References and Notes

1. W. S. Stiles, B. H. Crawford, *Proc. Roy. Soc. London B* **112**, 428 (1933).
2. B. O'Brien, *Wright-Patterson Air Force Base Rept. W.A.D.C. T.R. 53–198* (May, 1953).
3. J. Jean, B. O'Brien, *J. Opt. Soc. Am.* **39**, 1957 (1949); G. Toraldo di Francia, *ibid.* **39**, 324 (1949); *Proc. Phys. Soc. London B* **62**, 451 (1949).
4. J. M. Enoch, *Am. J. Ophthalmol.*, in press.
5. J. M. Enoch, *J. Opt. Soc. Am.* **50**, 1025 (1960). An article also dealing with the possible role of wave-guide modes in vision has been presented by A. Schroeder [*J. Opt. Soc. Am.* **50**, 945 (1960)].
6. This research was supported in part by grant B-2168 from the National Institute of Neurological Diseases and Blindness, U.S. Public Health Service. I would like to express my appreciation to E. Snitzer for his advice on several phases of this work.

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Does the Male Stimulate Oestrogen Secretion in Female Canaries?

Abstract. Female Border canaries treated with oestrogen during the nonbreeding season may build nests, regardless of winter lighting, temperature, and absence of partner. Incubation may follow completion of the nest although ovulation is suppressed. Reactions obtained in the breeding season suggest that the male does not initiate but accelerates oestrogen production through the stimulation he provides.

In seasonally breeding birds cyclical aspects of the environment have been associated with periodic changes in the gonads (*1*). It is also well known that the sequential changes in breeding behavior depend on changes in the hormonal state (*2*). The sequence of physiological and behavioral events does not depend on one environmental factor, but on several which occur simultaneously or in succession. Thus increasing day-length, a prime factor in inducing gonadal growth in many temperate zone species (*3*), may be less effective unless other changes also occur.

One factor of importance is the interaction between male and female (*4*): for example, stimuli from the male are important in inducing ovulation in female pigeons (*5*). In domesticated canaries nest building and egg laying in the spring are delayed when females are kept visually isolated from males (*6*). Since nest building can be induced by injections of oestrogen (*7*), it therefore seemed probable that one function of the male is to accelerate oestrogen production in the female. If this is the case, the presence or absence of the male should not affect the occurrence of nest building if the level of oestrogen is controlled. Accordingly, equal quantities of oestrogen were administered during the nonbreeding season to female canaries (i) kept in visual isolation from males, (ii) paired with untreated males, and (iii) paired with males treated with androgen.

Canaries were of the Border variety, purchased from a dealer. Eighteen females and twelve males were used. Three groups of birds were set up as follows: Group A, six females housed individually and visually isolated from other birds. Group B, six females each paired and housed with an untreated male. Group C, six females each paired and housed with a male receiving 2.0 mg of testosterone propionate three times a week.

All females in each group were given 0.5 mg oestradiol benzoate (oestroform aqueous BDH) in 0.05 cm³ of solution injected into the pectoral musculature thrice weekly.

Each cage was supplied with a felt-lined nest pan as a nest site. Two baskets of nesting material, one containing grass and the other feathers, were hooked to the outside of the cages. The baskets were so arranged that the birds could peck out grass or feathers at will. The supply of grass and feathers was replenished daily or when needed.

Birds were killed after the experiment to be sure of sex identity. The oviducts of the first four birds that completed nests regardless of group were compared with those of birds from the same group which had had an equal number of oestrogen injections but did not build.

The testosterone-treated males, unlike the untreated ones, were seen to sing, show courtship behavior, and mount. No attempt to compare quantitatively their sexual activity with that of males in the spring was made.

There were no apparent differences between groups in the nest building behavior of the females, or in the interval between the start of oestrogen injections and the occurrence of nest building. The results for each group were as follows:

Group A (isolated females). Four out of six showed building activity. Three of these built good nests. The fourth built an incomplete nest and was found to be a male on autopsy. Of the three females, each had four injections prior to the start of nest building (that is, before several scraps of nest material were found in the nest). Nests were completed in 7, 7, and 9 days from the start of building. The bird which took 9 days incubated the eggless nest when it was complete.

