

## BEHAVIORAL RESPONSES OF BROWN-HEADED COWBIRDS TO NESTS AND EGGS

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SEVERAL hypotheses have been advanced regarding a physiological basis for the absence of nest-building, incubation, and brooding in cowbirds and other birds that are obligate brood parasites. Theoretically, it is possible that this involves inherent deficiencies in the production of prolactin and other hormones which normally mediate these behaviors (see reviews by Lehrman, 1961, and Eisner, 1960), as suggested by several workers (Höhn, 1959, 1961; Selander, 1960; Friedmann, 1960), but more in line with modern concepts of the evolution of endocrine systems (Medawar, 1953; Beach, 1958; Zuckerman, 1955; Gorbman and Bern, 1962) is the alternate hypothesis that the development of brood parasitism involves genetic changes producing refractoriness to hormonal stimulation of the neural mechanisms controlling these behavior patterns (Höhn, 1962; Selander and Kuich, 1963: 85-86). This view is supported by Höhn's demonstration (1959, 1962) that the pituitaries of breeding female Brown-headed Cowbirds (*Molothrus ater*) contain prolactin in amounts similar to those found in the pituitaries of breeding females of the non-parasitic Red-winged Blackbird (*Agelaius phoeniceus*).

Selander and Kuich (1963: 86) suggested that hormonal treatment could not induce parasitic cowbirds to perform nest-building, incubation, or other behaviors that are not part of the normal behavioral repertoire of the species. This prediction was based on their failure to elicit these behaviors in Brown-headed Cowbirds in experiments involving the injection of estrogen, prolactin, and progesterone, alone and in combination, and the testing of responses to nests and cowbird eggs. However, Robinson and Warner (1964) have since claimed that captive female Brown-headed Cowbirds exhibit incubation behavior in response to nests containing eggs and (p. 323) that "more than a 30-fold increase in incubation behavior" can be induced in young (three to four month old) cowbirds by daily injections of prolactin.

The objective of the present work was to repeat and extend the experiments of Robinson and Warner (1964) with prolactin and to test the influence of progesterone and an estrogen on the behavior of captive female Brown-headed Cowbirds.

### METHODS AND MATERIALS

Our experiments entailed a standardized test of the reactions of caged female cowbirds to artificial nests and eggs. Comparisons were made between the performances of birds before hormone treatment and during treatment with prolactin (Experiment

1), progesterone (Experiment 2), and estradiol benzoate (Experiment 3). Additionally, we tested the response of two females to empty nests (Experiment 4).

*Conditions of confinement.*—In Experiment 1 eight female cowbirds (reference numbers 1 through 8) were confined singly to small cages ( $63 \times 46 \times 42$  cm) and four females (numbers 9 through 12) were housed in larger cages ( $152 \times 92 \times 60$  cm). (We found no evidence that cage-size influenced the behavior we studied.) In Experiments 2, 3, and 4 all birds were housed in the small cages. Individuals were visually isolated from birds in adjacent cages but not from birds in cages across the room.

Each cage contained two perches, a bowl of water for bathing, and a container of food (millet, chick starter, and chicken "scratch"). Drinking water and grit were provided in containers attached to the cage fronts. The birds, with one exception, remained in excellent physical condition throughout the study period.

Photoperiod in the laboratory was 12 hours and temperature was maintained at approximately  $20^{\circ}\text{C}$ .

*Nests and eggs.*—Artificial nests were prepared from grass (Experiments 2, 3, and 4) or from fine twigs and grass obtained from nests of the Great-tailed Grackle, *Quiscalus mexicanus* (Experiment 1). The material was shaped into a compact nest cup inside a glass bowl 11.6 cm in diameter and 5.2 cm deep (Figure 1). Because captive cowbirds frequently break real eggs by pecking them, we used plaster of Paris eggs cast in a mold formed from an egg of the Brown-headed Cowbird. The plaster eggs were painted with watercolors to resemble the eggs of this species. We repaired or replaced nests disrupted by the foraging activities of the cowbirds and replaced eggs as they became chipped.

*Test procedure.*—We placed a nest containing three eggs (or, in some cases, as indicated below, an empty nest) in each cage and observed the responses of the female cowbirds for a period of from 45 minutes to five hours. Observations were

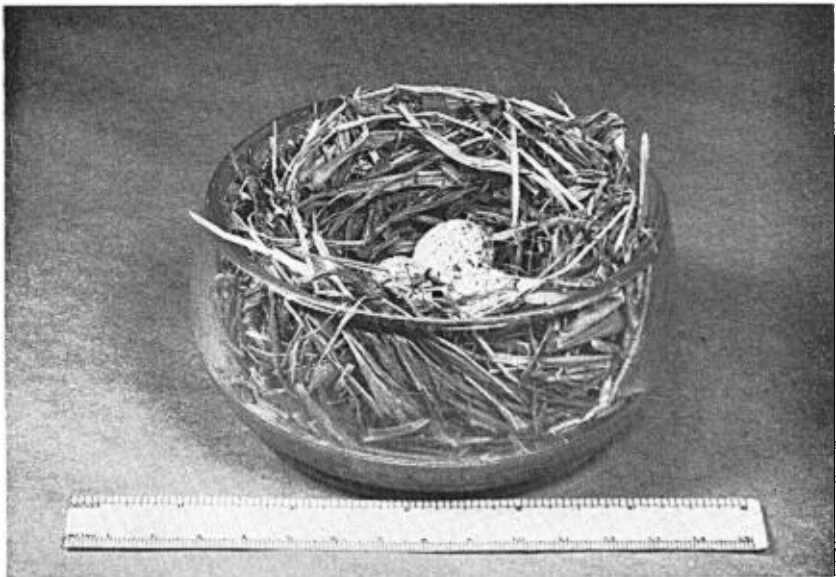


Figure 1. Artificial nest containing three plaster eggs.

made by two persons about 10 feet from the cages. At the end of each hour of observation, the nests were reshaped and eggs which had been covered with nest material or removed from the nests were replaced in the nest cups.

We originally intended to leave the nests and eggs in the cages throughout the course of an experiment, following the procedure of Robinson and Warner (1964: 316). Thus, nests containing three eggs were placed in the cages at the beginning of Phase 1 of Experiment 1 on 26 August; however, they were removed on 2 September when it became apparent that the cowbirds were introducing an uncontrollable variable in the experiment by altering the condition of the nests and eggs. With few exceptions, the cowbirds foraged in the nests, pulling out grass with the bill and scratching with the feet; the nests soon were disrupted and the eggs covered with nest material. Nests were often torn apart by the foraging birds and eggs were commonly removed from the nest and dropped on the cage floor. Therefore, to insure reasonable uniformity in the condition of the test objects, in all experiments after 2 September the nests and eggs were placed in the cages at the beginning of a test period and removed from the cages and from the sight of the cowbirds at the end of the period.

*Hormones.*—Prolactin used in Experiment 1 was an ovine preparation (NIH-P-S5) bioassayed at 17 IU per mg. This was dissolved in normal saline and injected subcutaneously in the breast region. Control birds were similarly injected with normal saline.

In Experiment 2, experimental birds were injected intramuscularly in the breast with progesterone (Proluton, Schering) in sesame oil and control birds were injected with sesame oil.

