

MATE FAMILIARITY AND THE REPRODUCTIVE BEHAVIOR OF RINGED TURTLE DOVES

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PAIR bond establishment in birds may be manifested through a variety of behavior patterns. Typically there is a tendency to remain in close proximity to a single individual while avoiding others. Often reproductive and protective behavior are restricted to that individual; aggressive behavior is usually directed only toward other conspecifics. Other behavioral adjustments may be an expression of pair formation as well. A previous study of Ringed Turtle Doves (*Streptopelia risoria*) (Erickson and Morris 1972) demonstrated that performance levels of two principal behavior patterns, bow-cooing, and nest soliciting, differed according to whether the male was displaying to an unfamiliar female or to a former mate. The functional significance of these behavior patterns is not positively known, but it was suggested that bow-cooing is effective in achieving reproductive isolation, and nest soliciting is important in establishing the pair at the nest site. It was found that much more bow-cooing was exhibited in the presence of unfamiliar females, while slightly more nest soliciting was displayed to former mates. Other investigators have reported such modifications in display and vocalization among mated pairs. Stettner et al. (1966) and Stettner et al. (1971) found more frequent aggression toward nonmates and greater frequency of copulation with mates in Bobwhite Quail (*Colinus virginianus*). Mundinger (1970) discovered that paired male and female cardueline finches modify their calls to resemble one another. He found changes of this sort even in mixed-species pairs where Pine Siskin (*Spinus pinus*) males were paired with European Siskin (*Carduelis spinus*) females. Perhaps most dramatic are the antiphonal duets that develop among pairs of several avian species. Such duets may be either very simple and occasional as occurs in the "hit-tuck" of the White-breasted Nuthatch (*Sitta carolinensis*) (Kilham 1972) or as elaborate and extended as the flutelike, multiphrased expositions of the African bou-bou shrieks (Thorpe and North 1965).

Although it is clear that pair formation may be reflected in modifications of social interaction with both mate and nonmate, as yet few investigators have systematically attempted to trace the development of such behavioral modifications. The present study was designed to follow the divergence in performance when animals are exposed to familiar and unfamiliar animals.

EXPERIMENT I

MATERIAL AND METHODS

Animals.—The subjects of the initial study were eight male and eight female adult Ringed Turtle Doves hatched in the laboratory. This species is also commonly known as the Ring Dove and Barbary Dove.

Housing in the colony.—Breeding cages were of wood and measured 32 inches wide, 18 inches deep, and 14 inches high, equipped with food and water dispensers, a glass nest bowl, and a supply of pine needles as nest-building material. Stock cages were 35-inch cubical units with wooden frames and mesh sides. Individual chambers for visual isolation were formed by placing an opaque partition in a breeding cage thus dividing it into 16 × 18 × 14-inch compartments. Clock-controlled illumination of the cages was from 08:00 to 22:00. Food and water were available ad libitum.

Experience of animals prior to testing.—All birds remained with their parents for 3 weeks after hatching. They were then banded for identification and transferred to a stock cage with 8 to 10 other squabs of similar age and remained there until 5 months of age. At 5 months their sex was determined by laparotomy, and they were paired for breeding. After completing at least one, but not more than two reproductive cycles, all birds were placed in visual isolation in the same large colony room for 4 weeks. Only doves that had successfully raised at least one squab in their prior reproductive cycles were used. Although some of the doves had shared a stock cage as juveniles, none had been housed together as adults prior to the study.

Procedure.—On the day of introduction four males were taken from isolation and placed into individual cages; a female was placed in the cage of each male, and the birds were then allowed to remain together as breeding pairs for 43 days. During this breeding cycle all pairs successfully produced and raised at least one squab. All birds were given their first test observation 2 to 4 hours after introduction. Subsequent observations were made on alternate days through day 13 and then again on alternate days from day 29 through day 43 of the reproductive cycle. These test observations were usually given between 10:00 and 13:00. They were omitted during the interval from day 13 to day 29 to avoid disruption of the nest immediately before and after hatching. On test days each male and female was observed twice. One test consisted of removing the bird from the home breeding cage and placing it in a neutral cage with its own mate for 15 minutes; in a second test of equal duration the bird was taken from the home breeding cage and observed with a bird of opposite sex taken from one of the other three pairs (nonmate). Thus on each test day all birds were exposed in neutral cages to their own mates as well as to the mates of other birds. The first egg appeared 5 to 9 days after the commencement of breeding; but except for this 4-day range of maximum variation, birds were in approximately the same stage of the reproductive cycle at the same time. On any given test day half of the birds were exposed to their own mate first, and half of them were exposed to the nonmate first. On successive test days birds were alternately given first exposure to their own mate, a nonmate, their own mate, a nonmate, etc.

