# THE ROLE OF EXPERIENCE IN THE NEST BUILDING OF THE ZEBRA FINCH

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IN 1867, Alfred Russel Wallace, speculating on the role of learning in the nest building of birds, wrote:

> During the time they are learning to fly and return often to the nest, they must be able to examine it inside and out in every detail, and as their daily search for food invariably leads them among the materials of which it is constructed, and among places similar to that in which it is placed, is it so very wonderful that when they want one themselves they should make one like it?

Wallace was one of the first to suggest that birds might build their nests on the basis of their previous experience. Although it now seems that nest building in birds is not solely a function of memory, the extent to which experience plays a role has not been determined.

The present experiments were carried out in an attempt to determine whether the early nestling and fledgling experience of the Zebra Finch (*Poephila guttata*; syn., *Taeniopygia castanotis*) would influence the selection of materials, substrate, and "habitat" for the first nest; and, further, whether previous nesting experiences would influence these selections upon renesting.

## HISTORICAL REVIEW

The information available to a nestling or fledgling bird about its nest might be treated at three levels.

*The materials and construction of the nest itself.*—Some experimental work has been carried out in which birds were reared in the absence of a nest, and later given appropriate materials as a test for innate nest building ability. Scott (1902, 1904) hand-reared American Robins (*Turdus migratorius*) and Rose-breasted Grosbeaks (*Pheucticus ludovicianus*) and found that these birds were totally unsuccessful at building nests when presented with appropriate materials at one to two years of age. All of Scott's females did lay eggs in artificial containers when these were provided, a fact indicating that his birds were in reproductive condition.

On the other hand, it has been shown that domestic canaries (*Serinus canarius*) (Verlaine, 1934; Hinde, 1958), Serins (*Serinus canarius*) (Thorpe, 1963), "Yellow Weaverbirds" (Marais, 1937), and African Village Weaverbirds (*Textor cucullatus*) (Collias and Collias, 1964) will build species-characteristic nests after having been hand-reared without nesting materials. It is possible, however, that the birds built these nests on the basis of innate nest-building movements, and that finer individual differences

among nests within the species concerned could be produced by rearing the birds in a variety of early nesting situations.

Verlaine (1934) has obtained evidence which suggests that some learning might occur during the nestling–fledgling period of canaries; birds that were reared in nests constructed by their parents made better nests upon reaching sexual maturity than birds reared in artificial containers.

*The immediate substrate of the nest.*—No experimental work on this topic has been carried out with birds to my knowledge. However, at least two field observations of unusual local nesting traditions which persisted for several years suggest some form of early learning of nesting substrates. Schiermann (1939) observed a small colony of Yellow Wagtails (*Motacilla flava*) in which all of the individuals built their nests in shrubs, as opposed to the normal ground-nesting habits of this species. Hochbaum (1955) has observed a few pairs of ground-nesting Redheads (*Aythya americana*) on the marsh at Delta, Manitoba, for several years, although these ducks usually nest in emergent vegetation over water.

*The habitat surrounding the nest.*—Recent experimental work by Klopfer (1962, 1963) indicates that the apparently innate preference for pine foliage in Chipping Sparrows (*Spizella passerina*) may be altered by hand-rearing young birds in oak foliage. There are a number of field studies which suggest that birds might learn the habitat around their rearing nest. Young birds commonly return to breed in the general area of their birthplace (e.g., Nice, 1937; Werth, 1947; Austin, 1949). Various workers have studied this tendency by transplanting the eggs and young of various species from one geographic area to another, and then checking both areas in subsequent years for returning birds. These studies indicate that birds will often return to breed in the area where they are fledged (e.g., Välikangas, 1933; McCabe, 1947; Löhrl, 1959).

However, all of this field work is equivocal, in that homing to a particular *geographic* area and recall of the original nesting situation could be involved, rather than "habitat imprinting" *per se*.

