

## INDUCTION OF INCUBATION BEHAVIOUR IN MALE RING DOVES (*STREPTOPELIA RISORIA*): A BEHAVIOURAL ANALYSIS\*

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**Summary.** Male ring doves (*Streptopelia risoria*) were treated with either progesterone or dexamethasone (a powerful ACTH inhibitor) and tested for incubation behaviour. Progesterone treatments shortened the latency of incubation response by facilitating nest-related pre-incubation behaviour patterns in the nest bowl and components of incubation behaviour. The accumulated rather than the daily dose level of progesterone injections appeared to be the determinant factor in mediating behavioural effects. Dexamethasone treatment at the dosage of 100 µg/day for 7 days inhibited the overall expression of male courtship behaviour. None of the dexamethasone-treated ring doves 'sat' in 2 weeks. It is suggested that the hormonal and situational (non-hormonal) cues are not only important contributory factors but also complement one another in the induction of incubation behaviour.

### INTRODUCTION

As a result of his experimental findings (Lehrman, 1958, 1961), Lehrman postulated that progesterone secretion which was believed to surge around the time of ovulation was the hormonal basis for the induction of incubation behaviour in male and female ring doves (*Streptopelia risoria*). This postulate was supplemented and confirmed in later studies in which the synergistic effect of androgen or oestrogen plus progesterone, but not of the gonadal hormones alone, was found to induce a shorter latency of incubation behaviour in castrated male doves (Stern & Lehrman, 1969; Stern, 1974). Other hormones, such as prolactin, were effective only in maintaining but not in inducing incubation behaviour (Lehrman & Brody, 1961).

Lehrman's postulate has recently been challenged by the observations of Silver & Buntin (1973) and Silver & Feder (1973) who concluded that changes in the progesterone level are not obligatory for the induction of incubation behaviour in male ring doves. Finding that there was no testis weight change throughout the breeding period (R. Silver & C. Barbieri, unpublished), and that male ring doves showed a basal level of progesterone throughout

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courtship and incubation (Silver, Reboulleau, Lehrman & Feder, 1974), the authors further concluded that endocrine factors are not necessary for the initiation of male incubation behaviour, and that situational (non-hormonal) cues from female behaviour, nest bowl and nest materials act in additive fashion to produce incubation behaviour in male doves (Silver, Feder & Lehrman, 1973).

Only the former of these two conclusions (that endocrine factors are not important in the induction of incubation behaviour) appears to be incompatible or irreconcilable with Lehrman's postulate, but these two sets of data may simply illustrate different aspects of the same physiological phenomenon. If endocrine factors are not important in the induction of incubation behaviour, the progesterone effect may be a pharmacological one or the progesterone-treated doves may be too drowsy to show any other behaviour due to the general anaesthetic effect of progesterone. The reason for a specific effect of progesterone on incubation behaviour is obscure, however, for a doped dove has a choice of crouching comfortably in the corner or on the top of the food can in the testing cage; the latter place is a favourite location for a rest. Furthermore, it is yet to be shown experimentally that the progesterone-treated doves are under the influence of a general anaesthetic effect.

An alternative view is that most of the conflicting findings simply result from differences in experimental procedure, i.e. in Lehrman's experiments, only the internal endocrine make-up of the doves was varied by progesterone injections while situational cues were minimized by keeping the males and females in isolation until they were tested. Thus, the experiments were designed to show the effect of progesterone injections, if any, on incubation behaviour; the measurements taken were the number of doves that 'sat' in 24 or 48 hr and the latency to 'sit'. In the experiments of Silver and her co-workers, the internal endocrine make-up was varied by dexamethasone (DEX) administrations, while all situational cues were maximized; male doves were exposed to the females in the breeding cages before and throughout the period of hormone administrations and most DEX treatments did not start until eggs were laid. The measurement taken in these experiments was the amount of time 'sitting' over a testing period of 15 days, i.e. Lehrman's testing period was extended to 15 days, and the latency to 'sit' was not measured at all. Thus, the experiments were concerned with the ability of the male doves to incubate after the blockade of progesterone with DEX, when all situational cues were normal.

Since experienced male doves do incubate in the testing procedures of Silver & Buntin (1973) and Silver & Feder (1973), non-hormonal cues must still be adequate for maintaining the incubation behaviour of such males for half or more of the incubation period. The induction of incubation behaviour was very difficult to evaluate, however, because (1) with the exception of one group, DEX administration did not start until several days after pairs of male and female doves were introduced into the breeding cages and the females laid eggs, in which case most components of incubation behaviour had already developed, and (2) the group that received treatments 2 days before pairing were not castrated so that gonadal progesterone might have been involved in the induction of incubation behaviour in these birds.