In Experiment 3, experimental birds were injected intramuscularly in the breast with estradiol benzoate (Progynon B, Schering) in aqueous suspension and control birds were injected with normal saline.

Each injection was 0.1 ml of fluid in Experiments 1 and 2, and 0.2 ml in Experiment 3. Doses are indicated in the descriptions of the experiments. Injections were given on alternate sides of the breast on alternate days.

The potency of the prolactin preparation used in Experiment 1 was confirmed by measuring the crop sac response (Riddle *et al.*, 1933; Lehrman and Brody, 1961) of albino Ring Doves (*Streptopelia risoria*).

#### EXPERIMENT 1 (PROLACTIN)

Brown-headed Cowbirds used in this experiment were captured at Devine, Texas, on 18 August 1964. All individuals were juveniles of an estimated average age of two and one-half months at the time of capture. The birds were in early stages of the postjuvinal molt when captured and had completed the molt by the end of Experiment 1 on 12 October.

On 20 August, a male and a female were placed in each of 12 cages in the laboratory. We had intended to leave the males in the cages throughout the experiment, but, as did Robinson and Warner (1964: 316), we found that aggressive behavior of the males interfered with the responses of the females to the nests and eggs. For this reason, the males were removed on 12 September, and the experiment was continued with each female housed alone.

Experiment 1 was divided into three phases, following a standard experimental design (McNemar, 1962: 86-88).

*Phase 1 (23 days: 26 August—17 September).*—This phase was designed to deter-

mine the "base level" of response of untreated females. Therefore, none of the 12 birds received injections. Observations were made on 12 days in test periods ranging from 45 minutes to three hours; each female was observed for a total of from 24.5 to 27.3 hours, with the exception of female 12, which was observed for 18.7 hours.

*Phase 2 (14 days: 21 September—4 October).*—Following Phase 1, the 11 surviving females were divided into experimental and control groups, both of which included some individuals which in Phase 1 failed to sit in the nest and others which sat frequently. For statistical purposes, five birds in the experimental group were paired with those in the control group, as follows: 10-1, 3-6, 7-8, 5-9, and 4-11. Beginning on 21 September, females of the experimental group received 13 daily injections of prolactin. From 21 through 27 September, the daily dose was 3.7 IU and, from 28 September through 3 October, the daily dose was 28.3 IU (total dose: 195.7 IU). Individuals of the control group received 13 daily injections of normal saline. Test periods were conducted daily (except on 2 October) from 23 September through 4 October, each bird being observed for 26.5 hours.

*Phase 3 (8 days: 5–12 October).*—This phase of the experiment involved only two birds. Female 8 of the control group of Phases 1 and 2 received daily injections of prolactin, as follows: 4 through 8 October, 28.3 IU; 9 October, 21.5 IU; and 10 October, 11.1 IU (total dose: 174.1 IU). In the same period, female 7 of the experimental group of Phases 1 and 2 received seven injections of normal saline. The two birds were observed for 15.0 hours in seven tests conducted from 5 through 12 October.

#### EXPERIMENT 2 (PROGESTERONE)

In this experiment, we used a new group of 16 first-year female Brown-headed Cowbirds captured in Austin, Texas, on 6 October 1964. The birds had completed the postjuvinal molt, but it was possible to determine their age by the presence of under wing coverts retained from the juvenal plumage (Selander and Giller, 1960). The estimated average age of these cowbirds at the beginning of the experiment was four and three-quarters months.

The 16 cowbirds were placed individually in cages on 6 October. Experiment 2 was divided into two phases, as follows:

*Phase 1 (10 days: 13–22 October).*—In this phase, we observed the responses of untreated cowbirds. Observations were made on all 10 days in periods ranging from one to three and one-half hours (on 8 of the 10 days, the test period lasted three hours); each cowbird was observed for 28.5 hours.

*Phase 2 (16 days: 23 October—7 November).*—Following Phase 1, the 16 females were divided into experimental and control groups; pairing for statistical purposes was as follows: 25-23, 35-31, 36-28, 33-32, 26-34, 30-22, 27-21, and 29-24. Beginning on 23 October, females of the experimental group received 15 daily injections of progesterone. The daily dose was 0.5 mg (total dose: 7.5 mg). Control birds received 15 injections of sesame oil. Tests were conducted on 10 days, and each female was observed for 22.0 hours.

#### EXPERIMENT 3 (ESTROGEN)

The subjects of this experiment were the 16 birds used in Experiment 2.

From 10 to 28 November, the eight birds which had served as controls in Experiment 2 were given 10 injections (administered every other day) of 0.625 mg estradiol benzoate (total dose: 6.250 mg), and the eight experimental birds of Experiment 2 were given 10 injections of saline. Tests were conducted on 10 days in the period from 17 through 29 November, and each female was observed for 20.0 hours.

## EXPERIMENT 4

This experiment was designed to test the effectiveness of empty nests in evoking sitting and crouching responses in untreated cowbirds. The subjects were two first-year females (numbers 40 and 41) which were captured on 6 October and had not had previous experience with artificial nests or eggs.

*Phase 1 (6 days: 7-12 November).*—The two cowbirds were presented with empty nests in six test periods; each bird was observed for 13.0 hours.

*Phase 2 (10 days: 13-22 November).*—The two birds were presented with nests containing three eggs in seven test periods; each bird was observed for 13.0 hours.

## RESULTS

## BEHAVIORAL RESPONSES OF FEMALE COWBIRDS TO NESTS AND EGGS

Captive female cowbirds directed the following behaviors to nests containing eggs and to empty nests.

*Sitting in nest.*—A cowbird stepped into the nest cup, with the body in a horizontal position, and lowered the body to a point at which the breast and abdomen rested on the eggs or, when the nest was empty, the bottom of the nest cup. The bird assumed a relaxed posture, with the body largely within the nest cup and, apparently, not supported by the tarsi (Figure 2A).

Sitting birds frequently moved or pecked at nest material on the rim of the nest with the bill. Sometimes the flight feathers of the folded wings were shuffled to adjust their positions.

Sitting is called the "incubation position" by Robinson and Warner (1964) but, as noted below, it is also the position assumed by wild female cowbirds visiting the nests of hosts to deposit eggs. Therefore, to avoid unwarranted implications concerning motivational aspects of this behavior, we will use the descriptive term "sitting."

Our criterion of "sitting" apparently is more rigorous than that applied by Robinson and Warner (1964: 317), who considered a bird to be in the "incubation position" when "in the observer's opinion, it lowered itself far enough into the nest to bring its belly into contact with the eggs or nest bottom." We presume that some part of the behavior that we have classified as crouching falls in the category of "incubation position" as defined by Robinson and Warner.

*Crouching in nest.*—In crouching, a cowbird stepped into the nest cup, with the body in a horizontal position, then lowered the body, but not to a point where the abdomen and breast rested on the eggs or, in empty nests, the bottom of the nest cup. Compared with a sitting bird, the body of a crouching bird was less completely within the nest cup (Figure 2, B and C).

