

Contributions of reproductive experience to observation-maintained crop growth and incubation in male and female ring doves

By: GEORGE F. MICHEL & CELIA L. MOORE

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Abstract:

Previous work has established that experienced male ring doves (*Streptopelia risoria*) can maintain prolactin-dependent crop growth and readiness to incubate by observing an incubating partner. We report that this is also true for female ring doves. The role of experience in this phenomenon was examined in separate experiments with males and females. Observation of an incubating mate from 3 days after completion of egg laying is sufficient to maintain crop growth and incubation in both male and female ring doves in their second, but not in their first, reproductive cycle. Male and female doves in their first cycle must incubate for a greater part of the cycle before observation of an incubating mate is an effective stimulus; there are no differences between first and second cycle doves separated by a glass plate from the mate and nest 8 days after laying. Experience obtained within the first cycle apparently ensures that previously neutral stimuli come to elicit prolactin secretion. The effectiveness of these stimuli is reinstated early in a second cycle.

Article:

Incubation and care of the young are shared by the male and female of a mated pair of ring doves. During incubation the crop sacs of both birds grow from an initial empty weight of about 600 mg to over 3000 mg (Hansen 1966; Friedman & Lehrman 1968). This rapid growth results in the sloughing off of epithelial cells into the lumen to form crop 'milk', the characteristic food for young doves and pigeons (Beams & Meyer 1931). Both parents regurgitate crop milk to the young as their principal source of nourishment during the early post-hatching period. By 3 weeks after hatching, crop weight has regressed to resting state in ring doves (Goldsmith et al. 1981), and the young are feeding independently.

Although there may be synergistic effects of other hormones, prolactin is necessary for crop growth (Bates et al. 1962). Furthermore, except at the extremes, there is a close correlation between circulating prolactin level and crop weight in incubating ring doves (Goldsmith et al. 1981; Cheng & Burke 1983). An increase in crop weight, therefore, can be used as a valid indicator of prolactin secretion and a valid estimator of plasma prolactin level over most of the range in which prolactin varies. Prolactin secretion may, however, escape detection by crop growth at the low levels characteristic of early incubation, and changes within the very high prolactin levels characteristic of late incubation may not be reflected in crop weight changes (Cheng & Burke 1983).

Prolactin is secreted during incubation in doves and pigeons as a result of exposure to the stimulus conditions associated with sitting on eggs. Thus, if incubating doves (Lehrman & Brody 1964) or pigeons (Patel 1936) are removed from their nests before crop growth has started, growth will not begin, and if they are removed from the nest after crop growth has begun, the crop will regress back to the resting state and prolactin levels will fall sharply (Silver 1984). However, if males are removed from their nests to an adjacent cage from which they can observe their incubating mates, then their crops will continue to grow as though they were also incubating (Patel 1936; Friedman & Lehrman 1968). Thus, observation of an incubating mate can provide the stimulus conditions required for maintaining prolactin secretion in males of these species during the incubation phase of a breeding cycle.

Friedman & Lehrman (1968) examined the conditions under which observation of an incubating mate would maintain crop growth and readiness to incubate in male ring doves separated from their mates by a glass plate. By testing incubation, and measuring crop growth at the end of the incubation phase of the cycle for nine different groups of males, each separated by a glass partition from their incubating mates at different phases of the cycle, they found that the male must have been sitting on a clutch of eggs for at least 3 days before observation was sufficient to maintain crop growth and incubation state. Separation before 3 days would prevent observation-maintained crop growth and readiness to incubate. Males that were separated after 3 days showed crop weights at the end of the incubation phase (9 days later) that were equivalent to those of males that had not been separated from contact with their mates and nests during that time. Thus, observation of their incubating mate provided the males with conditions that promoted a pattern of prolactin secretion similar to that which would have occurred if they had continued to participate in incubation.

Since males separated on the third day readily reestablished incubation at the end of their 9 days of separation from their mates, the prolactin secreted as a result of observing the mate not only continued the growth of the crop but also apparently maintained a state of readiness to incubate (Lehrman & Brody 1964). Thus, these males would have been quite capable of feeding and brooding newly hatched young, despite their physical separation from their mate and nest for most of the incubation phase of the cycle.