At the end of the 43-day breeding period, all birds were returned to individual visual isolation for 28 days. At the end of this isolation period the animals were again returned to breeding cages for mating and testing precisely as before.

The entire procedure was carried out with two subgroups of animals, four

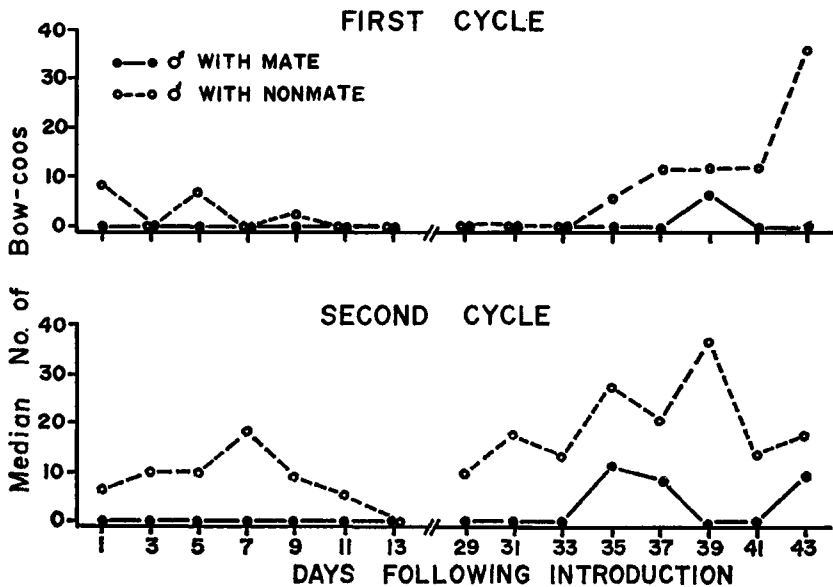


Figure 1. Frequency of bow-cooing by males.

males and four females in each subgroup. Both subgroups were treated equally and are combined for purposes of data analysis.

Observations.—The neutral test cage contained an opaque partition dividing it into two equal halves. The male was introduced on one side of the partition and the female on the other. After allowing several minutes for the animals to become accustomed to the cage, the partition was removed. During the 15-minute observation periods the following behavior patterns were recorded as discrete events: a) bow-coos, b) nest-coos of the male, (i.e. one of the two measures of nest soliciting), and c) copulations. In addition, the presence or absence of the following behavior patterns was noted in each of the 1-minute intervals of the observation period: d) chasing of the mate by male or female, e) aggressive pecking or wingslapping by male or female, f) handling of nest material by male or female, g) wingflipping by male or female (i.e. a second measure of nest soliciting), h) allopreening performed by male or female, and j) billing. (More detailed descriptions of these behavior patterns are reported in Miller and Miller 1958.)

All but a very few of the observations in this experiment were made by an observer who did not know the identities or pairing relationships of the birds being watched. Sexes were identified by green adhesive tape placed over the leg bands of females and yellow tape placed over those of males. An assistant transferred the birds from the breeding cages to the test cages in a sequence unknown to the observer.

Statistics.—The Wilcoxon matched-pairs signed-ranks test was applied in all comparisons (Siegel 1956), as scoring distributions were often highly skewed and performance comparisons were made on the same individuals under varying stimulus conditions. All statistical tests were two-tailed. Because of the skewed distributions, medians rather than means are presented as averages (Guilford 1956).