We observed complete gradation in behavior between crouching and sitting, so that many times the assignment of a behavior to one of these

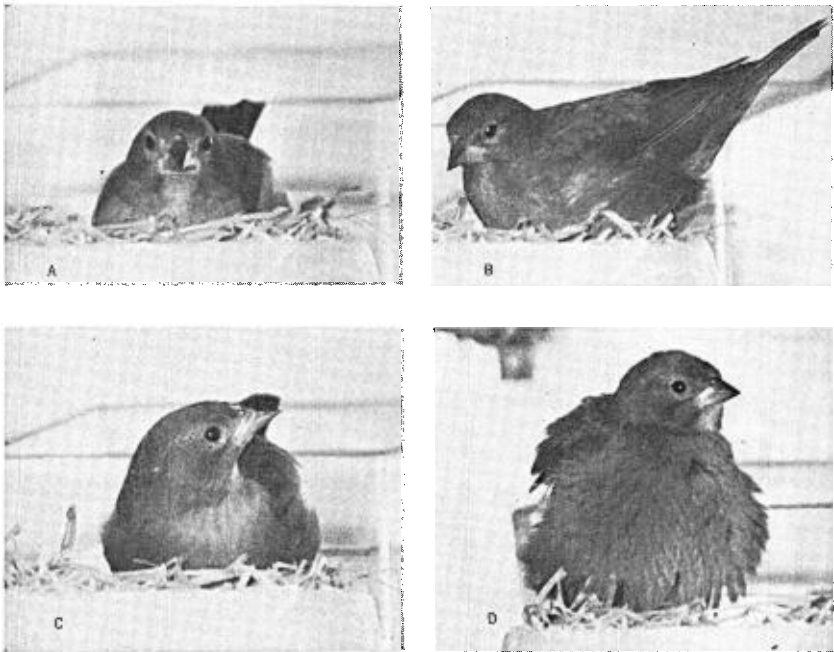


Figure 2. Female cowbird (number 26). A, sitting in nest cup. B and C, crouching in nest cup. D, fluffing feathers while perched on rim of glass nest bowl.

categories was arbitrary. Crouching is a low intensity form of sitting, and very brief crouches are merely intention movements to sit. We noted individual variation in intensity of the sitting posture; some individuals characteristically sat farther down in the nest and assumed a more relaxed posture than did others.

If a bird sat in the nest, rose to a crouched position, and sat again, we recorded the behavior as a single sitting period but, in recording the duration of the sitting period, we did not count the time spent crouching. However, if a sitting bird stood up fully in the nest cup and then sat again, the sequence was recorded as two sitting periods.

In Phase 1 of Experiment 1, we failed to record the duration of some periods of crouching and, in retrospect, we think that we may have overlooked some brief periods of crouching. Frequency and duration of crouching periods were recorded in Phases 2 and 3 of this experiment and in subsequent experiments.

*Foraging in nest material.*—This was a frequent response of all cowbirds observed. As the birds searched through the nest material, pieces of grass were picked up with the bill and mandibulated. Frequently, the birds made

rapid scratching movements in the nest with the feet, exhibiting behavior performed by birds foraging on the ground (Selander and Kuich, 1963: 81).

Some birds habitually foraged in the nest throughout most of the test periods, actually pulling the nest apart and scattering the material and eggs. In general, birds which often sat or crouched spent less time foraging in the nest than did those which rarely if ever sat, but some individuals which rarely sat only occasionally foraged in the nest.

*Pecking at eggs.*—This common response became more or less habitual with some birds. In addition to pecking at the eggs, some birds were prone to pick up the eggs (holding them by a piece of loose plaster) and carry them about the cage. Birds which frequently sat pecked at the eggs but rarely removed them. Commonly, birds pecked very lightly at the eggs just before sitting in the nest.

*Resting on rim of nest.*—Several birds perched on the rim of the nest for long periods and, on occasion, went to sleep there. These were, in general, birds which rarely crouched or sat.

*Additional comments.*—In the summary of their paper, Robinson and Warner (1964: 324) report that “no indication of increased nest-building activity in the prolactin-injected birds was observed.” This statement seems to imply that some nest-building behavior was performed by their cowbirds, yet this is not indicated in their paper. In the present study, as in an earlier investigation by Selander and Kuich (1963: 87), none of the cowbirds performed nest-building motions. We found no indication that treatment with prolactin, progesterone, or estradiol benzoate affected the frequency with which cowbirds moved or otherwise manifested “interest” in nest material.

Robinson and Warner (1964: 319–320) reported that:

on 36 occasions females receiving prolactin abducted the breast and belly feathers slowly while they stood on the rim of the nest or on the perch looking into a nest containing eggs. On these 36 occasions the birds did not assume the incubation position. . . . This feather abduction was never seen in the control birds. Since this activity was also observed when the prolactin-injected birds were about to assume the incubation position, we think that this abduction of the feathers represents an element of incubation behavior; i.e., exposure of the incubation patch as displayed by normal, incubating birds of other species.

We saw no behavior which would be interpretable as abduction of feathers to expose the abdominal and breast area. Both control and hormone-injected birds frequently fluffed the feathers of the body, including those of the breast and abdomen, while perched on the edge of the nest (Figure 2, D). In many cases feather erection was intense and was performed slowly, but it invariably involved feathers over most or all of the

body surface. The erected feathers were returned to their normal positions by a shake of the body around its longitudinal axis, as described for other passerines by Marler (1956: 13). Possibly the intense fluffing was an autonomic response to an ambivalent motivational situation involving conflicting tendencies to sit in the nest, peck at the eggs, remove the eggs, or leave the nest.

None of the sitting cowbirds turned the eggs or made wriggling movements of the body of the type that, when performed by incubating birds, functions to bring the eggs into contact with the incubation patch (see Marler, 1956: 132-133). Finally, none of the birds laid eggs or showed behavior indicative of gonadal activity.

#### EXPERIMENT 1 (PROLACTIN)

In Experiment 1, we essentially repeated the Experiment 1 of Robinson and Warner (1964), in which the injection of prolactin over a 14-day period supposedly produced a marked increase in "incubation behavior," as measured by the number of sitting periods per hour and the mean duration of sitting periods. However, our experimental design differed importantly from Robinson and Warner's in that we pretested our birds (Phase 1) before pairing them into matched control and experimental groups and administering prolactin to members of the experimental group in Phase 2. Also, whereas Robinson and Warner (1964) used a daily dose of 3.6 IU prolactin, in Phase 2 we injected 3.7 IU prolactin for seven days, then increased the daily dose to 28.3 IU for six days. The dose was increased when it became apparent that the lower dose did not influence the behavior of the experimental birds.

Results of Phases 1 and 2 of our Experiment 1 are summarized in Tables 1 and 2. These data and those from other experiments demonstrate marked individual variation among females in responsiveness to nests and eggs. It is also apparent that, with two exceptions (birds 7 and 8), the performance levels of individuals of the control and experimental groups were similar in Phases 1 and 2.

In frequency and duration of sitting periods, as well as in other measures of performance, the control and experimental groups show no statistically significant differences. The statistic employed was a two-sided  $t$  test of significance of differences between changes in scores of paired control and experimental birds from Phase 1 to Phase 2 (see McNemar, 1962: 104). The null hypothesis tested is that the mean difference between changes of pairs is zero. For number of sitting periods per hour,  $t = .979$ , with 4 df ( $P = .4$ ) and, for mean duration of sitting periods,  $t = 1.01$  ( $P = .4$ ). (In one-sided  $t$  tests, based on the *a priori* assumption that the prolactin-injected birds would respond *more* strongly than the controls,  $P = .2$ .)