The male's ability to maintain crop growth by observing his incubating mate has been assessed only in reproductively experienced doves. However, the secretion of prolactin and the growth of the crop are influenced by several different kinds of visual and tactile cues (Lehrman & Brody 1964; Hansen 1966, 1971a; Buntin 1977), and the effectiveness of these influences can differ according to the breeding experience of the doves being tested (Hansen 1971b, 1973). It is possible that reproductively naive and experienced males will differ in their responsiveness to stimuli provided by observing an incubating mate.

Although males and females share incubation and care of young, they may not respond equally to the various factors that regulate these behaviours. For example, incubation may be more dependent on endocrine state in females than in males (Silver & Buntin 1973), and females are more sensitive than males to certain non-tactile stimulation of crop growth by squabs during the post-hatching period (Buntin et al. 1977). Since females do most of the incubating and incubate throughout the dark phase of the diurnal cycle (Gerlach et al. 1975), the regulation of prolactin secretion by females during the incubation phase of the cycle may differ from that of males. Therefore, the present study examines the ability of reproductively naive and experienced male and female ring doves to maintain crop growth and readiness to incubate when they are prevented from incubating, but are allowed to observe the incubation of their companion.

EXPERIMENT 1

This experiment examines the effect of breeding experience on the male's ability to maintain crop growth by observing the incubation of the mate.

Methods

The subjects were 60 sexually mature male ring doves (*Streptopelia risoria*) bred in the psychology laboratory colony at the University of Massachusetts, Boston, from stock originally obtained from the Institute of Animal Behavior, Rutgers University.

Breeding cages were wooden, measuring 78 x 40 x 38 cm (with dispensers for food, water and grit) with wire-mesh front doors. Visual isolation cages were double-width rat cages, hanging in racks. Stock cages were 85 x 79 x 91 cm, with wooden frames and wire-mesh sides. Breeding, stock, and isolation cages were kept in separate rooms. A daily cycle of 14 h light: 10 h dark, with the light period beginning at 0700 hours, was controlled by Tork clocks. Temperature usually remained between 21 and 24°C. Doves were weaned to stock cages of 8-12 birds at 3 weeks after hatching and were sexed by exploratory laparotomy by 4 months of age. After sexing, each was placed in individual isolation cages.

Each male was assigned to one of five groups (12 per group) and treated as follows.

Group 8DE: 8-day experienced

At 6-7 months of age, each of these males was placed in a breeding cage with a reproductively experienced female and allowed to participate in a complete, successful breeding cycle. When his squabs were 3 weeks old, the male was removed to an isolation cage for 3-4 weeks. After isolation, the male was returned to a breeding cage containing an unfamiliar, reproductively experienced female and nest-building materials (nestbowl and hay). Eight full days after the appearance of the second egg (about 4 days before first hatching), a glass plate was inserted which partitioned the breeding cage and physically separated the male from his incubating mate. Thus, these males completed two-thirds of the incubation phase of a cycle before being separated from their mate by a glass plate so as to prevent incubation but allow observation of the incubating mate.

Group 3DE: 3-day experienced

Males in this group were treated as those in group 8DE except that the glass partition was inserted 3 days (72 h) after the second egg was laid. Thus, these males completed only a quarter of the incubation phase before being separated from their incubating mate. This group duplicates the group in Friedman & Lehrman (1968) which showed normal crop growth and readiness to incubate despite this period of separation.

Group 8DN: 8-day naive

These males remained in isolation until they were approximately 10 months old (median =10 months). Then each was placed in breeding cages with a reproductively experienced female and allowed to initiate a breeding cycle. Eight days after the appearance of the second egg the glass partition was inserted to separate the male from his incubating mate. Thus, these males were similar to group 8DE males except that they were reproductively naive before testing.

Group 3DN: 3-day naive

Males in this group were treated as those in group 8DN except that the glass partition was inserted 3 days after the second egg was laid. Thus, these males were similar to group 3DE males except that they were reproductively naive before testing.

Group NC: normal controls

These were males of reproductively experienced pairs that incubated normally in breeding cages that were not partitioned.

On the 13th day after the morning appearance of the first egg, 11 days after the second egg, a nest with eggs was placed on the male's side of the breeding cage, next to the glass partition. During the next hour, the male's incubation behaviour was assessed. A male was considered to be incubating if he erected his ventral feathers and kept his ventral apterium in contact with the eggs for two consecutive minutes. If the male had riot established incubation during the hour, then the partition and mate were removed and the male was observed for an additional 10 min to see if he would incubate his own eggs. At the end of this period, the male was autopsied and the crop was removed, cleaned of adhering fat and loose crop milk, rinsed in physiological saline, blotted dry, and weighed. The weights reported are for the area from the anterior to posterior ends of the crop sacs. There was no significant association between the age of the male at autopsy and his crop weight ($r=0.19$, $z=1.3$, $P> 0.10$).