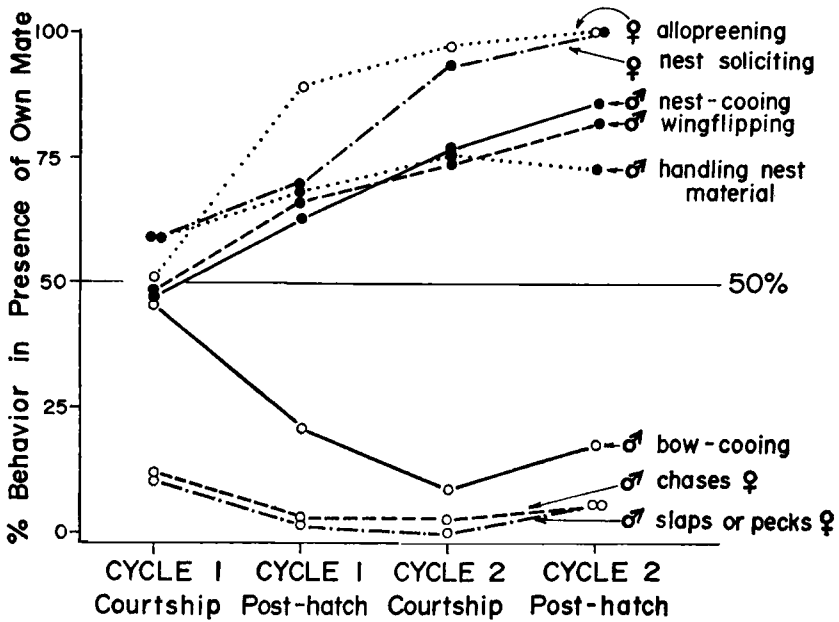


Figure 2. Percentage of each activity that animals performed with their own mates when tested in neutral cages.

RESULTS

Bow-cooing.—Without exception, all males exhibited less bow-cooing with mates than nonmates. This was true in both the first ($P < 0.01$) and second ($P < 0.01$) mating cycles. In fact for six of the eight animals in the first cycle and in all of the animals in the second, bow-cooing levels were more than twice as high for the nonmate as for the mate. It is apparent from Figure 1, which traces the changes in performance level, that bow-cooing is consistently higher in the presence of nonmates. Figure 1 also suggests that the difference in performance to mate and nonmate increases as the birds progress through the two cycles.

Figure 2 portrays the proportion of total bow-coos performed to the mate vs. the nonmate. Although in the opening stage of the first cycle the display was oriented about equally to mate and nonmate alike, in subsequent stages bow-cooing was directed primarily to the nonmate. It should be noted that bow-cooing levels varied as the animals proceeded through the reproductive cycle. For example, performance of this display declined during early incubation and rose again during the second week after squab hatching. Particularly interesting is the fact that at the end of both cycles bow-cooing markedly increased for the mate as well

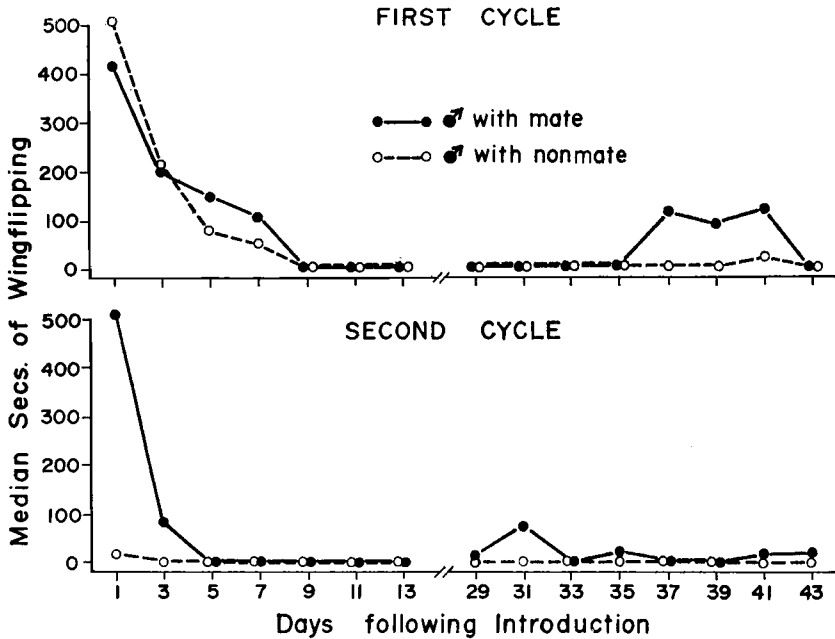


Figure 3. Duration of nest soliciting by the male as indicated by the wing-flipping component.

as the nonmate. Although bow-cooing frequently was accompanied by severe attacks upon the nonmate (see below), bow-cooing to mates often occurred without accompanying aggression, and female mates did not seem frightened or disturbed when bow-cooing occurred.