Group B (females with untreated males). Three out of six showed nest-building behavior after two, seven, and eight injections, respectively. Only one bird completed a nest, 15 days from the start of building activity. The other two nests were not completed. The bird that completed construction also incubated the eggless nest.

Group C (females with testosterone-treated males). Two of the six females started to build, one after the fourth and the other after the sixth injection, and completed nests in 6 and 5 days, respectively. Only the latter bird incubated.

Although only about half of the birds in each group built nests, resistance to exogenous oestrogens, especially with respect to behavioral effects, has frequently been reported elsewhere (*8*). Indeed, the quantity of hormone required to induce nest building under the conditions of this experiment cannot be withstood by some individuals (*7*). That the oestrogen was effective in influencing reproductive accessories even when it did not induce nest building was shown by observations of oviduct weight. Table 1 shows that these were comparable for birds that did and did not construct nests after equal numbers of injections.

These results indicate that during the nonbreeding period exogenous oestrogens will cause female canaries to show nest-building behavior with equal rapidity whether they are paired with a male or not, even if the male is showing courtship behavior. Thus neither the visual presence of the male, nor the temperature and light conditions of spring, are necessary for nest-building activity, providing certain levels of oestrogen are reached. These results thus support the view that, during the breeding season, the male acts together

Table 1. A comparison of the weights of oviducts after 11 oestrogen injections between birds that did (first four birds) and did not build nests. Groups A, B, and C represent females in isolation, with untreated males, and with treated males, respectively.

Group	Built nest			No nest		
	Females (No.)	Oviduct weight (mg)	Body weight (g)	Females (No.)	Oviduct weight (mg)	Body weight (g)
B	30	304	21.6	12	404	21.6
A	31	454	20.1	27	220	20.8
C	33	284	20.5	1	370	24.0
A	22	325	22.0	28	424	23.2

with other environmental changes to elevate oestrogen levels in the female. The fact that some females may eventually build nests in the spring without a male (6) suggests that the male does not initiate oestrogen production, but rather accelerates it so that levels sufficient to ensure nest building are reached early in the season.

Since exogenous oestrogen restricts hypophyseal secretion of gonadotrophins and thereby suppresses ovarian growth, the birds treated with the hormone did not lay eggs after nest building. However, one bird from each of the treated groups showed incubation behavior after completion of the nest. Incubation is easy to identify because, once it is firmly established, the female can actually be picked out of the nest; birds which are not incubating rarely sit in the completed nest, and if they do they fly from the nest as soon as the cage door is opened or a hand approaches them.

This incubation of the eggless nest indicates that eggs or egg-substitutes are not essential for incubation to occur. Nor is ovulation a *sine qua non* for incubation. That nest construction is not a prerequisite for ovulation has previously been shown. In the spring birds may ovulate (albeit delayed beyond the normal period), if they are prevented from building nests, and may even show incubation behavior (9).

Proper timing of the physiological changes associated with the successive phases of reproduction is essential for successful breeding. If young are to be raised and fledged at the biologically correct time, the proper hormonal states must occur appropriately. It is clear that none of these changes depend on single factors—rather, in each case a number of factors act synergistically to promote the next stage. In the absence of all the appropriate factors, those present may be effective if they continue to act over a long period. Thus incubation may occur without ovulation and even without a nest (10).