The number of incubating males for each group was cast in a 2 x 5 contingency table and analysed by a chi-squared test. Multiple 2 x 2 contingency analyses of incubation were performed for each pair of groups using the Silverstein (1978) Z-test for multiple comparisons. The crop weights were analysed by a Kruskal—Wallis analysis of variance. Multiple pair-wise comparisons of differences among the groups were assessed using the Silverstein Z-test.

Results

The percentage of males that maintained a readiness to incubate throughout the separation period differed significantly ($\chi^2=14.1$, $df=4$, $P<0.01$) among the groups (Fig. 1). The 3DN group had significantly fewer incubating males than any other group ($Z=2.8$ or larger, $P < 0.05$). No other differences were significant.

Table I shows the median crop weight for each group. The crop weights differed significantly across the groups ($K=15.3$, $df=4$, $P<0005$). The

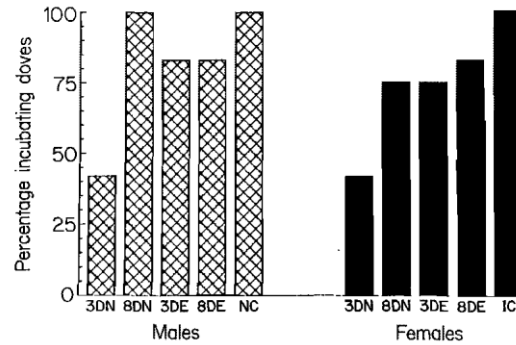


Figure 1. Percentage of males in experiment 1 (cross-hatched bars) and females in experiment 2 (solid bars) that maintained a readiness to incubate ($N=12$ per group).

Table I. Crop weights (in mg) of male and female ring doves in the different groups

	3DN	8DN	3DE	8DE	NIC
Experiment 1: Males					
Median	970	1348	2557	2465	2345
Semi-interquartile range	509	923	961	454	447
Experiment 2: Females					
Median	980	768	1213	1155	2111
Semi-interquartile range	324	170	581	294	447

crop weights of the 3DN group were significantly lighter than group NC ($Z=4.3$, $P<0.01$), group 3DE ($Z=4.2$, $P<0.01$), group 8DN ($Z=2.74$, $P<0.05$) and group 8DE ($Z=4.9$, $P<0.001$). No other differences were significant.

Discussion

The results demonstrate that breeding experience affects the ability of male doves to maintain prolactin-dependent crop growth and readiness to incubate through stimuli restricted to those obtained by observing the incubation of a mate. For reproductively experienced males it was found that observation of an incubating mate after 3 days of incubating a full clutch is as effective as normal participation in incubation for both crop growth and readiness to incubate, thus confirming Friedman & Lehrman (1968). However, reproductively naive males that were prevented from incubating, but were allowed to observe an incubating mate during the last three-quarters of the incubation phase of the cycle, failed to maintain a readiness to incubate and had strikingly lighter crops, thus indicating that stimuli obtained through observing an incubating mate were not sufficient to maintain prolactin secretion in males undergoing their first cycle. Although there was a striking difference in observation-maintained prolactin secretion between males with and without previous breeding experience when separation from the nest and mate occurred early in incubation, both first and second cycle males were able to maintain prolactin-dependent incubation and crop growth at levels equal to that of normally incubating males when separation occurred after 8 days of incubation.

EXPERIMENT 2

Experiment 1 showed that breeding experience facilitates the observation-maintained, prolactin-dependent

growth of the crop sacs and readiness to incubate in male ring doves. However, males incubate only about 6 h of every 24 (Gerlach et al. 1975). They normally obtain less stimulation from the act of incubation than females and hence may rely more on other sources of incubation-related stimulation, such as that provided by an incubating mate, for maintaining prolactin secretion. It is possible that female doves are more dependent than males on tactile or other stimuli provided by the act of incubation, even though after hatching they appear to be more sensitive to certain forms of non-tactile squab-related stimuli (Buntin 1977; Buntin et al. 1977). Therefore, it is of interest to know whether female doves can maintain crop growth and readiness to incubate by observation of an incubating companion and, secondly, whether breeding experience affects the female's response to these stimuli in ways similar to that of the male.