It is also interesting that bow-cooing to nonmates exhibited a significant increase ($P < 0.05$) from the first cycle to the second. Some males were extremely active during the second cycle, particularly during the post-hatch period. Male NR51, for example, bow-cooed almost continuously throughout the 15-minute observation period on day 31. He emitted 229 bow-coos in this interval. Bow-cooing to mates also increased (albeit not with statistical significance) from one cycle to the next.

Male nest soliciting.—In direct contrast to bow-cooing, more nest soliciting was performed in the presence of mates than nonmates. Both measures of nest soliciting were significant in this regard (nest-cooing, $P < 0.02$; wingflipping, $P < 0.01$). Figure 3 portrays the changes in wingflipping over the two cycles. (Nest-cooing changes are so similar to those of wingflipping that graphic depiction is unnecessary.) As in

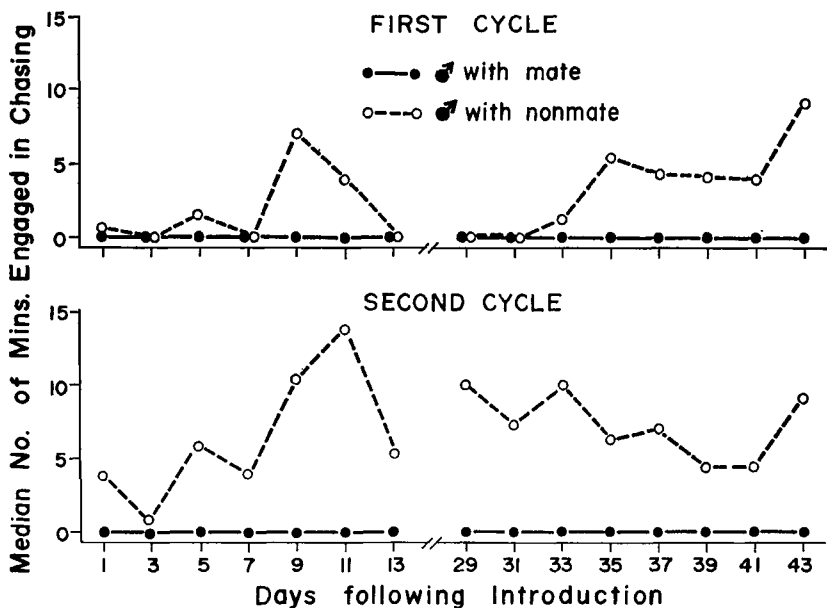


Figure 4. Male chasing of the female as indicated by the number of 1-minute intervals in which the behavior was observed.

the case of bow-cooing these differences increased progressively over the successive stages of the two cycles (see Figure 2). Although male nest soliciting was performed about equally for mate and nonmate alike throughout the early tests of the first cycle, in the comparable phase of the second cycle more nest soliciting was displayed in the presence of the mate, and the difference in wingflipping was statistically significant as early as the first day of this cycle ($P < 0.05$).

Male aggression.—It is common for male Ringed Turtle Doves to be aggressive toward females with which they have been paired, but this aggression usually is not severe and consists mainly of chasing the female and only occasionally pecking at her. Moreover this activity usually subsides rather quickly in the first few hours after introduction, and is much less severe, for instance, than that directed toward other males. In male-male encounters pecking may be frequent, and the animals often slap (box) each other with the wings, a severity of interaction seen only occasionally in mated animals.

Figures 2 and 4 show that males chased the nonmate more than the mate. (Separate statistical tests on the cumulative scores for each stage of each cycle indicate probability values of $P < 0.01$.)