If the hormonal and situational cues (Lehrman, 1965) are regarded not only as important contributory factors in the induction of reproductive behaviour but also as complementary to one another in the sense that one kind of cue manifests its specific effect whenever the other is held to a minimum, the two sets of data can be reconciled as illustrating different aspects of incubation behaviour.

Since non-hormonal cues were kept to a minimum in Lehrman's experiments, the effect on incubation behaviour of physiological changes was due to the exogenous progesterone, while in Silver's experiments, the adequacy of non-hormonal cues in maintaining the incubation behaviour of experienced males was demonstrated, since the hormonal state was upset by DEX.

Some of the experiments described below were designed to answer the following questions. (1) Is a high dosage of progesterone (100 µg/day for 7 days) really necessary in order to demonstrate its behavioural effects? (2) Does progesterone induce incubation behaviour or does it induce other behavioural patterns which precede and/or accompany incubation behaviour? (3) Does progesterone-induced incubation behaviour have any functional effect, such as hatching eggs?

## MATERIALS AND METHODS

### *Subjects*

The ring doves were hatched in the laboratory of the Institute of Animal Behavior, Rutgers University, and were maintained under a light cycle of 14-hr light/10-hr dark (lights on 06.00 hours, off 20.00 hours EST). Temperature was usually maintained between 21 and 22°C. At 21 days of age, the birds were transferred to stock cages which housed about fifteen young squabs. At 5 to 6 months of age, the birds were transferred to an isolation room where each bird was housed in an individual cage (isolation cage) rack mounted and measuring 35 × 20 × 15 cm. Birds in such cages could hear but not see the other birds. After 1 to 2 months in the isolation cage, each bird was put in a wooden breeding cage measuring 70 × 45 × 35 cm with wire-mesh doors. The bird was paired with a mate, given a nest bowl and nest materials and allowed to rear one or two squabs to 21 days of age. The pair were then separated and returned to the isolation cages. All birds bred successfully once or twice and were kept in the isolation cages for 3 to 5 weeks before being used in these studies.

### *Hormone administration*

All hormones were injected alternately into the right and left pectoral muscles.

**Progesterone.** A total of fifty reproductively experienced male doves were treated daily with 10 µg, 25 µg or 100 µg progesterone (Proluton: Schering Corporation, New Jersey, U.S.A.) in 0.1 ml sesame oil for 7 days in the isolation cages. As stimulus females, fifty-four reproductively experienced female doves in the isolation cages were given 100 µg progesterone daily during the same period as the male doves. Each breeding cage was partitioned into two compartments by a glass plate in the middle of the cage. A hand-made nest and two

sterile eggs were placed in each of these two compartments. On the day following the last injection, one male dove was put in one side of the cage and the stimulus female in the other. The testing situation used in these experiments differs from those of previous studies in that the male dove was separated from the female but could see her.

At the end of progesterone treatment, ten male doves (five received 100  $\mu\text{g}$  and five received 25  $\mu\text{g}$ /day for 7 days) were killed and the testes were removed for histological study. To test whether 100  $\mu\text{g}$  progesterone/day for 7 days was an excessive dose, six male doves were given 100  $\mu\text{g}$  progesterone/day for 2 days and two male doves were given 200  $\mu\text{g}$  progesterone for 1 day; all these birds were tested exactly as those in the first group.

In the 'hatching success' experiment, five birds were treated with 25  $\mu\text{g}$  progesterone/day for 7 days and were provided with fertile eggs laid by other breeding doves. One of the two sterile eggs was removed at the end of a 24-hr observation period and one fertile 1- to 3-day-old egg was replaced.

*Dexamethasone.* To test the hypothesis that situational cues and hormonal cues are complementary to each other, male doves were deprived of progesterone and allowed no access to the females until the time of the incubation test. The incubation test consisted of introducing a nest with two eggs and a female dove treated with 100  $\mu\text{g}$  progesterone/day. The anticipated result would be that these birds would not respond to the test situation by sitting on the eggs within a period of 24 to 48 hr, since both situational and hormonal cues would be minimized. After a prolonged association with female doves, however, the male doves should show some incubation behaviour which would be induced by an increased level of situational cues.

