

EXPERIENCE AND PROGESTERONE IN RING DOVE INCUBATION

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Abstract:

Doves were tested for progesterone-induced incubation after they had acquired previous experience with from one to five different phases of their initial breeding cycle. A sixth group had no previous breeding experience. Previous breeding experience inclusive of at least the nestbuilding phase of the cycle is a significant facilitator of incubation behaviour induced by injected progesterone, but previous experience with only the courtship phase was not sufficient. Experience with phases additional to nestbuilding increased overall nest-responsiveness without significantly increasing the number of birds incubating. The nature of a ring dove's previous experience is therefore an important influence in its behavioural response to exogenous progesterone.

Article:

The reproductive cycle of sexually mature ring doves can be divided into a sequence of functional phases: courtship, nestbuilding, egg-laying, incubation, and care of young. The organization of the behavioural patterns of each phase and the transitions between phases are influenced by both the external situation and the dove's hormonal condition (Lehrman 1965; Moore 1970; Cheng 1975). While recent studies have focused on the nature of the hormonal condition (e.g. Cheng 1973a, 1973b; Silver et al. 1974) and the details of the situational cues (e.g. Silver, Feder & Lehrman 1973), few studies have examined the role of previous individual experience in the organization of the ring dove's cycle (cf. Moore 1970).

In an earlier study of the hormonal initiation of incubation, Lehrman & Wortis (1960) reported that the occurrence of incubation in response to exogenous progesterone was dependent upon previous breeding experience. Reproductively experienced male and female doves that had received seven daily 100- μ g injections of progesterone, while in isolation, established incubation within 24 hr of introduction to a nest and eggs, whereas similarly treated and age-matched reproductively naïve doves did not initiate incubation. Subsequent study (Bruder & Lehrman 1967) showed that this experience-dependent progesterone-induced incubation was greatly facilitated, in both males and females by the presence of a similarly treated mate. Left unresolved by these studies was the question of what exactly is the previous breeding experience that is relevant for progesterone-induced incubation. That is, before behaving as an experienced bird in that situation, must a dove have completed an entire reproductive cycle, or have spent some time sitting on eggs, or have only initiated incubation? The present study examined this question by isolating and identifying those phases of an earlier cycle which are responsible for a dove's behaving like an experienced bird when tested for progesterone-induced incubation on a later occasion.

Methods

Ninety pairs of sexually-mature ring doves (*Streptopelia risoria*) of comparable ages at the time of testing were used. All birds lacked reproductive experience at the beginning of the study.

The testing cages were breeding cages of wood, measuring 70 x 45 x 35 cm, with dispensers for food, water and grit and having wire-mesh front doors. Isolation cages were double-width hanging rat-cages in racks. Breeding and isolation cages were kept in separate rooms. Lights were clock-controlled (Tork) to turn on at 06.00 hours and off at 20.00 hours E.S.T. Temperature was generally kept between 22° and 24°C.

Procedure

Each bird was randomly (within sex) assigned to one of six groups (N = 15 pairs per group). Except for group I, the members of each group were allowed to participate in only specific phases of their first breeding cycle as follows:

Group I 'reproductively naive'. These birds were kept in isolation cages throughout the period in which the birds of group VI were acquiring their breeding experience.

Group II 'courtship experienced'. These birds were placed for 8 days in a breeding cage which lacked nesting materials.

Group III 'nestbuilding experienced'. These birds were kept for 8 days in a breeding cage containing the usual nest materials (straw and a glass bowl). All pairs built nests at least three- fourths complete during this period.

Group IV 'egg-laying experienced'. These birds were kept in breeding cages containing the usual nesting materials until the day of the appearance of the second egg (about 11 to 12 days after introduction).

Group V 'incubation experienced'. These birds were allowed to breed until 12 days after the appearance of the first egg (approximately seventy-five per cent of the incubation phase of the cycle).

Group VI 'full-cycle experienced'. These birds were allowed to complete one breeding cycle from introduction to the breeding cage to 21 days after the young had hatched.

All birds were separated and returned to isolation cages after having completed their assigned portion of the cycle. Neither courtship experienced nor nestbuilding experienced females laid eggs during their 8 days in the breeding cage or during their 5 weeks in isolation cages before testing. Beginning 4 weeks after they had been returned to isolation cages, each bird received seven daily injections of 100 μ g of progesterone in 0.1 ml of sesame oil, injected into the right and left pectoral muscles on alternate days. The birds were tested in blocks that included animals from each group in a block. The birds in group I received their injections at an age comparable in time to those in group VI.

On the morning (between 08.00 hours and 09.15 hours E.S.T.) of the day following the last injection, each bird was placed in a breeding cage containing a nest with two fresh eggs and a similarly injected and experienced, but unfamiliar, mate. All of the birds' behaviour was recorded continuously, by hand, on sheets of paper divided into 15-s blocks, for 1 hr immediately following introduction and again for 10 min, 24 hr later.