Information influencing the selection of materials, substrates, and habitats for nesting in older birds might also derive from previous nesting experiences. Williams (1934) has obtained evidence which indicates that particular pairs of Baltimore Orioles (*Icterus galbula*), Eastern Kingbirds (*Tyrannus tyrannus*), and Cedar Waxwings (*Bombycilla cedrorum*), built distinctive nests of colored materials during successive years at his wildlife sanctuary. McCabe (1963) has shown a consistency in the choice of nesting substrates in Traill's Flycatchers (*Empidonax traillii*). He caused 25 pairs of these flycatchers to renest by destroying their original nests. By means of colored threads artificially woven into the first nests, he could

identify the second nest of each pair, since the birds re-used the original nesting material. He found high correlations between the heights, angles, and supports of the first and second nests of the renesting pairs.

There are also innumerable observations of breeding birds returning to the same nesting substrate or habitat year after year (e.g., Nice, 1937; Stoner, 1941; Delmée, 1954). But these observations could again involve homing to a particular geographic area, rather than to a particular habitat.

## MATERIALS AND METHODS

*The species.*—The Zebra Finch has been extensively studied in the field by Immelmann (1962) and in the laboratory by Morris (1954, 1958), Immelmann (1959), and Kunkel (1959). It is a xerophilic species which naturally occurs throughout the arid regions of Australia, but which has long been a popular cage bird.

In the wild, the normal nest is an untidy, domed structure with a side entrance and is constructed of both green and dry grasses. However, the Zebra Finch is extremely variable in its selection of nesting sites. Usually nests of several individuals are found together in a low clump of shrubs but nests have also been found on the ground, in fallen logs, in rabbit burrows, and in the foundations of hawk and eagle nests (Bourke, 1941; Immelmann, 1962). Both in the field and in the laboratory, the male indicates suitable nest sites, but the final choice is apparently made by the female. The male collects the nesting material and the female constructs the nest.

The incubation period lasts from 11 to 14 days, the nestling period about two weeks, and the fledgling period also about two weeks. During the fledgling period the young regularly spend the night in the nest. The young reach sexual maturity at about three months of age (Marshall and Serventy, 1958; Immelmann, 1962).

*Care of the birds.*—Most of the finches used were housed in Crown double-breeding cages (58.4 × 22.9 × 25.4 cm) which were arranged in tiers on four or five wooden shelves. Some of the finches were maintained for short periods between experiments in large flight cages (91.4 × 38.1 × 61.0 cm). The room in which the finches were kept was normally maintained within a temperature range of 75 to 85°F (24–29°C). There were windows opening into the room but they let in very little daylight and three 150-watt bulbs were kept on a "12-hour-on, 12-hour-off" schedule. The birds were given fresh water and feed daily. The seed mixture used was Kellogg's Finch Mixture No. 13. In addition, small petri dishes of gravel and Petamine and cuttlebone pieces were always available in every cage.

*Nest materials, substrates, and "habitats."*—The finches were given six-inch strands of burlap for nest building. These strands were available in three colors (bright red, deep green, and natural brown).

Two substrates were available for nest building: A, a box, 12.7 × 12.7 × 12.7 cm, made of hardware cloth and plywood; and B, two wire-mesh canary nest cups rigidly attached to each other at a 30° angle.

These substrates were situated in one of two "habitats": A, inside the cage; and B, outside the cage, within a 15.2 × 27.9 × 25.4 cm wood-enclosed extension area which the birds entered through a 12.7 × 12.7 cm doorway. "Habitat" B was considerably darker than "habitat" A because of its location in the wood-enclosed extension.

*General experimental procedures.*—Young finches were taken from their parents when independent (approximately 30 days old), color-banded, and transferred to holding cages with other members of their sex. In these holding cages the young birds did not have access to the nesting materials or substrates involved in the experiments. However, these birds were in habitat A (the cage) and could see into habitat B (the extension) during this period.