TABLE 2  
PERIODS OF CROUCHING IN NEST IN EXPERIMENT 1, PHASE 2<sup>1</sup>

<i>Bird</i>	<i>Average number per hour</i>	<i>Duration (sec.)</i>			
		<i>Average per hour</i>	<i>Mean</i>	<i>Median</i>	<i>Maximum</i>
Control Birds (Saline-injected)					
1	0.00	0.0	0.0	0.0	0
6	0.04	0.6	15.0	15.0	15
8	0.64	2.7	4.2	3.0	10
9	2.57	12.6	4.9	4.0	30
11	0.00	0.0	0.0	0.0	0
Averages:	0.65	3.2	4.8	4.4	
Experimental Birds (Prolactin-injected) <sup>2</sup>					
2	0.00	0.0	0.0	0.0	0
3	0.60	5.0	8.2	7.0	25
4	0.07	0.6	7.5	7.5	12
5	0.00	0.0	0.0	0.0	0
7	9.43	43.3	4.6	3.0	65
10	0.07	0.3	3.5	3.5	4
Averages:	1.69	8.2	4.0	3.5	
Averages: (all birds)	1.220	5.92	4.35	3.91	

<sup>1</sup> Birds observed 26.5 hours each.

<sup>2</sup> Total dose, 195.7 IU, administered in 13 daily injections.

Thus, prolactin had no demonstrable effect on the sitting response of the cowbirds to nests and eggs and our experimental results fail to confirm those previously reported by Robinson and Warner (1964). Before discussing the probable basis for the different results of the two experiments, we will examine more closely the performances of our birds in Experiment 1.

Control bird 1 and experimental bird 2 failed to respond by crouching or sitting in either Phase 1 or Phase 2 (Tables 1 and 2). Bird 10 failed to crouch or sit in Phase 1 but crouched twice (on 7 September) and sat once for 12 seconds (4 October) in Phase 2. Two birds (control 11 and experimental 4) showed weak responses in Phase 1 but failed to sit in Phase 2. In Phase 1, bird 4 sat once for 2 seconds and crouched 3 times (all on 11 September), then in Phase 2 crouched 2 times (30 September). All responses of bird 11 were recorded on 4 September in Phase 1; in Phase 2 it failed to crouch or sit.

The performances of control bird 8 and experimental bird 7 require special comment. Throughout most of Phase 1, bird 8 responded strongly, but the level of response had declined by the beginning of Phase 2. In Phase 2 the level was irregular from day to day but continued to decline (Figure 3). The performance of bird 7 was irregular in Phase 1, but in Phase 2 she reached a high and relatively uniform level of response which was maintained from 26 September on. To test the possibility that this high level of response was caused by prolactin treatment, the experiment

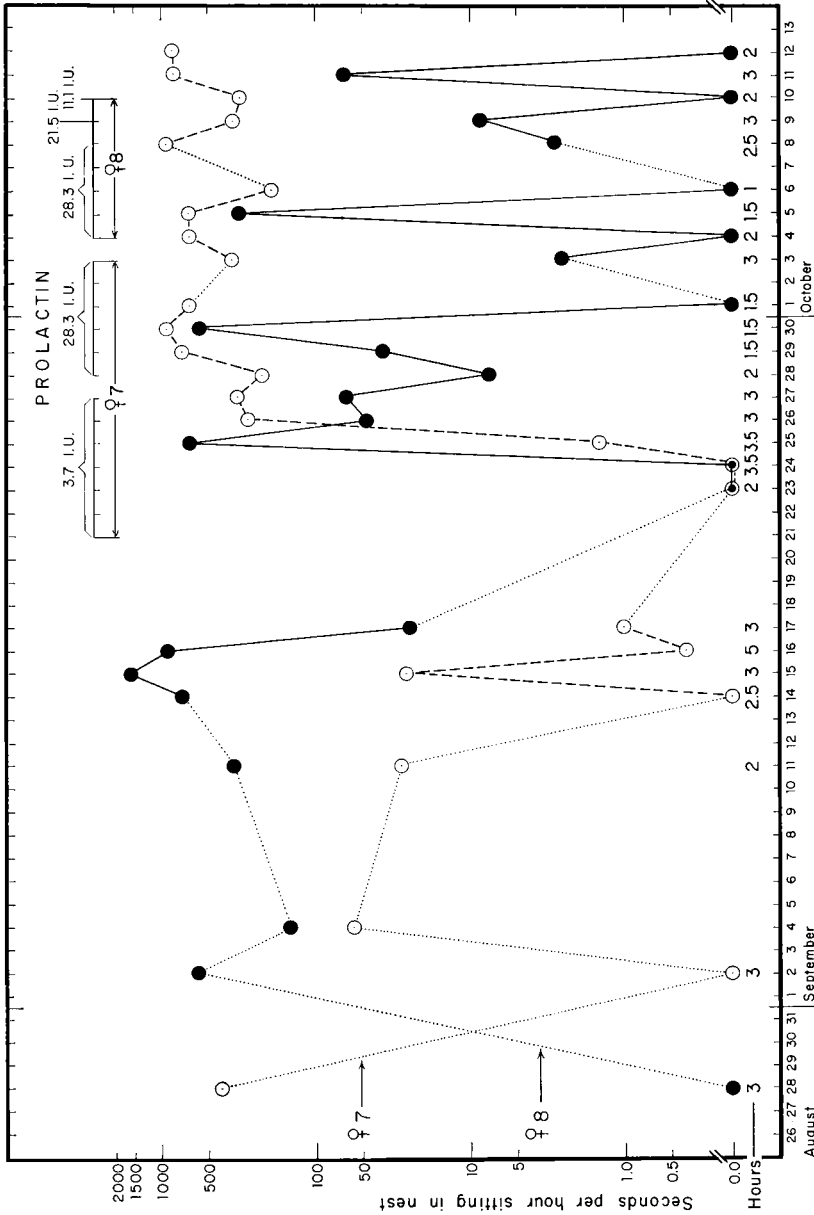


Figure 3. Seconds per hour sitting in nest by females 7 and 8 in Experiment 1. Dotted lines indicate gaps in records of one or more days.

TABLE 3  
RESPONSES OF BIRDS TO NESTS IN EXPERIMENT 1, PHASE 3<sup>1</sup>

<i>Bird</i>	<i>Response</i>	<i>Average number per hour</i>	<i>Duration (sec.)</i>			
			<i>Average per hour</i>	<i>Mean</i>	<i>Median</i>	<i>Maximum</i>
Saline-injected						
7	Sitting	17.93	613.7	34.2	12.0	515
	Crouching	14.00	114.9	8.2	5.0	44
Prolactin-injected <sup>2</sup>						
8	Sitting	0.87	46.4	53.5	15.0	260
	Crouching	1.13	7.7	6.8	7.0	13

<sup>1</sup> Birds observed 15.0 hours each.

<sup>2</sup> Total dose, 174.1 IU, administered in 7 daily injections.

was continued into Phase 3, in which treatments of birds 7 and 8 were reversed. Bird 7 was given daily injections of saline and bird 8 received daily injections of a high dose of prolactin. The reversal of treatment did not affect the levels of response of the two birds (Table 3 and Figure 3). Bird 7 maintained the high level she had shown in Phase 2, as demonstrated most clearly by the fact that mean and median durations of her sitting periods did not change from Phase 2 to Phase 3. In Phase 3, the performance of bird 8 remained irregular and, significantly, continued the declining trend which had been apparent in Phase 2. In sum, the results of Phase 3 provide evidence that the high level of response of bird 7 in Phase 2 is not attributable to the prolactin she had received in that phase of the experiment.