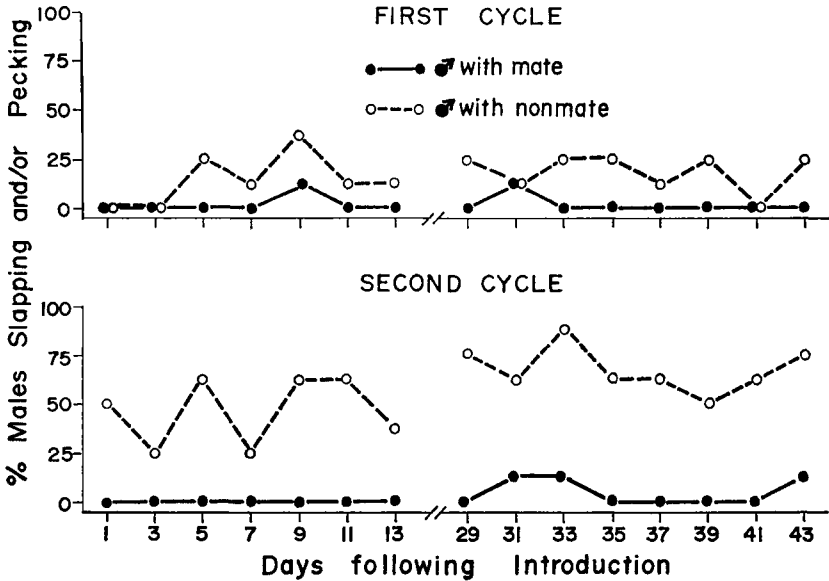


Figure 5. Aggressive slapping and pecking of the female by the male.

Because chasing may be construed as either sexual or aggressive behavior, the more violent activities of wingslapping and aggressive pecking were measured separately. Figure 5 indicates the percentage of animals that engaged in either slapping or pecking throughout the two cycles. During the first cycle only a minority of the animals directed such activities to either stimulus female, but in the second cycle all males exhibited these activities, and (except for one male, see below) they confined such attacks to the nonmate (see Figure 2 as well).

Thus across tests males were more aggressive to nonmates than to mates. Nevertheless there was some variability in the aggressiveness directed to nonmates. One particularly interesting case is that of male G54, who showed no aggression on 4 of the 17 tests, although he was typically aggressive to nonmates at other times. Further examination revealed that in all four cases the same test female (female Y44) was used, and she was exposed to this male at no other time. It appears that either this female had some quality capable of inhibiting the male's aggression or that she so resembled his own mate (female G95) as to be mistaken for her. The probability of the latter being the case was supported by additional analysis of the data. Female Y44 was the mate of male G55. If females Y44 and G95 were very similar to one another, one might expect male G55 to confuse them as well. Male G55 was indeed

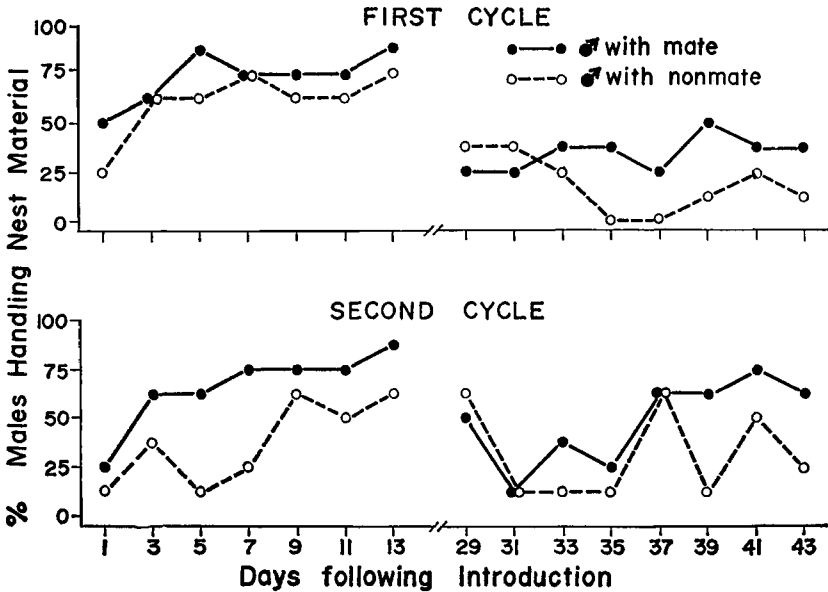


Figure 6. Handling of nest material by the male.

much less aggressive to female G95 than to other nonmate females, and generally treated both her and his own mate, Y44, much alike.