At approximately 90 days of age, these birds were paired in their first test situation. After a nest was built and a full clutch of four eggs laid in the substrate and habitat of their choice, the remaining substrate was removed. The birds were left together with their nest for about one month, when they were given their second test. Successive tests were spaced at one month intervals.

The experiments were so designed that they fall into two categories:

1. Birds nesting for the first time were tested for the retention of information from their rearing nests.

The birds of 12 pairs were reared in red, green, or brown burlap nests, and at maturity were presented with an excess of burlap strands of two colors which were thoroughly intermixed. (This mixing of the strands made a 100 per cent choice of one color unlikely, as the strands had a tendency to stick together.) Twice a day the number of strands in each test cage was brought up to a total of 400 (200 of each color). Upon completion of egg laying, I counted the strands making up each nest.

The birds of 35 pairs were reared in either the nest cups within the cage (substrate B, habitat A) or the nest box outside the cage (substrate A, habitat B). They were tested in situations which were designed to determine whether the rearing experience of the birds would influence their selection of a first nesting situation and, if so, whether their previous substrate or their previous habitat experience was more influential, and finally, whether their previous nestling or their previous fledgling period was more critical.

2. Renesting birds were tested for the retention of information from their previous nests.

In all, 17 pairs were given a variety of experiences with colored nesting materials. (Pairs would readily build nests of any of the colors, if given no choice.) The general procedure was the same as that followed with first nesting birds. All of these birds had been reared in brown burlap nests and

TABLE 1

EXPERIMENT 1: RESULTS OF PRESENTING BIRDS WITH A CHOICE BETWEEN THE BURLAP COLOR OF THEIR REARING EXPERIENCE AND A NOVEL COLOR AT THE TIME OF THEIR FIRST NESTING[1]

| *Test number* | *Rearing experience* | *Choices made (in per cent)* | | *Number of strands* | *Chi-square* | $p$[2] |
|---|---|---|---|---|---|---|
| 1. | Brown | Brown | Green | | | |
| | | 77 | 23 | 501 | 150 | *** |
| | | 90 | 10 | 305 | 192 | *** |
| | | 81 | 19 | 431 | 167 | *** |
| | | (82) | (18) | (1,237) | (496) | *** |
| 2. | Green | Brown | Green | | | |
| | | 46 | 54 | 366 | 3 | |
| | | 70 | 30 | 330 | 52 | *** |
| | | 56 | 44 | 257 | 4 | * |
| | | (57) | (43) | (953) | (19) | *** |
| 3. | Brown | Brown | Red | | | |
| | | 73 | 27 | 327 | 70 | *** |
| | | 80 | 20 | 389 | 138 | *** |
| | | 84 | 16 | 278 | 129 | *** |
| | | (79) | (21) | (994) | (332) | *** |
| 4. | Red | Brown | Red | | | |
| | | 83 | 17 | 408 | 178 | *** |
| | | 84 | 16 | 300 | 138 | *** |
| | | 75 | 25 | 291 | 73 | *** |
| | | (81) | (19) | (999) | (382) | *** |

[1] All numbers represent data from individual pairs, except those in parentheses, which represent the total for all birds in a given test.

[2] * = probability less than 0.05; ** = probability less than 0.01; *** = probability less than 0.001.

also had had one nesting experience with brown material. The tests were designed to determine whether a nesting experience with one color would result in a choice of that color over a novel color upon renesting, and whether the first nesting experience or the most recent nesting experience would dictate a subsequent preference.

Further, 44 pairs nested for the first time in one of the four substrate-habitat combinations. These birds were tested in situations designed to determine whether the first nesting experience of the birds would influence their selection of a second nesting situation and, if so, whether their previous substrate or their previous habitat experience was more important in dictating this selection.