Because of individual variation in responsiveness of female cowbirds to nests or to nests and eggs, proper control of experiments requires measurement of the performance levels of individuals before hormones are administered to the experimental group. The experimental results reported by Robinson and Warner (1964) are therefore inconclusive since there was no pretest period. These authors simply divided 10 birds into experimental and control groups and tested the responses to nests and eggs during a period in which the experimental birds received injections of prolactin. One

TABLE 4  
AVERAGE VALUES FOR PERIODS OF SITTING BY RESPONDING BIRDS  
IN EXPERIMENTS 1, 2, AND 3

<i>Experiment</i>	<i>Phase</i>	<i>Number of birds sitting</i>	<i>Number of periods per hour</i>	<i>Mean duration (sec.)</i>	<i>Median duration (sec.)</i>
1	1	9	0.96	31.0	9.6
1	2	6	1.92	29.3	14.6
2	1	9	0.76	44.6	25.8
2	2	8	1.00	39.5	20.4
3	—	10	1.90	21.1	7.9

TABLE 5  
PERIODS OF SITTING IN NEST IN EXPERIMENT 2

Bird	Phase 1 <sup>1</sup>				Phase 2 <sup>2</sup>				
	Average number per hour	Duration (sec.)		Average number per hour	Duration (sec.)		Average per hour	Maximum	
		Mean	Median		Mean	Median			
Control Birds									
Non-injected									
21	0.17	34.0	20.0	0.04	0.1	3.0	3.0	3	
22	0.98	61.0	16.0	1.40	36.5	25.9	9.0	308	
23	0.00	0.0	0.0	0.00	0.0	0.0	0.0	0	
24	0.20	103.2	72.0	0.27	11.3	41.3	41.0	80	
28	0.00	0.0	0.0	0.00	0.0	0.0	0.0	0	
31	0.00	0.0	0.0	0.00	0.0	0.0	0.0	0	
32	0.00	0.0	0.0	0.00	0.0	0.0	0.0	0	
34	2.42	25.1	17.0	2.63	184.4	69.9	16.0	1552	
Averages:	0.47	27.9	15.6	0.54	17.5	8.6			
Sesame oil-injected									
Experimental Birds									
Non-injected									
25	0.00	0.0	0.0	0.00	0.0	0.0	0.0	0	
26	1.37	57.5	18.0	0.86	56.1	65.0	40.0	232	
27	0.17	8.3	33.0	0.22	2.8	12.2	10.0	30	
29	0.70	19.8	14.0	2.36	24.4	10.3	7.0	37	
30	0.80	39.2	39.0	0.22	20.7	91.2	37.0	289	
33	0.04	3.0	3.0	0.00	0.0	0.0	0.0	0	
35	0.00	0.0	0.0	0.00	0.0	0.0	0.0	0	
36	0.00	0.0	0.0	0.00	0.0	0.0	0.0	0	
Averages:	0.39	22.3	13.4	0.46	22.3	11.7			
Averages: (all birds)	0.428	25.11	14.50	0.500	19.92	10.19			

<sup>1</sup> Birds observed 28.5 hours each.

<sup>2</sup> Birds observed 22.0 hours each.

<sup>3</sup> Total dose, 7.5 mg, administered in 15 daily injections.

TABLE 6  
PERIODS OF CROUCHING IN NEST IN EXPERIMENT 2

Bird	Phase 1 <sup>1</sup>			Phase 2 <sup>2</sup>				
	Average number per hour	Mean	Median	Maximum	Average number per hour	Mean	Median	Maximum
	Non-injected			Sesame oil-injected				
21	1.23	7.9	6.0	17	1.14	3.3	2.0	17
22	1.54	18.6	5.5	97	4.73	5.7	4.0	45
23	0.00	0.0	0.0	0	0.00	0.0	0.0	0
24	1.37	15.3	10.0	14	5.00	15.1	8.3	134
28	0.03	0.3	9.0	9	0.41	9.7	8.0	22
31	0.03	0.1	4.0	4	0.14	0.6	2.0	10
32	0.46	1.2	2.0	5	0.00	4.7	0.0	0
34	2.53	21.5	6.5	33	3.77	8.1	7.0	40
Averages:	0.90	6.7	5.4		1.90	5.8	3.9	
	Control Birds			Experimental Birds				
	Non-injected			Progesterone-injected <sup>3</sup>				
25	0.00	0.0	0.0	0	0.00	0.0	0.0	0
26	1.23	11.1	6.0	33	5.50	14.3	10.0	127
27	1.44	16.5	8.0	45	0.77	5.0	4.0	15
29	0.74	4.3	5.0	16	1.73	4.1	3.0	12
30	1.12	8.4	4.0	25	0.55	7.2	10.0	43
33	0.32	3.1	4.0	5	0.00	0.0	0.0	0
35	0.00	0.0	0.0	0	0.00	0.0	0.0	0
36	0.03	0.5	13.0	13	0.09	1.5	1.5	2
Averages:	0.61	6.2	5.0		1.08	4.8	3.6	
Averages: (all birds)	0.754	6.48	5.19		1.489	5.29	3.75	

<sup>1</sup> Birds observed 28.5 hours each.

<sup>2</sup> Birds observed 22.0 hours each.

<sup>3</sup> Total dose, 7.5 mg, administered in 15 daily injections.

bird of each group failed to sit and the fact that, in their Experiment 1, the four remaining experimental birds sat more frequently and for longer periods, on the average, than did the four responding control birds could be due to chance assignment of four relatively strong responders to the experimental group.

Evidence supporting the thesis that the results of the Experiment 1 of Robinson and Warner need not be attributed to a prolactin effect is the fact that their experimental birds did not respond differently to nests and eggs than did our untreated birds. According to these authors, the mean duration of sitting periods for their four responding, prolactin-injected birds varied from 31.0 to 36.8 seconds, with an average of 35.0 seconds. Mean duration for the nine untreated birds which sat in Phase 1 of our Experiment 1 was 31.0 seconds, while, in Phase 1 of our Experiment 2, the nine untreated birds which sat had a mean duration of 44.6 seconds (Table 4). In our Experiment 4 (Table 10), in which hormones were not administered, mean duration of sitting periods for bird 41 was greater than that of any bird studied by Robinson and Warner. Hence, as measured by mean duration of sitting periods, the response of the four prolactin-injected birds studied by Robinson and Warner was not stronger than that which may be expected in the average untreated female cowbird. Similarly, a comparison of maximal length of sitting periods reveals that periods as long as or longer than those recorded by Robinson and Warner for their prolactin-injected birds are to be expected in untreated cowbirds. Maximal lengths of sitting periods for their four responding experimental birds were 1095, 240, 205, and 150 seconds. In our experiments, two untreated birds (numbers 22 and 34, Phase 1, Experiment 2) sat for 1110 and 1552 seconds, respectively (Table 5), and in six other untreated birds the maximal length of sitting periods exceeded 240 seconds (*e.g.*, 704 seconds for bird 8, Phase 1, Experiment 1; Table 1).

