

## IS THE INCUBATION PATCH REQUIRED FOR THE CONSTRUCTION OF A NORMAL NEST?

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**ABSTRACT.**—New methods are presented for examining the function of the incubation patch in the nest-building process. These involve direct interference with the tactile sensitivity of the brood patch and hence its ability to assess nest size and texture. The patch may be covered with a pliable plastic apron or rendered completely insensitive to touch by surgical denervation.

Data from several experiments employing such methods indicate that the incubation patch is not required for construction of a nest of normal size and composition by Canaries. In addition, its absence does not affect the birds' disinterest in nest-building as egg-laying approaches. The results suggest that receptors in places other than the incubation patch may be used in its absence to assess nest quality and size.

More than two decades ago, Robert Hinde (1958) published his classic monograph on the nest-building behavior of Canaries (*Serinus canaria*). In this and later papers (e.g., Warren and Hinde 1959, Hinde and Steel 1962, 1975, Steel and Hinde 1963, 1966, 1972a, b, Hinde 1965, 1967), he and his associates catalogued the Canary's stereotypic nest-building behaviors, demonstrated that estrogen and long daily photoperiods evoke them, and showed that certain characteristics of the nest modify them. In brief, when female Canaries are given grass and feathers as nest material and then photostimulated or treated with estrogen, they build a nest that consists of two discrete layers: an outer grassy one and an inner feather-rich one. The bird's early preference for material of coarse texture and later preference for feathers depends on the size and the texture of the nest. Increased interest in feathers as building material occurs whenever the nest cavity is small *or* has a rough, grassy texture. In addition, building activity declines before the bird lays its clutch because the nest cavity is small *and* has a rough texture (Hinde 1958, 1965, Steel and Hinde 1977).

Photostimulated Canaries exhibit high endogenous levels of gonadotrophins and estrogen which induce the formation of an incubation patch in the ventral apterium near the time when the nest is being constructed (Steel and Hinde 1963, Hutchison et al. 1967, Follett et al. 1973). The incubation patch is well endowed with superficial nonmyelinated nerve fibers (Kern and Coruzzi 1979) and is highly sensitive to touch (Hinde et al. 1963). Several nest-

building behaviors (scrabbling, turning, weaving, and pressing down) bring it into intimate contact with the forming nest. Apparently, this area of skin provides the central nervous system with information about nest quality and size during such contact and in this way brings about modifications and cessation of building activities.

Hinde proposed these functions for the incubation patch on the basis of experiments in which he altered the Canary's nest-building activities by modifying the nest. In this paper, we reexamine the role of the incubation patch in the nest-building process by using different methods that directly affect the sensitivity of the skin. In some cases, we monitor building behavior directly, as did Hinde, but more often we use the structure of the nest to tell us about the bird's building behavior. Because the nest is built from the outside in, differences in the composition of its outer and inner layers reflect differences in the Canary's preference for materials such as grass and feathers.

### MATERIALS AND METHODS

We obtained female chopper Canaries from local merchants in Ithaca and Brooklyn, New York. (Females of this strain weigh 15–25 g.) Their sex was determined by laparotomy. In the experiments outlined below, nest-building was induced by either photostimulating the birds or treating them with combinations of a synthetic estrogen (*EC*: depo-estradiol cypionate, Upjohn Co., Kalamazoo, MI) and ovine prolactin *LTH*: NIH-P-S9 and -S10).

We modified the sensitivity of the incubation patch by covering it with a sheet of soft, pliable plastic or by surgically denervating it. The plastic aprons covered the ventral and lateral apteria and the intervening

TABLE 1. Effects of denervation on the histology of the incubation patch.