## RESULTS

### BIRDS NESTING FOR THE FIRST TIME

*Material of the nest.*—The results of testing birds with a choice between the burlap color of their rearing experience and a novel color at the time of their first nesting are shown in Table 1. All of the pairs tested showed a

EXPERIMENT 2

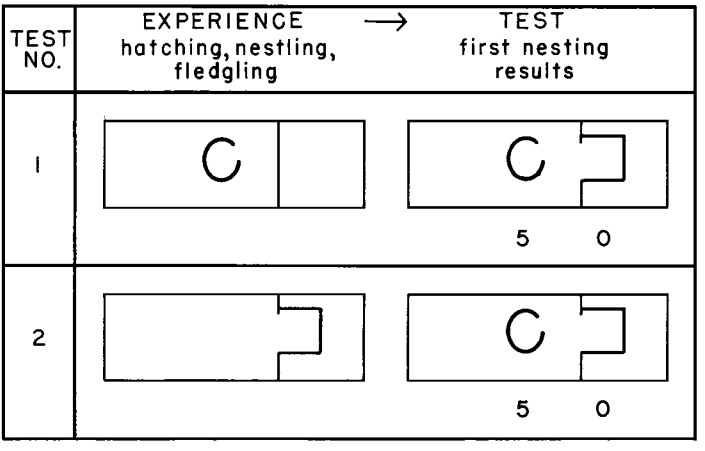


Figure 1. Experiment 2. The results of giving finches a choice between the substrate-habitat combination of their rearing experience and a novel substrate-habitat combination, at the time of their first nesting. The rectangular drawings depict the cages, with the wood-enclosed extension areas to the right. The nest cups are symbolized by open ovals, and the nest boxes by open squares. The number of pairs making each choice is shown under the appropriate substrate-habitat combination.

significant preference for brown strands with one exception (pair 1 in Test 2). Birds reared in brown nests selected brown over either green or red strands, and in approximately the same proportion in each case (compare Tests 1 and 3) (Chi-square of 3.4; p greater than 0.05). Birds reared in green nests selected a significantly greater total of green strands than did the birds from brown nests (compare Tests 1 and 2) (Chi-square of 165; p less than 0.001). Birds reared in red nests selected a total of red strands which was not significantly different from that selected by birds from brown nests (compare Tests 3 and 4) (Chi-square of 1.2; p greater than 0.20).

These results indicate that the colors can be ranked, in decreasing order of preference: brown, green, red. A rearing experience with green increased the acceptance of green, but a rearing experience with red did not increase the acceptance of red.

*Substrate and habitat of the nest.*—The birds of Experiment 2 were given a choice between the substrate-habitat combination of their experience and a novel substrate-habitat combination (Figure 1). All of these birds chose the cups inside, regardless of their rearing experience.

In Experiment 3 (Figure 2) the cups were placed outside and the box inside, in an attempt to determine whether the substrate or the habitat was

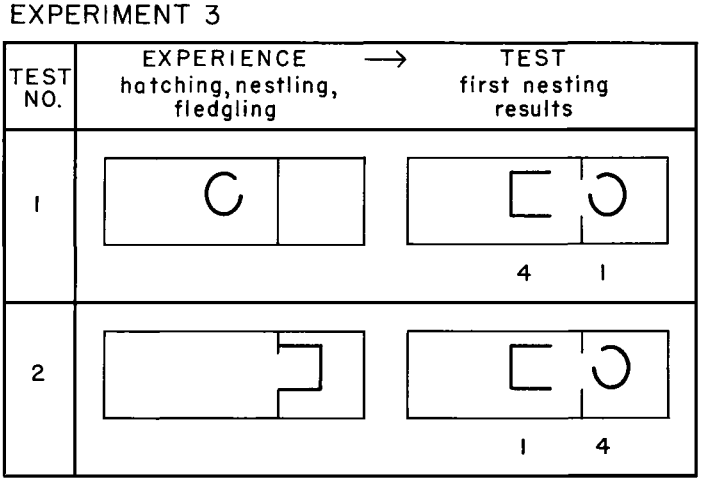


Figure 2. Experiment 3. The results of giving finches a choice between the substrate of their rearing experience in a novel habitat and a novel substrate in the habitat of their rearing experience, at the time of their first nesting. Symbols are the same as those of Figure 1.

dictating the preference shown by the birds in Experiment 2. However, the birds seemed to make different choices, depending on their rearing experience, indicating that they preferred the habitat of their experience, despite the differences in substrate. (The Fisher Exact Probability Test gives a p value of 0.10 for this distribution or one more extreme on one-tail.)