Ten male doves in isolation cages were given 100  $\mu\text{g}$  DEX daily for 7 days. On the day following the last injection, five birds were subjected to a testing procedure which was identical to that used for the progesterone-treated birds, while the other five birds were killed to determine the weight of their testes.

To check if the findings for DEX-treated birds could be attributed to the small number of birds tested, another ten pairs of male and female doves were used. Both male and female doves in isolation cages were given 100  $\mu\text{g}$  DEX/day for 7 days. After the last injection, they were placed in pairs in the breeding cages without the glass partitions and were observed daily for 15 days. The birds were then killed and their testes and ovaries were examined at autopsy. Samples of testes from four birds were stained with haematoxylin and eosin for subsequent examination of the morphological changes in these tissues.

*Control birds.* As a control group, ten male doves were given injections of 0.1 ml sesame oil/day for 7 days and were also tested for incubation behaviour. Another five intact birds were used for the determination of testis weight in normal male doves maintained in the isolation room and exposed to 14-hr light/day for 3 to 5 weeks. Finally, five male doves were castrated and similarly tested 2 weeks after surgery. This group provided data for comparison with the DEX-treated group.

*Behavioural observations.* Observations were conducted on each pair for the first hour after pairing. Further observations (four or five 20-min visits a day) were made over a 2- to 4-week period. The observations included (1) latency

of 'sitting', (2) the number of birds 'sitting', (3) the number of nests destroyed, (4) the behaviour patterns preceding and during 'sitting' in the nest, and (5) the hatching success for progesterone-treated birds.

## RESULTS

### *Dosage of progesterone and incubation response*

Exogenous injections of 10 µg progesterone/day for 7 days were still effective in inducing incubation behaviour (see Table 1). This was reflected in the shorter latency and the lower incidence of nest-destruction compared to the control group (i.e. the oil-treated birds). Of the dosages used in the first group, 25 µg/day for 7 days was found to be the most effective. Four of the six male doves treated with 100 µg progesterone/day for 2 days only showed incubation behaviour within 48 hr (Table 1), but male doves receiving 25 µg progesterone/day for 2 days failed to show incubation behaviour within 48 hr. A single injection of 200 µg progesterone induced some sporadic nest-cooing in the nest bowl but this did not develop into incubation behaviour.

### *Nest-cooing in the nest bowl*

The display of nest-cooing in the nest-bowl normally preceded the onset of incubation behaviour. This was true for the progesterone-induced as well as the naturally occurring incubation behaviour. The only difference between these two groups was the latency of displaying the behaviour pattern. The progesterone-treated birds showed behaviour patterns sooner than did the controls; the latter spent the first few hours, or even days, displaying either behaviour patterns which were characteristic of earlier courtship, such as bow-cooing and hop-charging, or other behaviour patterns which were not directed to the female mates.

### *Hatching success*

Four of the five fertile eggs given to the progesterone-treated birds were hatched and three squabs were raised successfully; their weight gains were comparable to those raised by normal parents. It is difficult to judge the significance of these hatching rates as the male doves were separated from females by a glass plate and were carrying alone the burden of incubating the eggs and feeding the young squabs.

### *Dexamethasone treatments and incubation behaviour*

The incubation responses of the DEX-treated and castrated male doves are shown in Table 1. None of the DEX-treated birds showed incubation behaviour within 24 to 48 hr. Even after 2 weeks of exposure to the female doves, only one male dove 'sat' and the rest did not. These male doves behaved very much like the castrated males (see Table 1). Their physical appearance, however, differed from that of the castrated doves in that their body feathers fluffed up to such an extent that the males looked like round balls.

The DEX-treated birds failed to display any courtship behaviour. All the birds had shrunken atrophic testes or ovaries. The histological preparations