| Region of the brood patch | Side of the brood patch | N | Epi-dermal thickness ( $\mu\text{m}$ ) | Dermis                       |                            |                            |  |      |      |      |      |
|---------------------------|-------------------------|---|--|------------------------------|----------------------------|----------------------------|--|------|------|------|------|
|                           |                         |   |  | Thick-ness ( $\mu\text{m}$ ) | Edema present <sup>a</sup> | Vascu-larity (ves-sels/mm) | Maximal vessel diameters ( $\mu\text{m}$ ) |      |      |      |      |
| Upper breast <sup>b</sup> | Control (unoperated)    | 5 | 8.39                                   | 92.4                         | 2.54                       | 7.66                       | 88.6                                       | 48.6 | 42.0 | 36.6 | 31.0 |
|                           | Denervated              | 5 | 10.74                                  | 116.9                        | 3.06                       | 8.92                       | 68.2                                       | 46.8 | 42.4 | 37.4 | 33.4 |
| Lower breast <sup>b</sup> | Control (unoperated)    | 5 | 10.36                                  | 139.9                        | 3.36                       | 8.90                       | 114.0                                      | 87.4 | 66.6 | 58.0 | 52.2 |
|                           | Denervated              | 5 | 11.38                                  | 181.5                        | 3.24                       | 10.35                      | 96.2                                       | 68.6 | 59.2 | 52.2 | 46.8 |
| Abdomen <sup>b</sup>      | Control (unoperated)    | 5 | 11.54                                  | 92.1                         | 2.36                       | 9.50                       | 66.4                                       | 52.4 | 45.2 | 41.4 | 36.2 |
|                           | Denervated              | 5 | 11.06                                  | 88.4                         | 2.50                       | 7.94                       | 67.6                                       | 50.0 | 43.0 | 36.0 | 32.8 |

<sup>a</sup> Rating scale for edema: 0 = none; 1 = mild; 3 = moderate; 5 = pronounced.

<sup>b</sup> Values in the table are means. None of the differences between the two sides is statistically significant in any region of the incubation patch (Mann-Whitney U tests, 2-tailed).

feather tracts and were tied in place along the dorsal midline. They had fine perforations that allowed air to circulate across the underlying skin. They did not interfere with the development of the incubation patch and can be presumed not to have prevented the bird from assessing the size of the nest cavity via the apteria. However, they probably would have prevented the bird from assessing the texture of the nest.

The surgical denervation procedure was one in which all of the cutaneous nerves to the brood patch were severed. We had good success with the procedure, rarely killing a bird and generally obtaining complete insensitivity of the skin for periods of months. The operation was performed on one side of the venter at a time, with an interval of 1–2 weeks between sides for healing. An incision was made in the skin immediately lateral to the ventral feather tract from near the vent to the axilla. The cutaneous nerves that supply the ventral apterium are on the surface of the body musculature beneath the lateral apterium and can be readily transected here. We removed a 2-mm segment of each nerve to minimize the possibility that it would regenerate. At the level of the subalar fat organ, one of the prominent cutaneous nerves to the apterium is accompanied by a branch of the incubation artery. Generally, the two can be teased apart, but if necessary the artery can be tied off and then cut along with the nerve. Interruption of this vessel does not appear to affect the development of the incubation patch (see below). We routinely anesthetized the birds with diethyl ether, but found that Equi-Thesin (Jensen-Salsbery Laboratories, Kansas City, MO) also works well. The location of the nerves and blood vessels that supply the Canary's ventral apterium can be obtained from Kern and Coruzzi (1979).

We evaluated the effectiveness of the denervation using a procedure suggested to us from methods used by Hinde et al. (1963). Canaries exhibit a "tickle response" when a fine glass needle is drawn lightly across their ventral apterium: they scratch at the unseen needle. Denervated birds do not show the tactile response and are assumed to be successfully denervated. The test is simple to administer and has been used successfully by naive workers in our laboratory to identify bilaterally and unilaterally denervated birds.

We also examined the possibility that surgical denervation interferes with the formation of a normal, if tactilely insensitive, brood patch. This does not appear to be the case. We treated unilaterally denervated canaries with combinations of EC and LTH that produce complete brood patch formation (50  $\mu\text{g}$  EC and 75 IU LTH given subcutaneously thrice weekly for 10 days).