In Experiment 4 (Figure 3) the cups were placed in both habitats. From the earlier experiments, one would predict a choice of the cups inside by the birds reared in the cups inside, and random choices (or a conflict situation) in the birds reared in the box outside. Such predictions were verified. The birds reared in the cups inside selected the cups inside, and the birds reared in the box outside showed evidence of conflict. Three of these latter pairs built nests in both situations; two females laid eggs in both nests (one egg in the inside cups, three eggs in the outside cups, in that order), and one female laid her eggs on the floor of the cage. (The Fisher Exact Probability Test gives a p value of 0.04 for this distribution or one more extreme on one-tail.)

Experiments 2, 3, and 4, taken together, suggest that there is an interaction in these birds between an unlearned preference for the cups inside, and an acquired habitat preference based on early experience. While 13 out of 27 pairs (48 per cent) chose the habitat of their experience when the cups inside were available (Chi-square of 0.4; p greater than 0.50),

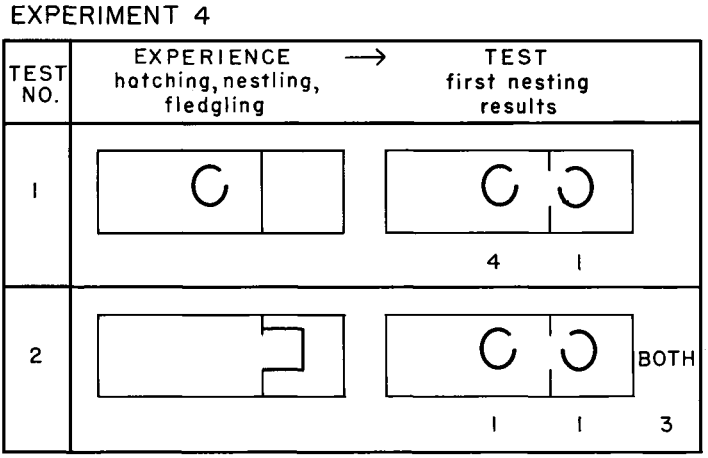


Figure 3. Experiment 4. The results of giving finches a choice between the habitat of their rearing experience and a novel habitat, both containing the same substrate, at the time of their first nesting. Symbols are the same as those of Figure 1.

8 out of 10 pairs (80 per cent) chose the habitat of their experience when the cups inside were not available (Chi-square of 3.6; p approximately 0.05).

*Nestling* versus *fledgling experience.*—Since the previous experiments indicated that young finches obtain information about the habitat of their nest during their rearing experience, Experiment 5 (Figure 4) was carried out in an attempt to determine whether the nestling or the fledgling period was more important in the acquisition of this information.

Several birds were reared in the box outside until they were almost ready

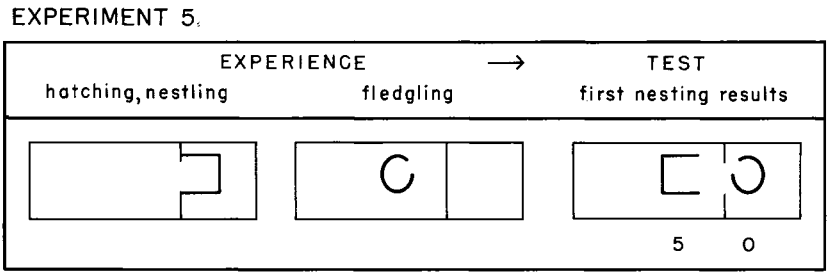


Figure 4. Experiment 5. The results of giving finches a choice, as in Experiment 3 (Figure 2), but with the birds having two previous experiences: a nestling period in the box outside, and a fledgling period in the cups inside. Symbols are the same as those of Figure 1.

to fledge, and were then transferred with their parents to a previously constructed nest in the cups inside. At maturity these birds were presented with a choice between the box inside and the cups outside.