In summary, doves were tested for progesterone-induced incubation after they had been allowed to complete from one to five different phases of a typical breeding cycle. As a control, group I was not permitted to initiate a breeding cycle before being tested for progesterone-induced incubation.

Observations

Data were collected on: (a) latency to stand near nest (i.e. to spend at least one full minute in the nest quadrant of the cage); (b) latency to stand on nest (i.e. to spend at least 30 s continuously on the nest); (c) latency to incubate (i.e. to erect the ventral feathers and bring the ventral aperture into contact with the eggs for two consecutive minutes); this measure of incubation eliminates its confusion with nest- site defensiveness and certain forms of nest- soliciting behaviour; (d) time spent on the nest; and (e) time spent incubating. Time was measured by the number of 15-s blocks in which the response occurred; and the time criteria for the latency measures were selected on the basis of pilot work to control for 'random' movements of the doves within the confines of the cage, resulting in occasional time on the nest and time in nest quadrant. If one member of the pair exhibited incubation at the 24-hr test, it was removed, and the remaining bird was observed for 10 min.

Results

Statistical analyses were performed on measures of the responses of each pair, rather than each bird. Since incubation is dependent, in part, on at least the presence of a mate (Bruder & Lehrman 1967), the animals were tested in pairs, eliminating the possibility of examining the male and female responses independently. Therefore, the latency measures represent the shortest latency exhibited within a pair and the tests were performed only on responding pairs (i.e. pairs in which either or both members responded). The duration measures represent the combined male and female times. It is possible for the male and female to simultaneously stand on the nest and impossible for the male and female to simultaneously incubate (as defined above). Again, analyses of these measures were performed only on responding pairs.

Table I shows that a greater number of pairs with nestbuilding experience (group III) established incubation within 1 hr after introduction than group I naïve pairs (Fisher-Yates test, $P = 0.025$ one-tailed) and group II pairs ($P = 0.005$). Tests of the other relevant differences in the 1-hr period were not significant. Although all groups showed increases in total number of pairs exhibiting incubation after 24 hr, the differences among the groups were unchanged. Again, significantly more group III pairs exhibited incubation than did group II pairs ($P = 0.05$). Interestingly, the incubation response of group II pairs at the 24-hr test is

Table I. Number of Pairs Incubating

	Group					
	I	II	III	IV	V	VI
1-hr test	1	0	7	11	8	10
24-hr test	4	7	13	15	13	13

Note. $N = 15$ per group.

equivalent to the incubation level exhibited by group III pairs during the 1-hr test.

When comparing the latencies to stand near or on the nest and to establish incubation (see Table II), there is an obvious difference between both naïve (I) and courtship-experienced (II) pairs and those with at least nestbuilding experience (groups III, IV, V, VI). Analysis of variance of the responding pairs in groups III, IV, V and VI revealed a further significant effect of previous breeding experience both for latency to stand near ($F = 8.8$; $df = 3, 56$; $P < 0.01$) and to stand on ($F = 7.43$; $df = 3, 56$; $P < 0.01$) the nest. Post hoc tests of the differences among the means indicated that group III pairs took reliably longer to stand near or on the nest than those pairs in the other three groups ($P < 0.01$, Newman-Kuels). There was no significant effect of previous breeding experience for latency to incubate among the pairs ($F = 1.15$; $df = 3, 33$; Ns).

For duration of responding to the nest and eggs during the 1-hr observation, group III again marks the phase of positive experiential influence. There was no discernible time spent incubating by either courtship-experienced or naïve pairs. The one dove establishing incubation in group I did so only during the last 30 s of the 1-hr test. Analysis of variance for groups III through VI revealed no significant influence of previous breeding experience for either time on the nest ($F = 2.1$; $df = 3, 55$; Ns) or time spent incubating ($F = 0.7$; $df = 3, 41$; Ns).

Though sex differences in progesterone-induced incubation were not examined in this study, the fact that the sexes differ in their reproductive physiology suggests that they might be differentially sensitive to progesterone injections. Table III shows that there are some differences in the number of males and females establishing incubation during the 1-hr and 24-hr tests. However, these differences are often slight and are subject to the qualification that both tests occurred during the time of day when the male would have begun his incubation turn in a normal cycle.