Using the criteria of Steel and Hinde (1963), we then compared the normal (unoperated) and denervated sides of the apterium (for defeathering, vascularity, and edema) as they developed into halves of the incubation patch. There were no visible differences. After the birds had well developed incubation patches, we took samples of skin from three regions of the apterium on each side, fixed them in 10% buffered neutral formalin, dehydrated them in alcohol, and embedded them in paraffin. Serial sections (7  $\mu\text{m}$  in thickness) were prepared from each skin sample, stained by the PAS or Pollak's trichrome methods (Humason 1962), and evaluated quantitatively. There were no histological differences between the two sides in any region of the incubation patch (Table 1). In summary, denervation per se does not apparently interfere with the conversion of the apterium into an incubation patch: feather loss, changes in the epidermis and dermis, increases in vascularity, and the accumulation of fluid in the dermis are similar in the presence and absence of cutaneous nerves.

Using these methods, we did several experiments designed to define the function of the incubation patch in the nest-building process. These experiments were done on visually isolated photosensitive Canaries kept on daily photocycles of LD 8:16 prior to use and housed in standard breeding cages (23  $\times$  36  $\times$  28 cm). The birds were freely provided with food, water, grit, and cuttlebone, as well as a standard plastic nest pan (diameter = 9.5 cm; depth = 6.0 cm) and a hopper of nest material. The latter was a mixture of coarse and soft materials: strands of shredded wood and horse hair cut in 4–5 inch lengths, and feathers (quail, pigeon, chicken), respectively, the two present in roughly equal proportions. The experiments were the following:

*Apron I experiment.* Six female Canaries were fitted with plastic aprons and six others with plastic halters, which did not cover the ventral apterium. They were allowed one week to adjust to their riggings and then exposed to a daily photocycle of LD 16:8. We observed the nest-building behavior of each photostimulated bird for 10–30 min daily from a blind. We routinely watched them for a 10-min period in the morning (beginning at 09:30), at midday (beginning at 11:30), and sometimes in the evening (beginning at 21:00). The order of observations for each watch was determined with a random number table. The number, kind, and duration of each nest-building behavior were recorded on paper with the help of a system of abbreviations and a wrist watch. The behaviors are those described by Hinde (1958) and include nest inspection; the gathering, carrying, and placing of nest material; weaving,

TABLE 2. The composition of nests built by reproductively active colony birds differs from that of nests built by estrogenized female Canaries<sup>a</sup>.

| Source of nests                     | N     | Pieces of material in outer layer of the nest <sup>b</sup> |          |                | Pieces of material in inner layer of the nest <sup>b</sup> |          |                | Total number of pieces in the nest <sup>b</sup> |
|-------------------------------------|-------|--|----------|----------------|--|----------|----------------|---|
|                                     |       | Shredded wood and hair                                     | Feathers | %F             | Shredded wood and hair                                     | Feathers | %F             |   |
| Colony birds                        | 20-23 | 626 ± 115<br>**  | 199 ± 22 | 28 ± 3<br>**** | 276 ± 47<br>****   | 285 ± 34 | 51 ± 3<br>**** | 1,398 ± 149<br>***                              |
| Estrogen-treated birds <sup>c</sup> | 6     | 1,383 ± 320  | 110 ± 24 | 8 ± 1          | 1,214 ± 416  | 205 ± 51 | 18 ± 4         | 2,911 ± 705                                     |

<sup>a</sup> Values in the table are means ± SEM.

<sup>b</sup> Asterisks between means indicate that they differ significantly at the 0.01 (\*\*), 0.005 (\*\*\*), or 0.001 (\*\*\*\*) levels (Mann-Whitney U tests, 2-tailed). The increase in preference for feathers (%F) late in the building period (i.e., in the inner layer of the nest) is significant for both groups of birds ( $P < 0.05$ , Wilcoxon paired-sample tests, 1-tailed).

<sup>c</sup> Birds received subcutaneous injections of 25 µg EC thrice weekly and were exposed to the long daily photoperiod of New York City during June and July while the experiment was in progress.

scrabbling, turning, pressing down, and bill-wiping; and the time spent sitting in the nest. Observations continued until each bird laid the first egg in the clutch. Its nest was then removed and disassembled. The pieces of shredded wood, hair, and feathers in the outer coarse layer and inner feather-rich layer of the nest were determined.

*Apron II experiment.* The number of birds and the design of this experiment were the same as before, except that the material in the nest bowl was removed at 16:00 each day and counted and nest-building activity was not watched. Collections continued until each bird laid the first egg of the clutch.