If the nestling period were more important in learning the habitat of the nest, one would expect a selection of the outside habitat, as in Test 2 of Experiment 3; whereas, if the fledgling period were more important, one would expect a selection of the inside habitat, as in Test 1 of Experiment 3 (compare Figures 6 and 8). Since the birds selected the box inside, it appears that the fledgling period was the one in which information about the habitat of the rearing nest was acquired.

### RENESTING BIRDS

*Material of the nest.*—The results of testing birds with a choice of burlap colors, after previous nesting experiences with various colors, are shown in Table 2. All of the pairs tested showed a significant preference for one

TABLE 2

EXPERIMENT 6: RESULTS OF PRESENTING RENESTING FINCHES WITH A CHOICE OF BURLAP COLORS, AFTER PREVIOUS NESTING EXPERIENCES WITH VARIOUS COLORS[1]

| *Test number* | *Previous experience(s)* | *Choices made (in per cent)* | | *Number of strands* | *Chi-square* | $p$[2] |
|---|---|---|---|---|---|---|
| 1. | Brown | Brown | Green | | | |
| | | 67 | 33 | 339 | 40 | *** |
| | | 41 | 59 | 370 | 14 | *** |
| | | 70 | 30 | 367 | 58 | *** |
| | | 89 | 11 | 278 | 168 | *** |
| | | (65) | (35) | (1,354) | (124) | *** |
| 2. | Brown | Green | Red | | | |
| | | 74 | 26 | 478 | 114 | *** |
| | | 77 | 23 | 386 | 112 | *** |
| | | 83 | 17 | 287 | 122 | *** |
| | | (77) | (23) | (1,151) | (336) | *** |
| 3. | Brown, Green | Green | Red | | | |
| | | 76 | 24 | 566 | 156 | *** |
| | | 65 | 35 | 617 | 56 | *** |
| | | 76 | 24 | 496 | 138 | *** |
| | | (72) | (28) | (1,679) | (332) | *** |
| 4. | Brown, Green | Green | Brown | | | |
| | | 88 | 12 | 320 | 184 | *** |
| | | 62 | 38 | 439 | 28 | *** |
| | | 73 | 27 | 488 | 100 | *** |
| | | (73) | (27) | (1,247) | (262) | *** |
| 5. | Brown, Red | Green | Red | | | |
| | | 81 | 19 | 284 | 106 | *** |
| | | 74 | 26 | 458 | 102 | *** |
| | | 55 | 45 | 431 | 5 | * |
| | | 70 | 30 | 269 | 40 | *** |
| | | (69) | (31) | (1,442) | (202) | *** |

[1] All numbers represent data from individual pairs, except those in parentheses, which represent the total for all birds in a given test.

[2] * = probability less than 0.05; ** = probability less than 0.01; *** = probability less than 0.001.