Similar recognition lapses may account for the beatings male NR56 gave his own mate. The male had never been aggressive to his mate until day 31 of the second cycle. On that day he attacked his mate severely, and again on day 35 and day 43. Such isolated incidents may reflect recognition failure in the neutral cage. On many occasions one had the impression that animals performed a "double-take"; that is, when the partition was removed, a male would immediately bristle and begin to charge the female. Frequently, if it was his own mate, he would halt in his tracks and preen or feed. Conversely, several cases were noted where the male ignored the test nonmate for several minutes, then suddenly, as if first recognizing her as a stranger, he charged at her and pecked her head and neck savagely.

Manipulation of nest material by males.—Overall, all males spent more observation time handling nest material in the presence of their mates than in the presence of nonmates ($P = 0.01$). Although this difference increased slightly over the two cycles, the increase was not as marked as for some of the other behavior patterns (see Figure 2). As expected, nest material handling was the highest at those times during the cycle when males would be expected to be building or repairing nests

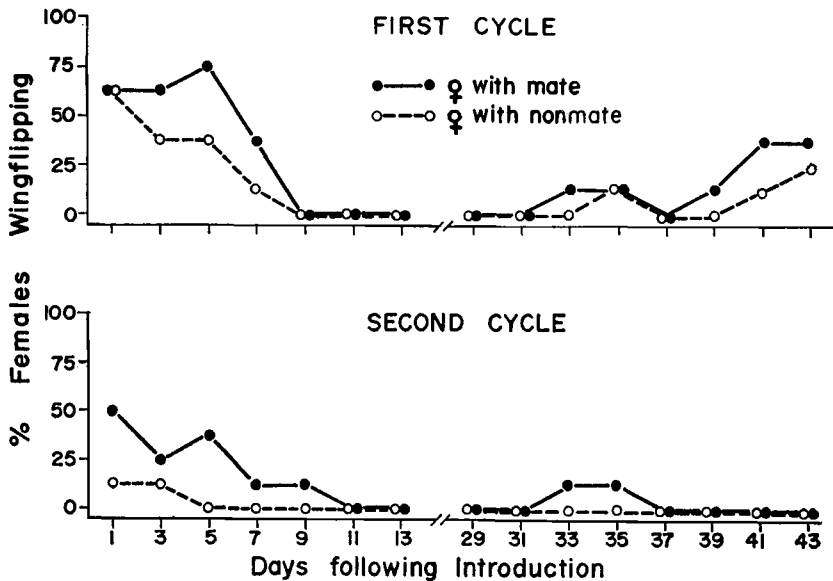


Figure 7. Nest soliciting by the female as indicated by the number of 1-minute intervals in which the wingflipping component was observed.

in their home cages. At other times few males engaged in the activity. Because medians would fail to reflect the low but varying changes in nest material handling, Figure 6 depicts this behavior in terms of the percentage of animals responding.

Female nest soliciting.—Nest soliciting by females was relatively infrequent. Also overall occurrence of this behavior pattern diminished significantly from the first to the second cycle ($P < 0.02$). Figure 7 traces the changes in this activity (as represented by the presence or absence of wingflipping) throughout the two reproductive cycles. Because of its infrequency, the nest soliciting of females is also plotted in terms of the percentage of animals responding. In general more nest soliciting was performed in the presence of familiar males, but differences did not approach statistical significance until the second cycle ($P = 0.05$). Figure 2 shows that the percentage of nest soliciting performed in the presence of the mate increased progressively over the two cycles.