Data on the frequency of sitting periods are not presented by Robinson and Warner in a fashion permitting quantitative comparison with our data. However, from examination of their graph (Figure 1, p. 318) of mean values for their experimental and control birds, it is apparent that the frequency of sitting by their birds was no greater than that of our untreated birds.

#### EXPERIMENT 2 (PROGESTERONE)

Progesterone had no effect on the frequency or duration of periods of sitting or crouching (Tables 5 and 6). Two-sided *t* tests of differences between changes in scores shown by the paired control and experimental birds yielded the following results:

Item	<i>t</i>	df	P
Number of sitting periods per hour	.004	7	> .9
Mean duration of sitting periods	.822	7	> .4
Number of crouching periods per hour	.749	7	> .4
Mean duration of crouching periods	.219	7	> .8

From Phase 1 to Phase 2, the 16 birds used in this experiment, taken as a group, showed a slight increase in frequency of sitting periods and a slight decrease in mean and median durations of sitting periods (Table 5), but the observed differences between average values for the two phases are not statistically significant. For example, for mean duration of sitting periods, a two-sided *t* test of changes in correlated means for the 16 birds gave a *t* value of .779, with 15 df ( $P > .4$ ).

As a group, the 16 birds also showed an increase in average frequency of crouching from Phase 1 to Phase 2, but the observed difference is doubtfully significant ( $t = 1.88$ ,  $P = .07$ ). Mean and median durations of crouching periods decreased in Phase 2, but not significantly (for mean duration of crouching periods,  $t = 1.00$ ,  $P > .3$ ).

TABLE 7  
PERIODS OF SITTING IN NEST IN EXPERIMENT 3<sup>1</sup>

<i>Bird</i>	<i>Average number per hour</i>	<i>Duration (sec.)</i>			
		<i>Average per hour</i>	<i>Mean</i>	<i>Median</i>	<i>Maximum</i>
Control Birds (Saline-injected)					
25	0.00	0.0	0.0	0.0	0
26	1.85	33.4	18.0	13.0	117
27	1.35	15.5	11.5	7.0	49
29	4.85	172.0	35.5	7.0	879
30	0.05	0.1	2.0	2.0	2
33	0.10	1.2	12.5	12.5	15
35	0.00	0.0	0.0	0.0	0
36	0.00	0.0	0.0	0.0	0
Averages:	1.03		9.9	5.2	
Experimental Birds (Estradiol Benzoate-injected) <sup>2</sup>					
21	0.70	2.7	3.9	3.0	8
22	3.10	19.7	6.4	4.0	39
23	0.00	0.0	0.0	0.0	0
24	3.00	143.0	47.7	8.0	506
28	1.75	19.7	11.3	9.0	37
31	0.00	0.0	0.0	0.0	0
32	0.00	0.0	0.0	0.0	0
34	2.25	139.5	62.0	13.0	1024
Averages:	1.35		16.4	4.6	
Averages: (all birds)	1.187		13.17	4.91	

<sup>1</sup> Birds observed 20.0 hours each.

<sup>2</sup> Total dose, 6.250 mg, in 10 injections administered every other day.



TABLE 8  
PERIODS OF CROUCHING IN NEST IN EXPERIMENT 3<sup>1</sup>

Bird	Average number per hour	Duration (sec.)			
		Average per hour	Mean	Median	Maximum
Control Birds (Saline-injected)					
25	0.05	0.1	2.0	2.0	2
26	2.65	13.0	4.9	4.0	18
27	2.65	11.7	4.4	3.0	25
29	2.25	6.6	3.0	3.0	9
30	1.80	9.2	5.1	4.0	24
33	2.00	8.0	4.0	3.0	16
35	0.05	0.1	2.0	2.0	2
36	0.10	0.9	8.5	8.5	15
Averages:	1.44		4.2	3.7	
Experimental Birds (Estradiol Benzoate-injected)					
21	1.25	3.6	2.9	3.0	6
22	1.25	4.7	3.8	3.0	10
23	0.00	0.0	0.0	0.0	0
24	3.40	16.5	4.8	4.0	23
28	2.85	19.0	6.7	5.0	23
31	0.45	1.4	3.0	3.0	7
32	0.10	0.3	2.5	2.5	3
34	3.05	17.4	5.7	4.0	25
Averages:	1.54		3.7	3.1	
Averages: (all birds)	1.494		3.96	3.38	

<sup>1</sup> Birds observed 20.0 hours each.

<sup>2</sup> Total dose, 6.250 mg, in 10 injections administered every other day.

EXPERIMENT 3 (ESTROGEN)

Data on sitting and crouching by birds in Experiment 3 are summarized in Tables 7 and 8. To evaluate the performance of the controls and estradiol benzoate-injected experimentals, we have calculated the differences in changes of scores of paired birds from Phase 2 of Experiment 2 to the single phase of Experiment 3. The levels of response of the experimentals and controls in Experiment 3 do not differ significantly:

Item	<i>t</i>	df	P
Number of sitting periods per hour	.454	7	> .6
Mean duration of sitting periods	.787	7	> .4
Number of crouching periods per hour	.616	7	> .5
Mean duration of crouching periods	.534	7	> .6

Thus, estradiol benzoate had no demonstrable effect on the response of female cowbirds to nests and eggs.

From Phase 2 of Experiment 2 to Experiment 3, the 16 cowbirds, taken as a group, showed a significant increase in average frequency of sitting periods ( $t = 2.756$ ,  $P = .015$ ) but no change in frequency of crouching.

Duration of sitting and crouching periods decreased, but not significantly ( $t = 1.00$ ,  $P > .3$ ;  $t = 1.134$ ,  $P > .2$ ).

Approximately one week after receiving their first injection of estradiol benzoate, birds 21, 22, 31, and 32 began giving a chattering call which in wild cowbirds (Friedmann, 1929) is given only in the breeding season when the ovaries are active. In addition, females 22 and 31 periodically uttered syllables which suggested parts of the male song. Since these vocalizations were not given by the controls or by birds in other experiments, their appearance may be attributed to the injected estrogen.

#### EXPERIMENT 4 (RESPONSE TO EMPTY NESTS)

In interpreting the sitting response of captive female cowbirds as "incubation behavior," Robinson and Warner (1964) assume that the birds are responding to the eggs as well as to the nest, but there is evidence that the response is elicited primarily by the nest itself.

In experiments reported by Selander and Kuich (1963: 80-81), five female cowbirds sat in empty nests for periods from 2 to 60 seconds, and even one male cowbird sat in an empty nest four times for periods of 3 seconds each. Each of these birds sat in an empty nest without previously having been exposed to nests containing eggs, at least under conditions of captivity, and similar behavior was noted in the present study. For example, the first time female 27 was presented with a nest (empty), she made strong intention movements to sit, then sat for 60 seconds, stood up in the nest cup, and sat again for 20 seconds.

In Experiment 3 of Robinson and Warner (1964), several female cowbirds sat in empty nests and in depressions in clumps of grass. This presented a problem to these authors in their attempt to interpret sitting as incubation behavior and prompted them to suggest (p. 318) that "it does not seem that in this instance this activity really represented a drive to incubate."