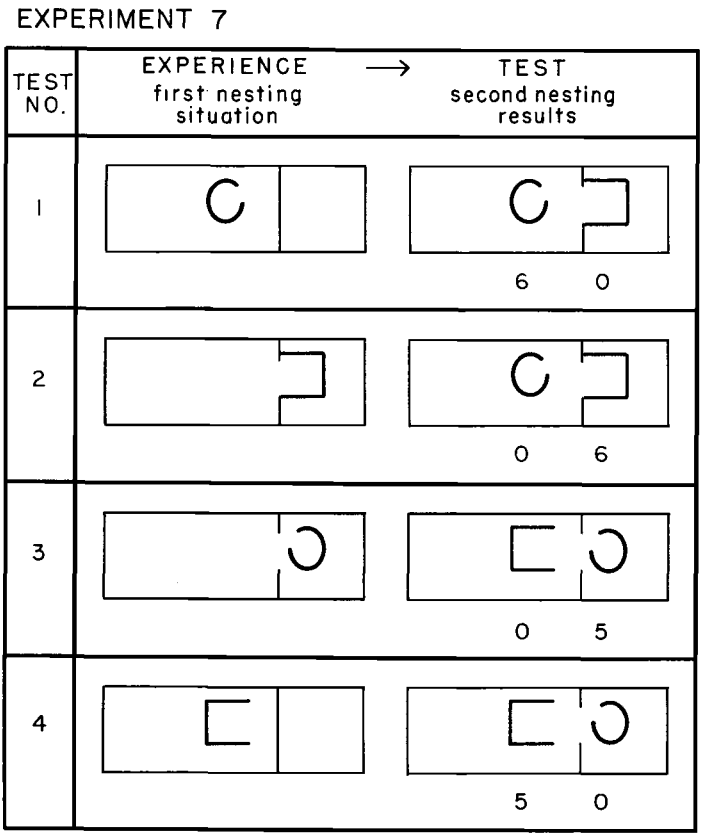


Figure 5. Experiment 7. The results of giving finches a choice between the substrate-habitat combination of their first nesting experience and a novel substrate-habitat combination, at the time of their second nesting. Symbols are the same as those of Figure 1.

of the colors presented to them and, with one exception, all of the pairs in any given test situation showed the same preference (pair 2 in Test 1). The preference reversal of this latter pair seems inexplicable at present.

A nesting experience with brown strands resulted in a choice of brown over green strands (Test 1), and a choice of green over red strands (Test 2) upon renesting. This indicates that the colors can be ranked, in decreasing order of preference after one nesting experience with brown strands, as brown, green, red.

A nesting experience with brown strands, followed by one with green strands, resulted in a choice of green over red strands (Test 3), and a choice of green over brown strands (Test 4). This latter result indicates

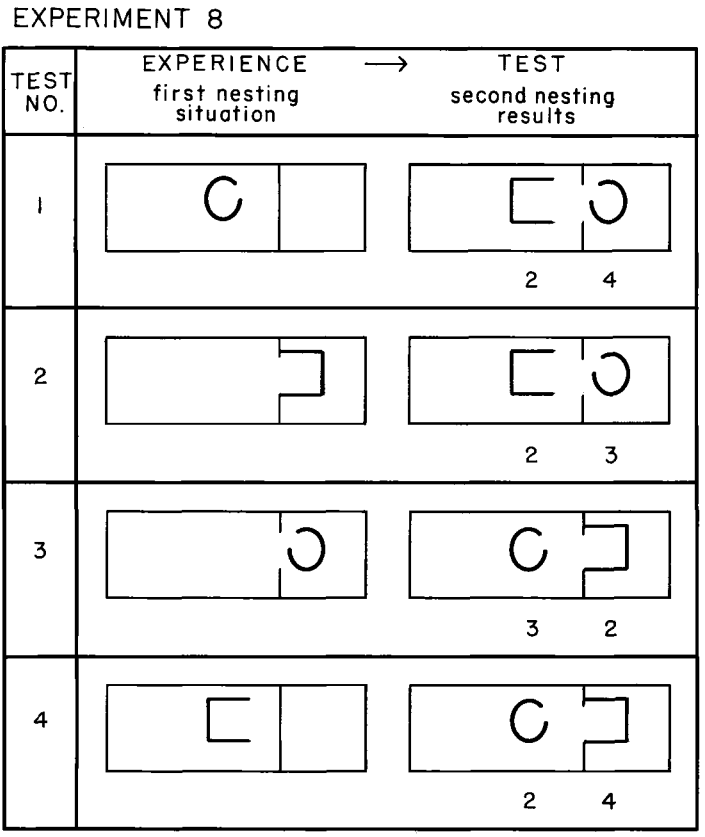


Figure 6. Experiment 8. The results of giving finches a choice between the substrate of their first nesting experience in a novel habitat and a novel substrate in the habitat of their first nesting experience, at the time of their second nesting. Symbols are the same as those of Figure 1.

that the previously found preference for brown over green (Test 1) could be reversed by one nest-building experience with green strands. This result also suggests that, with brown or green strands, the more recent experience exerts a stronger influence on the choice of colored strands than an earlier one.