*Denervation I experiment.* Four sham-operated and eight bilaterally denervated female Canaries were photostimulated (the daily photocycle was LD 16:8) and allowed to build a nest and lay the first egg of the clutch. Nests were then removed, measured, and dismantled as above. In addition, the gross appearance of the apterium (presence or absence of feathers and dermal edema; vascularity) was recorded at the beginning and end of the experiment and a tickle test was ad-

ministered. (All birds developed incubation patches; denervated ones had tactilely insensitive apteria throughout the experiment.)

*Denervation II experiment.* Ten sham-operated and 13 bilaterally denervated female Canaries were exposed to the natural (long) daily photoperiod of New York City during May-August. Each received subcutaneous injections of 25 µg EC and 50 IU ovine prolactin thrice weekly, after a week (three injections) of EC injections alone. Injections continued until the birds built a visibly complete nest that did not increase more than 0.5 g in weight over two successive days. The nest was then removed, measured, and dismantled as above. In addition, the amount of nest material on the floor of the cage was counted daily, and the visible appearance and tactile sensitivity of the ventral apterium was determined periodically. (All birds developed brood patches; three denervated individuals which built nests regained limited sensitivity in the abdomen [only] during the experiment.)

Nests built by normal Canaries during spring and summer differ in some important ways from those pro-

TABLE 3. Apron I experiment: effects of covering the incubation patch with a plastic apron on the nest-related activities of photostimulated Canaries. Values in the table are means ± SEM.

| Nest-related activity             | Frequency of each activity (number/h) |                              | Duration of each activity (s/h) |                              |
|-----------------------------------|---------------------------------------|------------------------------|---------------------------------|------------------------------|
|                                   | Birds wearing halters (N = 3)         | Birds wearing aprons (N = 4) | Birds wearing halters (N = 3)   | Birds wearing aprons (N = 4) |
| Inspection of nest pan            | 98 ± 24                               | 85 ± 23                      | 181 ± 47                        | 140 ± 45                     |
| Gathering nest material           |                                       |                              |                                 |                              |
| Shredded wood and hair            | 23 ± 5                                | 23 ± 5                       | 56 ± 13                         | 96 ± 32                      |
| Feathers                          | 26 ± 7                                | 14 ± 5                       | 107 ± 28                        | 62 ± 25                      |
| % feathers                        | 51 ± 5                                | 38 ± 7                       | 65 ± 3                          | 40 ± 10                      |
| Carrying nest material            |                                       |                              |                                 |                              |
| Shredded wood and hair            | 14 ± 6                                | 16 ± 5                       | 64 ± 33                         | 57 ± 24                      |
| Feathers                          | 14 ± 5                                | 10 ± 4                       | 46 ± 28                         | 39 ± 22                      |
| % feathers                        | 52 ± 5                                | 40 ± 7                       | 39 ± 9                          | 34 ± 8                       |
| Placing nest material in nest pan |                                       |                              |                                 |                              |
| Shredded wood and hair            | 9 ± 3                                 | 11 ± 3                       | 9 ± 3                           | 12 ± 3                       |
| Feathers                          | 10 ± 3                                | 6 ± 1                        | 10 ± 4                          | 7 ± 2                        |
| % feathers                        | 18 ± 5                                | 18 ± 3                       | 52 ± 6                          | 40 ± 9                       |
| Nest-building activities          |                                       |                              |                                 |                              |
| Weaves                            | 14 ± 8                                | 10 ± 6                       | —                               | —                            |
| Scrabbles                         | 11 ± 6                                | 7 ± 3                        | —                               | —                            |
| Turns                             | 5 ± 3                                 | 4 ± 1                        | —                               | —                            |
| Sits or presses down              | 17 ± 7                                | 18 ± 5                       | 119 ± 54                        | 92 ± 30                      |

TABLE 4. Effects of covering the Canary's incubation patch with a plastic apron or denervating it on nest composition<sup>a</sup>.