Unfortunately, separating the female from her incubating male mate with a glass partition does not create conditions that are comparable to those created for males in experiment 1. Incubating males with mates on the other side of a glass partition will soon abandon the nest (Patel 1936; unpublished preliminary observations). Thus, separated females would observe an empty nest for more time than they would observe an incubating male. Neither males nor females in this situation show crop growth (Patel 1936; Silver 1984). However, because females will pair bond with other females, it is possible to provide a separated female with a continuously incubating mate. Paired females can be separated, allowing one to observe the other incubating. Experiment 2 was designed to examine the effect of observing an incubating mate on the maintenance of crop growth and readiness to incubate for reproductively naive and experienced female doves.

Methods

The subjects were 60 sexually mature female ring doves obtained and maintained as in experiment 1.

As in experiment 1, 12 females were assigned to each of 5 groups, the first four of which duplicated those of experiment 1. Like the males in experiment 1, each female was paired with a reproductively experienced female during the test breeding cycle. Because there were two females to lay eggs, separation was timed from the first eggs to appear, regardless of which female laid them. Thus, the second consecutive day on which an egg was found was considered the day of appearance of the second egg; extra eggs were removed so that the females incubated a clutch of two eggs.

The fifth group was an incubation comparison group (labelled IC) and consisted of the reproductively experienced stimulus female companions of group 8DE females. These females shared incubation with their mates through 8 days after the second egg, after which they had continuous access to the nest during the remaining time before testing and autopsy. Periodic checks indicated that these females incubated virtually continuously during these 3 days. Thus, female group IC was not equivalent to male group NC because the females in IC had to prolong their daily incubation time during the last part of incubation, unlike normally incubating males or females. Secondly, these females incubated infertile eggs, which may have affected their hormonal condition (Cheng 1977).

On the 12th day after the second egg, a nest with eggs was placed on the subject female's side of the breeding cage, next to the glass partition, and readiness to incubate was assessed as in experiment 1. Crops were removed at autopsy, prepared and weighed as in experiment 1. Again, there was no significant association of age with crop weight ($r = 0.08$). Data analysis was performed as in experiment 1.

Results

There was a significant difference ($\chi^2 = 11.2$, $df = 3$, $P < 0.025$) across groups in the percentage of females that maintained a readiness to incubate (Fig. 1). Group 3DN had significantly fewer incubating females than any other group ($Z = 2.73$ or larger, $P < 0.05$). No other differences were significant.

Crop weights differed significantly across groups ($K = 11.7$, $df = 4$, $P < 0.025$, Table I). Crop weights of 8DN females were significantly lighter than those of females in groups 3DE ($Z = 3.2$, $P < 0.05$), 8DE ($Z = 3.1$, $P = 0.05$) and IC (the incubation comparison group) ($Z = 4.1$, $P < 0.001$). Crop weights of 3DN females were also

significantly lighter than those of IC females ($Z= 3.1, P < 0.05$). No other differences were significant. Because there was no difference between separation after 3 or 8 days for either naive or experienced females, the crop weights of the 8DE and 3DE females were combined and compared with the combined crop weights of the 8DN and 3DN females. The crops of experienced females were significantly heavier ($Z=4.2, P<001$).

Discussion

Observation of an incubating mate can provide the stimulation necessary for maintaining prolactin-dependent crop growth and readiness to incubate in female as well as male doves. Breeding experience also seems to facilitate observation- maintained prolactin secretion in females. If the female is engaged in her first breeding cycle, preventing her from participating in incubation, even after 8 days of incubating a full clutch, significantly prevents growth of her crop. Incubating for 8 days before separation does allow the naive female to maintain a readiness to incubate which is lost if separation occurs after only 3 days of incubation. Since crop growth can occur rapidly in response to stimuli provided by sitting on squabs (Buntin 1977; Buntin et al. 1977), the 8DN females that maintained a readiness to incubate would be more likely to rear young successfully after a period of interrupted incubation than the 3DN females that were not ready to incubate.

Because duration of incubating a full clutch before separation from the nest was a major variable of interest in this study, it was held constant despite the fact that subject females sometimes laid before, sometimes after, and sometimes coincident with their stimulus female partners. This meant that the separated females varied somewhat in their endocrine status because of differences in the timing of their egg-laying with respect to the separation schedule. Although the same scatter of laying intervals was observed across conditions, this kind of variation is rather different from that which could occur in males. Therefore, direct comparison with males is not permissible.