A nesting experience with brown strands, followed by one with red strands, resulted in a choice of green over red strands (Test 5). Although these birds did select a significantly greater total of red strands than did the birds with a green nesting experience (compare Tests 3 and 5) (Chi-square of 8.0; p less than 0.01), their clear preference for green indicates

that the previously found "aversion" to red strands (Test 2) could not be appreciably overcome by one nesting experience with red strands.

*Substrate and habitat of the nest.*—All of the finches which were given a choice between the substrate-habitat combination of their first nesting experience and a novel substrate-habitat combination chose the situation of their experience (Experiment 7; Figure 5). Two of the pairs in Test 2 were retested after three months in a holding cage, to determine whether the influence of a nesting experience would persist over this longer period. These two pairs again chose the box outside.

Experiment 8 (Figure 6) was carried out in an attempt to determine whether the substrate or the habitat was more important in dictating the choices of Experiment 7. Accordingly, the substrates were reversed so that the familiar substrate was now in a novel habitat, and the familiar habitat contained a novel substrate. Under these conditions the birds chose their nesting situations randomly, indicating that either the substrate or the habitat could influence the choice of any individual pair.

## DISCUSSION

The foregoing experiments demonstrate slight effects of rearing experiences, and larger effects of adult nesting experiences on subsequent nest-building in the Zebra Finch. These effects varied, however, with the particular choices presented. Thus, birds having experience with red nests showed virtually no effects of this experience when later confronted with an opportunity to use red materials for nest building. Similarly, birds reared in the box outside the cage tended to ignore this situation when the cups inside the cage were available for nesting. These observations indicate that experience played a limited role in the experiments. Apparently, innate predispositions tended to bias the birds in favor of the more "natural" or species-characteristic nesting materials and situations.

Nest building in this species thus seems to involve an interaction of innate and learned components, and it is suggested that nesting experiences, in order to influence subsequent behavior, must lie within a limited portion of the range of experiences available to the species. Such restrictions on the effects of experience would allow this species a number of adaptive responses within a limited diversity.

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SUMMARY

Experiments were carried out with caged Zebra Finches to determine whether nestling and fledgling experiences would influence the first nest buildings of these birds and whether previous nesting experiences would influence subsequent nestings.

The experiments involved presenting choices of materials, substrates, and "habitats" to breeding pairs of finches. The materials available were brown, green, and red burlap strands; the substrates were nesting cups and nesting boxes; and the habitats were the insides of the cages and wood-enclosed extension areas outside the cages.

Birds nesting for the first time were tested two months after their removal from the rearing nest, and renesting pairs were tested at subsequent one month intervals.

The rearing experience affected the selection of colored nesting materials by birds nesting for the first time, provided that the colors involved were brown and green. The birds tended to reject red material, even if they had been reared in red nests.

Birds nesting for the first time tended to select the habitat, but not the substrate, of their rearing experience, although one particular substrate-habitat combination (the nesting cups inside the cage) tended to mask this effect. The fledgling period was apparently more important than the nestling period for the young birds' acquisition of information about the habitat of the nest.

Renesting birds selected the colored nesting material of their preceding nest, if this material was either brown or green. Again, as with birds nesting for the first time, red material tended to be rejected, even by birds whose previous nest was constructed of red strands.

All of the finches selected the substrate-habitat combination of their previous nesting experience for renesting when it was available. The substrate and habitat were equally important in dictating this selection.

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