*
Controls	3	11–16 August	3.5	73	62
Deprived	3	10–15 August	3.5	69	26
Controls	3	12–25 November	3.5	95	77
Deprived	3	13–25 November	3.5	158	52

the controls. The difference was significant to the 5 per cent level by the Rank-sum Test (see Dixon and Massey, 1957).

After the first experiment the nest materials were left with the birds, and then a fresh supply of reed grass was maintained constantly in the aviaries. By the middle of November, 1961, after some three months' opportunity to practice, the deprived males had improved considerably and (Table 4) had doubled the percentage of strips woven over their performance in August. The difference in the percentage of strips woven by the controls and the deprived birds was no longer significant by the Rank-sum Test ($P = 0.20$).

In the three-month practice period, two of the males reared in absence of nest materials managed to weave 2 nests. In the same period, the three control males built 11 nests. There was no obvious difference in the quality of nests built by controls and experimentals.

In the case of the simple cup nest of the canary, Hinde (1958) observed that three females reared from eight days after hatching without access to normal nest materials, would, when they reached breeding condition, go through all the movements of building in a nest pan. When appropriate materials were presented for the first time these females responded rapidly and built nests that appeared as large and tidy as those built by experienced ones. As in the case of our deprived young weaverbirds, these deprived canaries showed a pronounced tendency to pull at and carry their own feathers or those of cage-mates. Of course, the normal nest materials of canaries, being relatively short pieces of grass as well as feathers, are more like their own body feathers than are the long, flexible strips of grass or palm leaf used by a male weaverbird to weave his nest, and the integration of basic movements involved in building a nest is far less complicated in the canary.

It appears that some practice is important to successful weaving, and the next question that arises is just what the birds learn. It is interesting to watch the initial reactions to nest materials of young male weavers that have been reared without normal nest materials to an age where the control males can weave. These deprived males already possess certain basic motor elements of the act of weaving. They can select suitable materials, hold a strip under one foot or in the beak, mandibulate to one end of the strip, and poke it toward or alongside the perch, or into the interstices of the wire meshwork of the cage. Somewhat later the young birds develop the ability to reach around to the other side of the twig while standing on a strip, seize the strip anew in the beak and wind it around the twig.

In watching the attempts of a young weaver to fasten its initial strips of nest materials and the gradual improvement of weaving, it seemed to us that in general what every young male weaver has to learn is what in subjective terminology we would call "judgement." But we can break down the things apparently learned into more objective descriptions of our impressions after watching a great many instances where a young weaverbird was attempting to "weave." Frequently the young bird attempts to weave with materials that are too short or too stiff. But it is channelized into the right direction by its normal tendency to develop a preference for green, flexible, and longer materials. Before the bird can succeed in firmly fastening a strip in place it must learn to carry out the basic movements in an *effective sequence.* It must learn not to pull a strip out again before it is firmly fastened in place. Often the bird starts to weave one end of its strip and, instead of following through, *shifts* its point of attack in an ineffective way. In contrast, the adult is much more likely to *persist* in its weaving at one end of the strip, or at a given site. Often the young bird will push a strip partly into a wire mesh and just as promptly pull it right out again, making no attempt to let go in order to shift its hold through to the next mesh. Learning *when to let go* of a strip is an important requirement of weaving. But even when let go, the strip frequently may fall out of place, of its own weight or resilience, before the young bird can reach around to the other side of the twig or wire and seize it anew. The bird apparently has to learn to push the strip through *far enough* so that it doesn't fall out or spring back at once when released. Unless the bird has also learned to hold a strip *under foot*, the strip may even fall to the ground when the bird shifts its beak-hold on the strip.

Even when a young weaver can effectively make several stitches, it still fails to make a nest. For one reason or another, the bird generally ends up *removing* each strip before he has thoroughly woven it into place; we have seen this repeatedly. For example, in 1962, a deprived young weaverbird, Male WY, on its first exposure to reed grass, was observed for one hour daily for five days, the reed grass being removed after each hour of observation, and in this time he was seen to weave a total of 36 stitches, gradually increasing the number each day to a total of 21 on the last day. But, in contrast to the usual behavior of controls, not one of these stitches or strips was left in place by the bird by the end of each observation hour, so WY ended his first week of exposure to normal nest materials with not a single strip in place. This tendency to undo one's own weaving we dubbed the "Penelope act" for convenient reference.