GENERAL DISCUSSION

The data from these two experiments confirm the observations of Patel on pigeons (1936) and Friedman & Lehrman on doves (1968), that crop growth and readiness to incubate can be maintained after separation from contact with nest and mate, provided that the incubating mate can be observed. Our experiments extend these observations to include female as well as male doves. Further, we have shown that the ability of doves to use stimuli provided by observing an incubating mate to maintain both crop sac growth and readiness to incubate depends upon their previous reproductive experience. Both male and female reproductively experienced doves may be prevented from incubating from as early as 3 days after the second egg is laid and still maintain normal crop growth and readiness to incubate, provided that they can observe their incubating companion; such observation is not sufficient in male or female doves undergoing their first reproductive cycle.

Previous breeding experience enables doves to secrete prolactin under highly restrictive and otherwise inadequate stimulus conditions. It is conceivable that the previous breeding experience functions simply by allowing associations to be formed and strengthened between stimuli that initially promote prolactin secretion and other stimuli, initially ineffective, provided by an incubating mate. Because incubation, once established, can be maintained by prolactin (Lehrman & Brody 1964), continued stimulation of prolactin secretion after separation can account for both crop sac growth and incubation readiness in these experienced male and female doves. Although it is insensitive to changes in prolactin level at both the lowest and highest levels observed during a cycle, crop weight has been demonstrated to be a good indicator of changes in plasma prolactin over the rest of the normal range in both males and females (Goldsmith et al. 1981; Cheng & Burke 1983). Thus, the changes in crop weight observed in the present study are likely to reflect changes in prolactin secretion.

Reproductively naive males can also maintain both crop growth and readiness to incubate, and naive females can maintain at least readiness to incubate, if they have participated in incubation for three-quarters of the incubation phase of the cycle. Thus, progress through the incubation phase of the cycle provides at least some of the experience that allows for observation-maintained prolactin secretion. This is consistent with the idea that experience in this instance consists of the opportunity to form and strengthen associations between various stimuli that can promote prolactin secretion. The intra- and intercycle experiential effects observed by comparing

3DN doves with SDN and 3DE doves may be equivalent. Thus, it is conceivable that the processes that promote observation-maintained prolactin secretion during an initial cycle may be the same as those that operate across cycles (see Moore 1976a).

The experience obtained within a breeding cycle apparently enables ring doves to use a wider range of relevant stimuli to maintain both crop growth and incubation behaviour. This process may enable the two parents to coordinate more effectively with one another and may permit both parents to adjust to the changed stimulus situation when young appear in the nest at hatching. The experience provided by the progression of a breeding cycle does contribute to the successful transition from incubation to brooding (Moore 1976a, b). The increased range of effective stimuli in experienced doves also produces some redundancy in the stimulus support of parental condition, which may contribute to successful hatching and feeding of young by enabling doves to maintain a parental state under suboptimal natural conditions where the regular daily pattern of incubation may be disrupted. Finally, the fact that these experiential effects carry over between cycles may contribute to the increased efficiency and greater reproductive success that have been reported in previously experienced doves (Lehrman & Wortis 1967; Michel, in press).

Males and females were similar in their general pattern of response. Both could use mate-provided stimuli to maintain crop growth and incubation readiness, both required more than 3 days' experience with incubation before these stimuli were effective during an initial breeding cycle, and both could make use of experience from a previous breeding cycle to reinstate the effectiveness of mate-provided stimuli within the first 3 days of incubation during a subsequent cycle. It is not possible to tell whether the crops of females in experiment 2 were lighter than those of males in experiment 1 as a result of procedural differences or as a result of a sex difference in the relative importance of the different stimuli that promote prolactin production. Sex differences in crop weight have not typically been reported (see Buntin 1977; Buntin et al. 1977). In addition to being paired with a same-sex partner and having a more variable internal state at separation because of their egg-laying schedule, the females incubated infertile eggs. There is evidence that doves can sense when the eggs are infertile and that this raises luteinizing hormone levels causing them to begin to recycle 2-3 weeks after laying (Cheng 1977). Therefore, while incubating in this study, the females may have had a rather different hormonal condition than if they had laid fertile eggs. Thus, the relative importance of incubation-related tactile and other stimuli for males and females remains an open question for future work.

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