**Table 1.** The effect of different treatments on the induction of incubation behaviour by male ring doves

Group	No. of doves	Duration of treatment (days)	% 'Sitting' in 24 hr	% Not 'sitting' in 3 weeks	Latency to 'sitting' (hr) Median      Range	Latency to cooing in nest bowl Median      Range	Nests destroyed in 24 hr in 24 hr (%)
P <sub>100</sub> *	10	7	60.0	—	25.8 3.0 to 26.5	26.5 0.5 to 26.5	20.0
	6	2	66.7	—	10.0 1.0 to 26	2.5 0.5 to 10.5	0.0
P <sub>25</sub> *	15	7	86.8	—	2.0 0.6 to 23	0.5 0.5 to 1.0	6.6
	6	2	16.7	—	30.8 5.0 to 98	(50.0) 0.8 to (160)	16.7
P <sub>10</sub> *	15	7	40.0	—	28.0 5.8 to 30	3.5 0.8 to 30	13.3
Intact (oil)	10	7	20.0	0	49.0 0.8 to 120	(49.0) 0.5 to (120)	30.0
DEX <sub>100</sub> †	5	7	0	100	— 336	(336)	60.0
	10 M	7	0	100	—	—	—
	10 F	7	0	100	—	—	—
Castrated	5	7	0	100	—	—	60.0
P <sub>200</sub> *	2	1	0	—	—	28.0 26 to 30	50.0

M = male; F = female; the inclusion of female birds is explained in 'Materials and Methods'.

\* Male birds treated with progesterone at doses of 100, 25, or 10 µg/day for 7 days.

† Male birds treated with dexamethasone at a dose of 100 µg/day for 7 days.

revealed shrinkage of the seminiferous tubules. Table 2 gives the weights of the testes of those progesterone-treated, DEX-treated and intact birds obtained at the end of seven treatments.

**Table 2.** The testicular and body weights of male ring doves in different treatment groups

	<i>Intact males in isolation (N = 10)</i>	<i>Progesterone (25 µg/day) for 7 days (N = 5)</i>	<i>Progesterone (100 µg/day) for 7 days (N = 5)</i>	<i>DEX (100 µg/day) for 7 days (N = 10)</i>
Weight of paired testes (mg)	1018.8 ± 52.5	988.9 ± 35.2	892.5 ± 42.5	320.2 ± 20.7**
Body weight (g)	155.2 ± 14.8	145.9 ± 18.5	160.9 ± 9.2	118.5 ± 10.4*

Values are expressed in terms of mean ± S.E.M. Comparisons between groups were made using the Duncan's test for unequal n. DEX = dexamethasone; N = number of doves.

\*\*  $P < 0.01$ ; \*  $P < 0.05$ .

## DISCUSSION

The results of the present experiments indicate that (1) the accumulated rather than the daily dose level of progesterone injections appears to be the determinant factor in mediating behavioural effects. The optimal (accumulated) dosage probably is of the order of 200 µg, (2) The level of progesterone at the dosage used in the earlier studies (100 µg/day for 7 days) is indeed non-physiological, and (3) the behavioural effect of progesterone is unlikely to be due to any anaesthetic properties, since 25 µg/day for 7 days or 100 µg/day for 2 days are more effective than 100 µg/day for 7 days.

In order to gain a fuller understanding of the rôle of progesterone in induction of the incubation behaviour of male ring doves, it is important to have some knowledge of the preceding behavioural patterns. These may be categorized into four stages: (1) aggressive behaviour—bow-cooing and hop-charging; (2) nest-soliciting (wing-flipping and cooing in an oblique posture at the potential nest site) and copulatory behaviour; (3) nest-building and nest-cooing behaviour (wing-flipping and cooing in a partly crouched posture in the nest-bowl with the tail somewhat lowered); (4) 'sitting' in the nest—wing-flipping or nest-cooing occasionally. When the nest is occupied by the female, the male usually perches quietly near the nest, occasionally heteropreening her. Stage 4 is followed by egg-laying and subsequent incubation by both sexes.

The behavioural components of Stage 4 usually consist of (a) rearranging the nest materials, (b) components of settling movements, (c) exposure of the mid-line apterium area as the dove arises from the nest, (d) mild nest-defensive behaviour, and (e) occasional nest-cooing or wing-flipping. During incubation, both sexes display all these behavioural components with even greater intensity. They also show behavioural components specifically associated with the presence of eggs. Thus, Stage 4 may be regarded as a stage of 'pseudo-incubation' (incubation without eggs). The presence of eggs apparently does not

cause any abrupt behavioural change in a dove which has been 'sitting' in the nest and the behavioural transition from courtship to incubation may, therefore be regarded as a continuous process. This is supported by the observation that both male and female doves could be induced to incubate eggs even before their own eggs were laid, provided that the foster eggs were given to them during the last part of the pre-laying period (Lehrman, Brody & Wortis, 1961). Since the behavioural data needed to determine the stage of male courtship were not given by these authors, it is not possible to tell at which behavioural stage their doves were provided with foster eggs. The best results were usually obtained, however, with those doves which had been paired for 5 to 8 days, and therefore the behavioural stage was probably either Stage 3 or Stage 4.