| Experiment <sup>b</sup> | Group         | N   | Pieces of material in outer layer of the nest |           |         | Pieces of material in inner layer of the nest |           |         | %F            | Total number of pieces in the nest |
|-------------------------|---------------|-----|---|-----------|---------|---|-----------|---------|---------------|------------------------------------|
|                         |               |     | Shredded wood and hair                        | Feathers  | %F      | Shredded wood and hair                        | Feathers  | %F      |               |                                    |
| Apron I                 | Halter        | 3   | 1,193 ± 165                                   | 247 ± 108 | 18 ± 8  | 89 ± 30                                       | 226 ± 115 | 72 ± 3  | 1,754 ± 186   |                                    |
|                         | Apron         | 3-4 | 655 ± 84                                      | 188 ± 52  | 22 ± 15 | 98 ± 67                                       | 158 ± 59  | 69 ± 10 | 1,030 ± 76(4) |                                    |
| Denervation I           | Sham-operated | 2   | 1,514   | 781       | 34      | 77  | 223       | 74      | 2,596         |                                    |
|                         | Denervated    | 2   | 1,231   | 434       | 23      | 100   | 242       | 70      | 2,006         |                                    |
| Denervation II          | Sham-operated | 8   | 795 ± 120                                     | 180 ± 27  | 24 ± 3  | 766 ± 138                                     | 246 ± 44  | 33 ± 2  | 1,561 ± 234   |                                    |
|                         | Denervated    | 6   | 1,293 ± 470                                   | 174 ± 54  | 20 ± 6  | 980 ± 316                                     | 331 ± 97  | 38 ± 6  | 2,272 ± 757   |                                    |

<sup>a</sup> Values in the table are means ± SEM. No statistically meaningful differences exist among sham-operated and denervated groups in the denervation I experiment ( $P > 0.05$ , Mann-Whitney U tests, 2-tailed).  
<sup>b</sup> Canaries in the apron I and denervation I experiment were treated with estrogen and prolactin. Those in the denervation II experiment were treated with estrogen and prolactin. Both procedures stimulate Canaries to build nests.

TABLE 5. Placing activity during the apron experiments: effects of decreasing size of the nest cavity on the Canaries' preference for feathers during the nest-building period. Preference for feathers is expressed as the percentage of the total material placed in the nest pan that was feathers (%F). Values in the table are means.

| Experiment | Treatment | N | Preference for feathers (%F) during |        |       |
|------------|-----------|---|-------------------------------------|--------|-------|
|            |           |   | initial                             | middle | final |
| Apron I    | Halter    | 3 | 0                                   | 32     | 69    |
|            | Apron     | 4 | 30                                  | 34     | 64    |
| Apron II   | Halter    | 3 | 19                                  | 14     | 20    |
|            | Apron     | 2 | 13                                  | 11     | 19    |

duced by birds treated with estrogen. The dimensions are not much different: 32.9 vs. 28.0 cm<sup>2</sup>, 4.6 vs. 4.0 cm, and 128.6 vs. 132.0 cm<sup>3</sup> for the cross-sectional area, depth, and volume of the nests, respectively (natural vs. estrogen-induced nests; only the cross-sectional areas differ significantly,  $P < 0.05$ , Mann-Whitney U test, 2-tailed). Nest composition in the two groups, however, is considerably different (Table 2). Estrogen appears to exaggerate nest-building, with the result that the nest contains abnormally large amounts of material, especially coarse material. These compositional differences suggest that estrogen *alone* is not responsible for the entire spectrum of nest-building activities, although it clearly induces building. Steel and Hinde (1966, 1972a, b) made the same point on other grounds. Such differences must be recognized when comparisons are attempted between experiments in which nest-building has been induced by different methods.

RESULTS AND DISCUSSION

APRON EXPERIMENTS

Seven photostimulated Canaries (three control birds and four birds with aprons) built complete nests in the apron I experiment. The number is too small to permit statistical comparisons by group, but examination of their behaviors (Table 3) and nests (Table 4) shows that they did not differ in any major way. All birds produced nests with coarse outer layers and inner feather-rich linings. All exhibited a marked preference for feathers as building material late in the building period. This is evident in the structure of the nests (Table 4 and Fig. 1) and the nest-building behavior itself (Table 5). In fact, combining the data of the two groups (permissible given the similarity of their responses), we found that the inner layer of the nest contained a significantly higher percentage of feathers than the outer layer (Table 4). Furthermore, Canaries placed significantly more feathers in the nest late in the nest-building period than they did earlier (Table 5;  $P < 0.025$  in both cases, Wilcoxon paired-sample tests, 1-tailed,  $n = 6$ ).