TABLE 9  
PERIODS OF SITTING IN EMPTY NESTS AND NESTS CONTAINING EGGS

Stimulus	Time	Average number per hour	Duration (sec.)			Maxi- mum
			Average per hour	Mean	Median	
Female 8 (Exp. 1, Phase 1) on 16 September						
Nest with 3 eggs	1025-1255	8.4	903.5	107.5	30.0	644
Empty nest	1300-1530	8.0	908.4	113.5	29.5	517
Female 7 (Exp. 1, Phase 2) on 3 October						
Nest with 3 eggs	1500-1522	51.8	1188.0	22.9	10.0	120
Empty nest	1522-1540	36.7	450.0	12.3	6.0	55
Nest with 3 eggs	1540-1630	25.2	576.2	22.8	11.0	155

In the course of Experiment 1, female 8 was exposed for two and one-half hours to a nest containing three eggs, followed by a similar period in which she was exposed to an empty nest (Table 9). There was no significant change in her level of response following removal of the eggs. In a similar test involving bird 7 (Table 9), the level of response decreased in the 18 minutes during which the bird was exposed to an empty nest, but the period was too short to provide reliable estimates of mean duration of sitting and other measures of response.

From 7 through 12 November, we tested two females (numbers 40 and 41) with empty nests (Phase 1 of Experiment 4; Table 10). Both birds showed levels of response equivalent to those of the more strongly responding birds of other experiments. In Phase 2 of the experiment (13 through 22 November), the birds were tested with nests containing eggs, and the response levels were actually lower than in Phase 1.

#### POSSIBLE AGE VARIATION IN RESPONSIVENESS

Robinson and Warner (1964) suggested that captive female cowbirds may become less responsive to nests and eggs with increasing age. They obtained strong responses from first-year birds in the second half of October, but the same individuals failed to respond when tested from 19 January through 6 February, and only low levels of response were shown by these birds in test periods from 25 March through 9 April and from 27 May through 11 June.

Although there was no conspicuous change in the performance levels of our birds from 26 August through 29 November, mean and median durations of sitting periods for responding birds gradually decreased in Experiments 2 and 3 (Table 4). We intend to test these birds again in January for evidence of decreased responsiveness.\*

An age factor cannot explain our failure to demonstrate an effect of prolactin on the sitting response, since the birds used in our prolactin ex-

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\* From 25 to 30 January 1965, the responses of eight birds were measured; the birds were numbers 7 and 8 of Experiment 1 and numbers 22, 24, 26, 28, 29, and 34 of Experiment 3. Hormones were not administered. In 10 hours of observation, the following results were obtained. Bird 7: mean number of sitting periods per hour, 22.00; mean duration of sitting periods, 36.4 sec.; maximum length of sitting periods, 288 sec. Bird 8: 0.40, 28.5, 65; Bird 22: 9.30, 207.5, 1883; Bird 24: 0.20, 15.0, 20; Bird 26: failed to sit; Bird 28: 0.30, 250.0, 725; Bird 29: 3.90, 219.5, 1896; Bird 34: failed to sit.

With the exception of numbers 26 and 34, the birds continued to show moderate to high levels of response. Of the six responding birds, two (8 and 24) showed a slight decrease in responsiveness, while four (7, 22, 28, and 29) showed an increase. These results do not support the view that there is marked age variation in responsiveness to nests and eggs.

TABLE 10  
PERIODS OF SITTING AND CROUCHING IN NEST IN EXPERIMENT 4

Bird	Phase 1 <sup>1</sup> : Empty nest						Phase 2 <sup>1</sup> : Nest with 3 eggs					
	Average number per hour			Duration (sec.)			Average number per hour			Duration (sec.)		
	Average number per hour	Mean	Median	Maximum	Average number per hour	Mean	Median	Maximum	Average per hour	Mean	Median	Maximum
40	4.08	38.8	9.5	9.0	1.00	7.6	7.0	14	7.6	7.6	7.0	14
41	3.77	223.8	59.4	23.0	0.62	39.2	25.5	350	63.7	63.7	25.5	350
40	13.61	95.3	7.0	5.0	4.38	19.5	4.0	13	4.5	4.5	4.0	13
41	3.77	27.3	7.2	5.0	1.85	9.4	4.5	13	5.1	5.1	4.5	13

<sup>1</sup> Birds observed 13.0 hours each.

periment were at least as young as those used by Robinson and Warner in their Experiment 1.

#### DISCUSSION

The sitting behavior of captive cowbirds was first reported by Selander and Kuich (1963: 87), who interpreted it as a response which wild females normally make to nests of host species when they visit them to deposit eggs. However, Robinson and Warner (1964) do not consider this possibility but, instead, conclude that sitting of captive cowbirds is "incubation behavior." An explicit corollary of this interpretation is the assumption that a "drive" to incubate has remained latent in the cowbird.

We may now examine the available evidence bearing on the question as to whether or not the sitting response of captive cowbirds is part of the normal behavioral repertoire of the species.

First, we call attention to field observations of female cowbirds sitting in the nests of hosts at the time of egg laying. A cowbird watched by Friedmann (1929: 185) at the nest of an American Robin (*Turdus migratorius*) "lit on the Robin's nest, looked around a little, and then settled on it. She shifted her position three times, a little bit each time and then *settled down in the same way that a Robin does on the nest* [italics ours]." Photographs by Hann (1941: Figures 2 and 3) of female cowbirds on nests of the Ovenbird (*Seiurus aurocapillus*) show the birds in sitting postures similar to those assumed by incubating passerines and by captive cowbirds responding to nests.

Available data on the duration of sitting by wild female cowbirds are as follows: Hann (1941: 220) notes that the cowbird "spends from a few seconds to a minute in the nest when laying." Mayfield (1960) reports that female cowbirds remain on the nests of the Kirtland's Warbler (*Dendroica kirtlandii*) for periods up to 25 seconds. Howell (1914) saw a female cowbird remain on the nest of a Red-eyed Vireo (*Vireo olivaceus*) for "about two minutes," in which period the bird apparently laid an egg. Thus, wild female cowbirds are known to sit on nests of hosts for periods varying from a few to 120 seconds, and, predictably, the maximum recorded duration will increase as more records become available. Considered in light of this information, the average duration of sitting periods of captive birds is not unexpectedly long. Mean duration for the responding birds in our study was about 33 seconds, while the median duration, which is more indicative of the "typical" duration, was only about 16 seconds (Table 4). Similarly, in the study by Robinson and Warner (1964), mean duration for eight responding birds in Experiment 1 was 20.1 seconds (median duration not reported).