There was no predictive association (Goodman & Kruskal index of predictive association in Hays 1963) between mates for the establishment of incubation during the 1-hr test. Nor was there any predictive association

between the males and females for latency to stand on the nest or to establish incubation during the 1-hr test. However, the chance of error in predicting whether the male spends a long or short time on the nest is reduced about thirty-seven per cent on the average, given the information as to whether his mate spends a long or short time on the nest. That is, the male's time on the nest seems to be somewhat influenced by the female's time on the nest; the longer she is on, the shorter he is on. There was no predictive association for the female's time on the nest, given information

Table II. Latency and Duration of Responsiveness to Eggs and Nest during the 1-hr Observation Period

	Latency			Duration	
	Near nest	On nest	Incubation	On nest	Incubation
I	69, 33, 7	141, 72, 4	—	47, 42, 4	—
II	129, 42, 5	209, 24, 2	—	40, 22, 3	—
III	37, 27, 15	35, 27, 14	150, 61, 7	169, 110, 14	52, 50, 7
IV	10, 10, 15	9, 11, 15	144, 61, 11	226, 95, 15	79, 49, 11
V	16, 21, 15	17, 22, 15	110, 65, 8	207, 63, 15	62, 44, 8
VI	7, 6, 15	8, 5, 15	161, 57, 10	244, 61, 15	62, 41, 10

Note. Time was measured in terms of numbers of 15-s intervals. The numbers in each column represent the mean, SD, and *N* for each group.

about the male's time on the nest. There was, also, no predictive association between the male's time on the nest and his latency to incubate or his likelihood of incubating during the 1-hr test.

Discussion

Previous experience with the activities of courtship plus nestbuilding appears to be the source of the difference between experienced and naive doves' progesterone-induced incubation. Experience with additional phases of the breeding cycle reduces the latency for nest orientation without necessarily increasing the probability of the establishment of incubation within the 24-hr test period. These results are concordant with Lehrman's (1958) observation that the onset of incubation during a breeding cycle is facilitated when pairs of reproductively experienced doves can engage in both courtship and nestbuilding activity for some 7 days. The present study indicates that previous courtship and nestbuilding activity also facilitates progesterone-induced incubation.

There are at least two alternative explanations for why previous courtship and nestbuilding experience facilitates progesterone-induced incubation in the female dove. Cheng & Silver (1975) have shown that during a normal reproductive cycle, both nestbuilding and incubation in the female are dependent upon the presence of both oestrogen and progesterone. Therefore in the present study, female doves engaging in nestbuilding for the first time are also experiencing increases in endogenous oestrogen and progesterone. It is conceivable that solely as a result of exposure to her endogenous hormonal condition during nestbuilding, the female's nervous system may become sensitized to progesterone so that, at a later time, exposure to exogenous progesterone will facilitate the initiation of incubation. However, it is also possible that the behavioural and socio-environmental experiences concomitant with courtship and nestbuilding are the agents solely responsible for the change in sensitivity of the female to exogenous progesterone. These alternative explanations are currently being investigated, and the results will be reported at a later time.

The situation for the male dove is more ambiguous. It has been argued (Silver & Buntin 1973; Silver & Feder 1973) that the initiation of incubation in the male dove is not dependent upon progesterone. Rather, situational cues from the female's behaviour, the nest bowl, and nest materials are responsible for the initiation of incubation in reproductively experienced male doves (Silver et al. 1973). Indeed, Martinez- Vargas & Erickson (1973) found that oestrogen—progesterone treatment of female ring doves facilitated the nestbuilding behaviour of their untreated mates. White (1975a, b) also observed that the male's nestbuilding behaviour and

time in the nest was, in part, determined by his mate's nest-soliciting and nestbuilding behaviour. Moreover, radio-immunoassay results suggest that the male's plasma progesterone levels do not change during courtship and incubation (Silver et al. 1974). Therefore, it is possible that the male's incubation response during testing is a consequence of the cues provided by the mate and nesting material (Martinez-Vargas 1974) and not the result of his hormonal condition. However, this appears less likely given the lack of any predictive association between the incubation behaviour of mates.

Cheng (1975) has demonstrated that situational cues and hormonal condition complement one another in the induction of incubation.

Table III. Number of Males and Females that Established Incubation during the 1-hr and 24-hr Tests

	Group						Total
	I	II	III	IV	V	VI	
1-hr test:							
males	1	0	5	9	7	6	28
females	0	0	4	5	2	7	18
24-hr test:							
males	2	5	9	14	12	10	52
females	2	5	10	11	10	11	49

Note. $N = 15$ per cell.

However, if progesterone injections are responsible for the male incubation behaviour observed in the present study, and endogenous progesterone is not responsible for the male's nest-building experience, then it seems likely that it is the behavioural, socio-environmental factors of previously experienced courtship and nest-building that sensitize the male's nervous system for progesterone-induced incubation. Investigations of this hypothesis require a more programmatic analysis of the influence of different situational cues on the nest responsiveness and incubation performance of both males and females in the progesterone-induced-incubation test situation. Until this has been done one cannot say whether the mechanisms involved in the performance of the male in progesterone-induced incubation are different than those governing the female's performance. The results of the present study do show that experience with eggs and incubation is not necessary for progesterone-induced incubation and that the investigation of experiential influences is an important component of hormone-behaviour research.

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