FIGURE 1. The composition of the nest reflects a female Canary's preference for coarse and fine building materials. Initially, she selects coarse materials (shredded wood and hair) and later, she uses feathers.

The Canaries that built nests in this and the other experiments reported in this paper developed brood patches and displayed the normal sequence of nest-building activities described by Hinde (1958). A representative sequence is presented in Figures 2 and 3.

Five of the 12 females in the apron II experiment built nests and laid eggs. All birds failed to show a preference for feathers late in the building period, in distinct contrast to birds in the apron I experiment (Table 5).

On the basis of Hinde's work, we anticipated that the building behavior and nest composition of the two groups in the apron I experiment would be similar because the apron did not prevent the bird from tactilely assessing changes in the size of the nest cavity and the latter is sufficient to increase the bird's interest in feathers. We also predicted that the Canaries would not develop a marked preference for feathers in the apron II experiment because the nest pan was cleaned out daily so that nest size did not diminish.

On the other hand, we did not expect the building activities of the birds to decline with the approach of egg-laying because both a small nest cavity and a nest of coarse texture are required to stop building (Hinde 1958, 1965). In the apron I experiment, females with aprons presumably could not obtain information about nest texture. In the

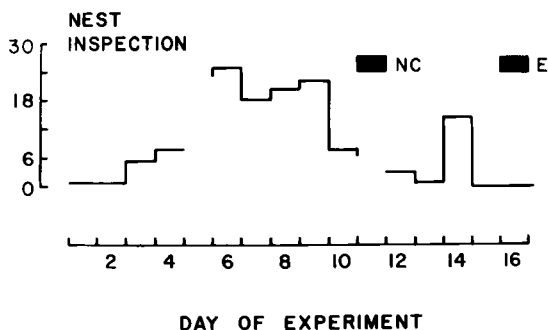


FIGURE 2. Nest inspections of Canary no. 23199 during the apron I experiment. Values on the ordinate are the number of nest inspections in a 10-min period. Nest-building behavior was not observed on days 5 and 11 of photostimulation. NC: day when the nest was completed; E: day on which the first egg in the clutch was laid.

apron II experiment, they not only were unable to assess nest texture, but also did not experience a diminishing nest cavity. (It does not seem likely to us that the plastic apron acted as a source of tactile stimulation which the bird interpreted as a small nest bowl. Had this been the case, the birds would have developed a marked preference for feathers near the end of the building period in the second experiment, but they did not.) Nonetheless, all four birds wearing aprons, as well as two of the three controls that built nests, in the apron I experiment stopped building shortly before laying eggs. In addition, two of three controls and one of two females with aprons in the apron II experiment stopped building before they laid. These findings are at variance with Hinde's postulate concerning the function of the incubation patch in regulating the duration of the building period.

#### DENERVATION EXPERIMENTS

Four of 12 birds in the denervation I experiment constructed nests when photostimulated. Two were sham-operated individuals; the others were successfully denervated. All constructed nests with an outer coarse layer and an inner feather-rich lining (Table 4). In other words, they exhibited a distinct preference for feathers late in the building period. We found no obvious differences in the composition of their nests (Table 4) or in nest dimensions: 26.0 vs. 24.3 cm<sup>2</sup>, 4.5 vs. 4.8 cm, and 115.8 vs. 115.0 cm<sup>3</sup> for the cross-sectional area, depth, and volume of the nest cavity, respectively (sham-operated vs. denervated birds). In addition, all four became disinterested in nest-building shortly before they laid eggs.