Mean duration of sitting periods is strongly affected by a small number

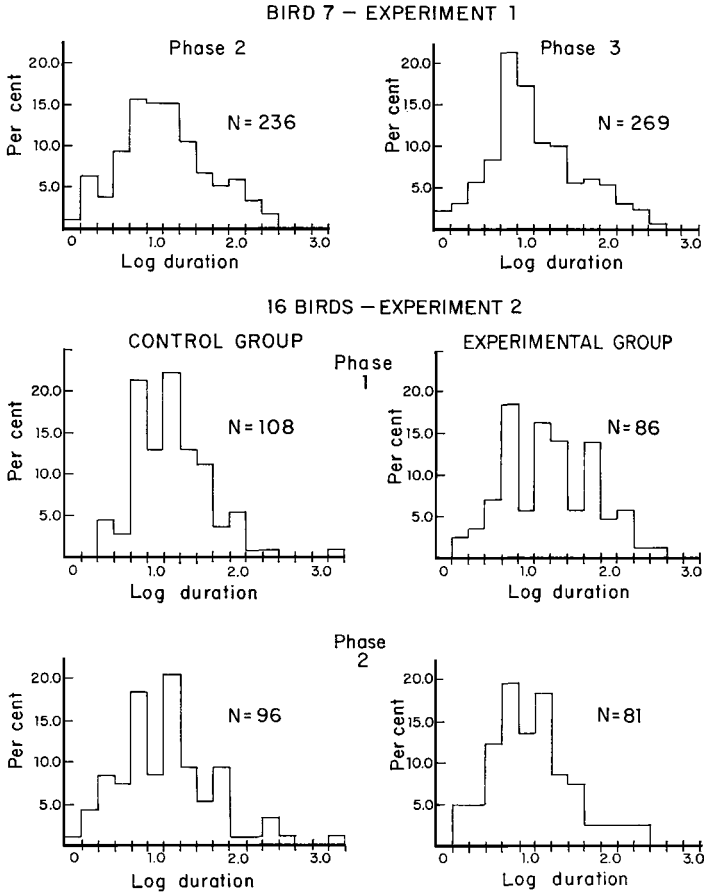


Figure 4. Variation in duration (expressed as logarithms) of sitting periods for bird 7 in Phases 2 and 3 of Experiment 1 and for all birds in Experiment 2.

of unusually long periods, but, because the logarithms of durations show an approximately normal distribution (Figure 4), there is no reason to invoke special causal factors to account for the longer sitting periods. While it is perhaps unlikely that wild female cowbirds ever remain sitting in nests for periods as long as the extremes recorded for captive birds, it is important to consider the following points in evaluating the behavior. (1) Entirely normal behavior is hardly to be expected in captive animals, especially when they are confined to small cages. Moreover, our captive cowbirds, as well as those studied by Robinson and Warner (1964), were young individuals which had not had breeding experience and, hence, had not, in all probability, previously responded to the stimulus of the nest. (2) All

very long periods of sitting in our study occurred when there was minimal "restless" activity and noise by our caged birds; in several instances it was apparent that the sitting bird was sleeping. One could argue that, in this situation, although the "motivation" underlying the response to the nest might be low, the cowbird, once having assumed the sitting position, remains there in the absence of stimuli which would induce it to move. (3) Finally, under normal circumstances egg deposition in the nest is the consummatory act in a behavioral sequence of searching for, approaching, and sitting in a nest. In captive birds there is no consummatory act, and we might therefore expect the last appetitive element in the sequence (sitting) to persist for unusually long periods.

Considering all aspects of the problem, we conclude that the behavior of captive cowbirds in responding to nests by sitting in them represents a stimulus-response sequence and a motor pattern which are part of the normal behavior of the female. One cannot justifiably refer to sitting as "incubation behavior" or infer that the behavior is motivated by a "drive" to incubate.

Selander and Kuich (1963: 87) suggest that the Brown-headed Cowbird, which parasitizes a large variety of bird species having diverse nest types (Friedmann, 1963), is, for adaptive reasons, capable of being stimulated by more "generalized" features of nest structure than are non-parasitic species. Paradoxical as it may seem on first consideration, brood parasitic species may, in some respects, manifest greater "interest" in nests than do non-parasitic forms. Mayfield (1961: 162) finds that the female cowbird "gives a continuing and discriminating attention to the nests in which it lays its eggs, and consequently might be said to manifest, in moderate degree, a vestigial proprietary interest in those nests."

It would be interesting to determine if the sight of a host building a nest or mere exposure to nests influences gonadal development of the female cowbird or other brood parasitic species (see discussions by Lehrman, 1959: 482-484, and 1961: 1281-1282). Hann (1941: 220) thought that the cowbird is brought to ovulation by the experience of watching nest-building by hosts (see comment by Mayfield, 1961: 162) and Miller (1946: 241) suggests that the sexual behavior of the hosts may also stimulate seasonal gonadal development and ovulation. It would also be worthwhile to test captive cowbirds to determine the features of a nest which are essential in evoking the sitting response.

There is no conclusive evidence that hormonal treatment can induce Brown-headed Cowbirds to perform nest-building, incubation, brooding behavior, or other behavior patterns that are not part of the normal repertoire of the species. We therefore conclude that the physiological basis for the loss of these behaviors in this species involves a refractoriness of

neural tissue to hormonal stimulation, as suggested previously by Höhn (1962) and Selander and Kuich' (1963: 86). In comparable fashion, the loss of the incubation patch in parasitic cowbirds has been achieved by the integument of the breast and abdomen having become unresponsive to those hormones which mediate formation of the patch in related icterids and other passerines (Selander, 1960; Höhn, 1962; Selander and Kuich, 1963). These findings, relating to both behavioral and morphological features, are compatible with the Medawar-Hisaw generalization (Medawar, 1953) regarding the evolution of endocrine systems (i.e., endocrine evolution is largely an evolution not of hormones but of reactivities and tissue competences).

Our conclusion was reached with full recognition of the difficulty of proving a negative hypothesis. Since it is difficult by hormonal treatment to induce out-of-season nest-building even in domestic canaries (Warren and Hinde, 1959), failure to evoke nest-building or incubation in cowbirds by hormone injection is not final proof that these behaviors are not latent in the birds. However, the conclusion we have reached is the only one justified by the available evidence.

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#### SUMMARY

Captive first-year female Brown-headed Cowbirds respond to empty nests and to nests containing eggs by crouching and sitting in the nest cup. In sitting, the female cowbird assumes a posture similar to that of an incubating passerine. Of 30 females tested, 22 (73 per cent) sat in the nest and 6 additional birds crouched in the nest at least one time. Mean and median durations of sitting periods of responding individuals were approximately 33 and 16 seconds, respectively; maximum duration was 1552 seconds. Responding females sat with a mean frequency of 1.3 times per hour.

Tests of responses of cowbirds to empty nests suggest that sitting behavior is elicited primarily, if not entirely, by the visual stimulus of the nest, the eggs being a minor, if not insignificant, aspect of the stimulus situation.



Injections of prolactin, progesterone, and an estrogen (estradiol benzoate) had no appreciable effect on the response of female cowbirds to nests and eggs. Hence, the present study failed to confirm an earlier report (Robinson and Warner, 1964) that prolactin injections increase the frequency and duration of the sitting response.

The sitting behavior of captive female cowbirds is interpreted as a normal part of the behavioral repertoire of the species which is performed by breeding females when they visit the nests of hosts to deposit eggs. There is no factual basis for referring to the response as "incubation behavior" or postulating a latent incubation "drive" to account for the behavior.

In the absence of convincing evidence that hormonal treatment can induce Brown-headed Cowbirds to perform nest-building, incubation, or other behaviors that are not part of the normal repertoire of the species, we conclude that the physiological basis for the loss of these behaviors in this species involves an insensitivity of neural tissues to hormones which mediate these behaviors in non-parasitic species. This inference and previously reported findings related to the physiological basis for the absence of an incubation patch in parasitic cowbirds are compatible with the Medawar-Hisaw generalization regarding the evolution of endocrine systems.

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