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References and Notes

1. W. Rowan, *The Riddle of Migration* (Williams and Wilkins, Baltimore, 1931); A. J. Marshall, *Bower-Birds, Their Displays and Breeding Cycles: A Preliminary Statement* (Oxford Univ. Press, New York, 1954).
2. A. J. Marshall, *Ibis* **101**, 456 (1959).
3. D. S. Farner, in *Photoperiodism and Related Phenomena in Plants and Animals*, R. B. Withrow, Ed. (AAAS, Washington, D.C., 1959), p. 717.
4. F. H. Herrick, *Brit. J. Animal Behaviour* **1**, 159 (1911).
5. L. H. Matthews, *Proc. Roy. Soc. London* **B126**, 557 (1939).
6. R. P. Warren and R. A. Hinde, "Roles of the male and the nest cup in controlling the reproduction of female canaries," *Animal Behavior*, in press.
7. ———, *Animal Behaviour* **7**, 209 (1959).
8. J. T. Emlen and F. W. Lorenz, *Auk* **59**, 369 (1942); G. K. Noble and M. Wurm, *Endocrinology* **26**, 837 (1940); H. H. Shoemaker, *Proc. Soc. Exptl. Biol. Med.* **41**, 299 (1939).
9. R. A. Hinde and R. P. Warren, *Animal Behaviour* **7**, 35 (1959).
10. This research was supported in part by the Air Force Office of Scientific Research, Air Research and Development Command, U.S. Air Force, through its European office.
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Specificity of Discrimination Learning to the Original Context

Abstract. Rats learned a black-white discrimination at one location in a maze. Subsequently, most rats required over half as many trials to learn the same discrimination when it was placed in another location in the maze. Additional evidence was consistent with the assumption that the relevant cues are, in effect, modified by interaction with the contextual stimuli.

The fact that a change in the background contextual environment produces some disruption in the performance of learned behavior is widely recognized. However, there are not many clear-cut demonstrations of this fact, particularly in a laboratory setting. The purpose of this report is to describe a striking and somewhat unexpected instance encountered during research designed for other purposes.

Rats were being run in a maze whose floor plan is shown in Fig. 1. As depicted, if the rat turned to the right after leaving the start box, it would take two additional right turns and then arrive at a second choice point displaying a black-white discrimination problem. That is to say, reward at the goal was contingent on the rats' selecting, let us say, the black swinging door regardless of its position at that choice point.

If, alternatively, the rat turned to the left after leaving the start box, it would take two additional left turns and then be forced to take a left (or, on half of the trials, a right) turn through a grey swinging door. Frequency of reward in this case was matched to the level of success on the discrimination problem. Specifically, when early in training the rats had strong position preferences at the discrimination choice point, so that they were obtaining reward on that half of the trials when the positive cue was in their preferred position, they were also rewarded on half the trials in the other wing of the maze. Subsequently, as the rats mastered the dis-

crimination problem in the right wing of the maze, the reward frequency in the left wing rose correspondingly. Throughout, the reward was arranged so as to be nondifferential with respect to position at any choice point.

The data of immediate interest arose when, in order to evaluate the strength of the general preference for the nondiscrimination wing of the maze, the location of the discrimination was changed to the left wing of the maze. It was expected that, after perhaps a slight disruption, the animals would transfer their previous learning. As will be seen, however, the degree of transfer was small.

Eight hooded rats were run on the problem schematized in Fig. 1, some with white positive and some with black, and some with the discrimination in the right wing and some with it in the left wing. The maze was illuminated by six 7-watt bulbs spaced equally 1 foot above the maze to minimize differential extra-maze cues. The rats were run after 23 hours' deprivation on a 12 g/day maintenance schedule and were given four 45-mg pellets as reward when appropriate. Both free and forced trails were given at the first choice point to equate the number of runs in each wing. All trials at the discrimination choice point were free, and all trials at the nondiscrimination choice point were forced in such a way as to insure equal and nondifferential reinforcement. The number of trials given in the original problem varied, but all rats used in the experiment had attained a criterion of 15 correct choices out of 16 at the discrimination choice point before its location was changed to the opposite wing.

One rat showed essentially perfect transfer in that it met the above criterion in its first 16 trials with the discrimination in its new location. The other rats, however, adopted position responses, their savings scores being 56, 32, 31, 28, 19, 15, and 13 percent. The median number of trials to learn the original discrimination was 424. The median number of trials to learn the same discrimination in its new position was 280.

Two somewhat different (though not incompatible) interpretations of the role of context might be advanced to account for this finding. According to one, contextual stimuli interact with the relevant cues, modifying them by patterning so that a change in context changes the pattern and hence disrupts performance. That is to say, a white door in the right wing of the maze is different from the same white door in the left wing, and there is a generalization decrement when shifting from