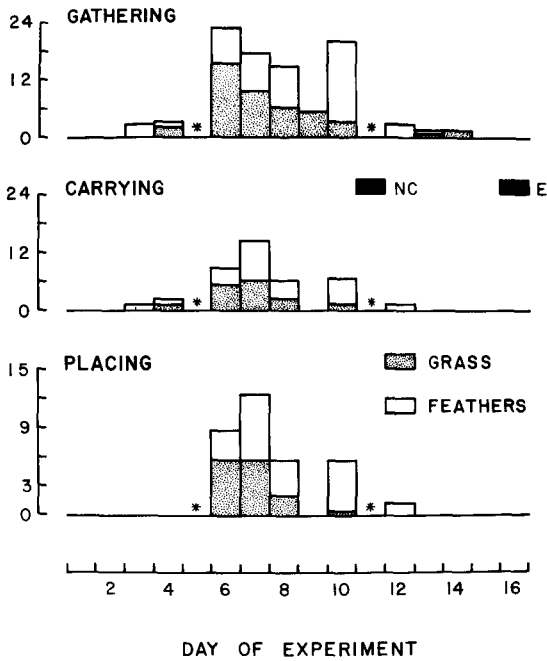


FIGURE 3. Phenology of nest-building by Canary no. 23199 during the apron I experiment. Values on the ordinates are the number of items gathered, carried or placed in the nest pan in a 10-min period. Nest-building behavior was not observed on days 5 and 11 of photostimulation (asterisks). Abbreviations as in Figure 2.

Fourteen birds constructed nests in the denervation II experiment. Eight were sham-operated; six were denervated. The composition of nests in the two groups was similar ( $P > 0.05$  for each characteristic of the nest shown in Table 4). In every case, there was a coarse outer layer of shredded wood and hair and an inner feather-rich lining (Fig. 1). In other words, females in both groups exhibited a distinct preference for feathers late in the nest-building period. In terms of the nests, this increase (in %F) was statistically significant ( $P < 0.05$  for each group). Furthermore, there were no significant differences (1) in nest dimensions by group: 23.7 vs. 25.7 cm<sup>2</sup>, 4.6 vs. 4.2 cm, and 109.2 vs. 110.8 cm<sup>3</sup> for the cross-sectional area, depth, and volume of the nest cavity, respectively (sham-operated vs. denervated birds), or (2) in nest weight by group: 6.4 vs. 7.4 g.

Because nest-building was induced with estrogen in the denervation II experiment, the birds did not lay eggs. We therefore assessed their interest in nest-building by weighing the nest pan (indicates placing activity) and counting the pieces of nest material on the floor of the cage (indicates gathering activity) on a daily basis. Seven of

eight sham-operated and five of the six denervated Canaries showed a perceptible decline in building activity at or just before their nests were completed. (The changes in nest weight per day and the type and amount of nest material on the floor of the cage per day were not statistically different by group on days -1 to -10, with day 0 being the day when the nest was complete; Mann-Whitney U tests, 2-tailed.)

Our experiments with surgically denervated Canaries, whose ventral apteria were unresponsive to tactile stimulation (in marked contrast to sham-operated birds), yielded results that are difficult to reconcile with Hinde's findings concerning the function of the incubation patch in the nest-building process. Presumably, denervated Canaries can neither assess the texture nor the size of the nest via the incubation patch and accordingly would not be expected to develop a preference for feathers late in the building period nor to stop building near the time of egg-laying.

GENERAL THEMES

The methods that we used to study nest-building have not been widely used previously. As far as we can determine, surgical denervation of the ventral apterium has been employed only once, to examine the relative importance of the eyes and the venter in the brooding behavior of pigeons (Medway 1961). Several behavioral studies have demonstrated that the ventral apterium is temperature-sensitive and regulates egg temperature (e.g., Franks 1967, Drent et al. 1970), but in only one study was the sensitivity of the apterium modified directly and in this case only briefly with the anesthetic, Xylocaine (White and Kinney 1974). Various investigators have dismantled nests (e.g., Riehm 1970), but none apparently as a means of assessing changes in building behavior.

The data we have presented are modest, yet they raise some intriguing questions about the role of receptor systems in the nest-building process. In some respects (apron experiments), they support Hinde's findings that the incubation patch participates in this process. However, in other respects (especially the denervation experiments), they suggest that additional receptor systems are also involved. A tactilely sensitive brood patch is well suited to provide the central nervous system with information about the nest. However, other systems apparently operate in its absence. Likely examples include the eyes and tactile recep-

tors at the base of the bill or in the lateral apertures.

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