INFLUENCE OF OTHER BIRDS ON LEARNING TO WEAVE

An important influence on the development of ability to build would seem to be the restriction of learning opportunities relative to position in the dominance order. Village Weaverbirds have a social ranking system based on habits of aggressive domination and subordination, and, at least in an aviary, this social order is as rigorous and almost as rigid as that seen in the domestic fowl. A much subordinated male has far fewer chances to practice weaving than does a dominant male. No sooner does a male low in dominance gather a strip than a dominant bird is likely to come and take it from him. In each of our groups, the most subordinate male wove a much smaller percentage of strips carried than did other birds, and it was evident that the main, though not the only, reason was his low social position.

The role of tuition by example from other birds, especially older males, is a factor we have not yet quantitatively assessed. It appears likely that some social facilitation exists for nest building, since the birds tend to show interest in nest materials at about the same time, just as in the case of their other activities. Marais (1937), studying the South African "yellow weaverbird," took eggs from the nest and had them hatched by canaries. The nestlings were then reared out of sight of both adult weavers and normal nest materials. These young weaverbirds were able to weave nests, indicating that tuition from older birds was not needed. Unfortunately, he gave no further details, as, for example, concerning possible improvement in skill of the birds in building their nests, nor did he certainly indicate the species concerned.

We do have some information of a qualitative nature bearing on this problem. A male Village Weaverbird was taken from a nest in our colony before his eyes opened and reared in our home in complete visual isolation from all other weaverbirds to an age of more than two years. He was supplied with normal nest materials from an early age, and gradually developed the ability to construct normal nests, the first appearance in development of the different acts involved in nest building being in the following sequence: mandibulation, biting and pulling at various objects with the beak, poking of raffia into any nearby object with the beak, poking raffia into the wire meshwork of the cage, tearing of strips, and standing on strips with the feet. At five and one-half months of age he

Figure 2. A male Village Weaverbird, hand-reared in complete visual isolation from other weaverbirds, but supplied with nest materials from an early age, built the nest illustrated here. The entrance is to the lower left, the brood chamber is at the right.

wove his first stitch into the wire but at once pulled it loose. Then, at six months of age he wove the first strip (with three stitches) that he left in place. At seven months he managed to fasten a strip onto a perch, at eleven months made a ring, and by one year made his first nest (of raffia). He subsequently wove several nests of reed grass or palm strips (Figure 2), which to us appeared no different from those built by other males of comparable age.

We concluded, from the case of this male reared in isolation from other weaverbirds, that tuition by example is not necessary to the development of the ability to build a nest in the Village Weaverbird. However, it is not unlikely that example may have a facilitation role, since two control males were each seen to weave their first strip in the outdoor aviary in which they were hatched by four months and one week of age, more than a month earlier than did the isolated male.

SUMMARY

Fledglings of the African Village Weaverbird, *Textor cucullatus*, begin to manipulate all sorts of materials very frequently soon after they leave the nest, and the males build crude nests long before attaining sexual maturity.

Some 30 young were hatched in outdoor aviaries. Half were reared by their parents. The rest were removed before their eyes opened and were hand-reared in the absence of nest materials. The hand-reared young, unlike the controls, often manipulated or tried to "weave" their own feathers or those of cage-mates. As did controls, when given equal chances for selection, they preferred green nest material to yellow, blue, red, black, or white. The hand-reared young quickly developed a preference for green within the first few days after initial exposure to artificial

nest materials. They also had the normal preference for flexible as against stiff nest materials, when tested with vinyl plastic strips.

When about one year old, the survivors were given their first normal nest materials, and the hand-reared males wove a much smaller percentage of strips than did control males. But this discrepancy greatly diminished with about three months' practice in handling strips, and two of three hand-reared males managed to weave 2 nests. Three control males wove 11 nests during the same period.

One male, hand-reared in complete visual isolation from other weaver-birds, but supplied with nest materials from an early age, gradually developed the ability to construct normal nests.

We conclude that practice, channelized by specific response tendencies, but not necessarily tuition by example, is needed for development of the ability to build a normal nest by the male of this species.

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