Progesterone appeared to facilitate the occurrence of the behavioural patterns characteristic of Stage 3, i.e. nest-cooing in the nest in a partly crouched posture. The control doves injected with the vehicle alone did not show these behaviour patterns until much later (see Table 1). Their initial behaviour patterns were those characteristic of early courtship, i.e., Stage 1 and/or Stage 2 behaviour. Since all birds tested in the experiments reported in this paper were provided with fully constructed nests, it is not surprising that they failed to show nest-building behaviour (White, 1974).

It may be concluded that treatment with progesterone facilitates an incubation response by way of inducing nest-related activities. It should be emphasized, however, that this conclusion does not necessarily imply the existence of a parallel function of endogenous progesterone. Endogenous progesterone may have an excitatory effect on behaviour depending on its differential ratio with respect to the levels of other hormones (such as testosterone), which may fluctuate during the breeding cycle. There is also a possibility, however, that progesterone secretion may surge (or fluctuate) at a time which was not sampled in the previous studies of ring doves.

Since the most effective hormone regimen for inducing an incubation response in the castrated doves is the combined treatment with testosterone (or oestrogen) and progesterone (Stern & Lehrman, 1969; Stern, 1974), the underlying mechanism for incubation behaviour seems to be the synergistic effect of the two hormones.

In a recent study, Korenbrot, Schomberg & Erickson (1974) showed that the plasma oestrogen level of the female ring dove rises immediately after male courtship, reaching a peak in a few days and then beginning to decline around the time of the nest-building period. If the testosterone level in the male ring dove changes in a similar manner during the breeding cycle, it is conceivable that when it drops to a critical point, the progesterone, which is at a relatively low and steady level, may then interact synergistically with the testosterone to produce the behavioural effect. It is a well-established fact that the synergistic effect of progesterone and oestrogen is best manifested when the oestrogen level is relatively low (Mason, 1952; Lisk, 1971; Diakow, Pfaff & Komisaruk, 1973).

The finding that none of the DEX-treated doves in the present study showed 'sitting' behaviour within a 2-week period is in favour of the hypothesis that hormonal and non-hormonal (situational) cues are complementary to one another for the induction of incubation behaviour in ring doves and contrary to



to the expectations aroused by the findings of Silver and her co-workers. The optimal dose of DEX which is sufficient to achieve an ACTH-blocking effect in ring doves but not too strong to cause other side effects has not so far, however, been determined.

Depending on the relative importance of hormonal and situational cues in a given experimental situation, there are four conditions which can be tested experimentally with ring doves to illustrate the complementary rôle of these cues. The conditions are summarized in Table 3. The first three have been

**Table 3.** Complementary rôle of hormonal and situational cues in the induction of male incubation behaviour in ring doves

Conditions	Hormonal cues	Situational cues	Incubation behaviour	Experimental studies
1	Max	Min	Yes	Lehrman <i>et al.</i> (1958, 1961), Stern <i>et al.</i> (1969, 1974)
2	Min	Max	Yes	Silver <i>et al.</i> (1973, 1974)
3	Min	Min	No	Present study
4	Max	Max	Yes	Prediction

Max = maximized; Min = minimized.

discussed in the present paper. The outcome of the fourth condition hardly seems in question. Since we know already from Lehrman's study and the present findings that progesterone injections (maximized hormonal cues) have the effect of shortening the time it takes to induce incubation behaviour in a short testing procedure (minimized situational cues), it follows that, in an extended testing procedure (maximized situational cues), progesterone injections should have the same effect on the induction of incubation behaviour. One interesting consideration is the possibility of controlling the induction of incubation behaviour by manipulating the relative importance of these two kinds of cues.

The rôle of sexual experience in modifying the relative importance of hormones in eliciting sexual behaviour has been demonstrated by Rosenblatt & Aronson (1958) in their study of the copulatory behaviour of castrated male cats. We hope to examine the possible rôle of such a factor in the complementary relationships of hormonal and situational cues in the induction of the incubation behaviour of male ring doves.

Finally, since weather, food and predators are important factors influencing the incubation behaviour of herring gulls in the field (Drent, 1967), it seems reasonable to assume that they are important situational cues for the incubation behaviour of doves under natural conditions.

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