Allopreening by the female.—More allopreening was directed at mates than nonmates ($P = 0.05$), and, in fact, during the post-hatch phase of cycle 2 no nonmate was allopreened. Figure 8 provides a comparison of the percentage of animals that engaged in the activity in each cycle. As was the case for nest soliciting, an increasing proportion of the total

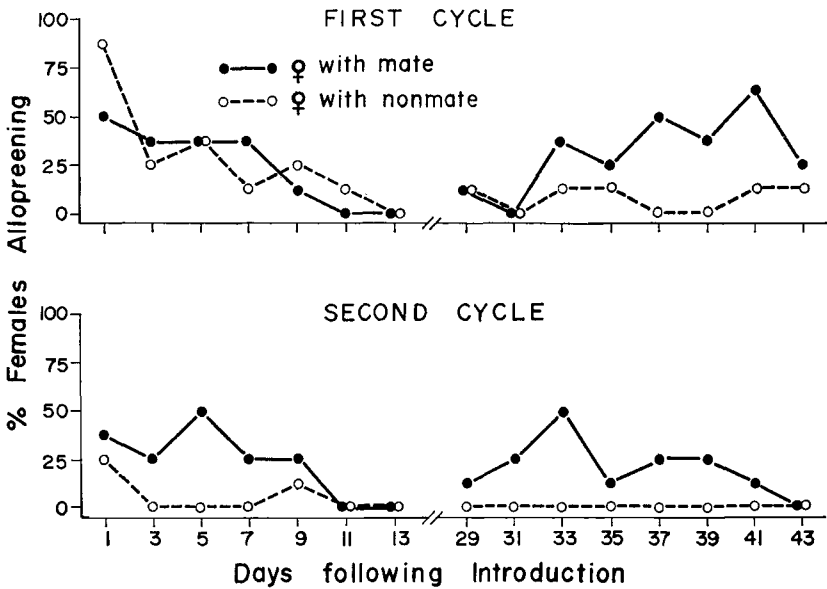


Figure 8. Female allopreening of the male.

allopreening was directed at the mate as testing progressed throughout the two cycles.

Other behavior.—Billing, courtship feeding, and allopreening by the male were too rare to be evaluated meaningfully. Copulation attempts by the male occurred quite frequently, especially with the nonmate. These usually occurred when the female was cornered during aggressive chasing, and she would crouch to avoid the pecking and slapping of the male. The crouch seemed to elicit mounting by the male, and he frequently showed the full copulatory pattern including the terminating “kah” call. On the other hand, the female rarely showed the full response; she did not avert the tail or elicit the typical “kah” call and feather shaking that follow a normal copulation. The copulatory sequence also lacked the billing and courtship feeding which often precedes copulation in mated pairs. These partial copulations were often effective in reducing the male’s activity, especially his aggressiveness, for several minutes afterward.

EXPERIMENT II

Because Experiment I was designed to trace behavioral changes over a long series of tests, and because the pool of nonmates available as test animals was limited in numbers, it was necessary to expose each animal

to the same nonmate as many as five times throughout the test sequence. Thus, as testing progressed, nonmates could have become increasingly familiar with one another. It is possible that such familiarity of nonmates might act to diminish differences in behavior toward mates and nonmates. On the other hand, such repeated exposure to the same animals could allow greater opportunity for learned discriminations to take place, and this could diminish confusion of mate and nonmate. In the latter case behavior distinctions might be enhanced.

This second experiment was performed in part as a replication of the first, but with an alteration to remove the possible confounding influence of repeated testing with the same nonmates. In order to accomplish this, fewer tests were performed in each cycle, but all tests with nonmates were performed with totally unfamiliar animals throughout both cycles.

METHODS

Subjects.—Four males and four females comprised the experimental pairs; 12 females bred in the colony and mated at approximately the same time as the experimental pairs served as stimulus nonmates.

Procedure.—The procedure was similar to that in Experiment I except that experimental males were tested with mates and nonmates only on days 1, 9, 13, 29, 33, and 39 of each cycle. The four experimental females were not tested with nonmates, and thus no replication of prior results is available for females.

RESULTS

Because of the small number of animals involved, no statistical tests were performed. Nonetheless the pattern of results supported the findings of Experiment I. Figure 9 illustrates the differences in male behavior in the presence of mates and nonmates. Medians are based on the summed scores of the three tests of each male at each stage of the cycle. (Sum of days 1, 9, and 13 of the first cycle; sum of days 29, 33, and 39 of the first cycle; sum of days 1, 9, and 13 of the second cycle; sum of days 29, 33, and 39 of the second cycle.)

Aggression toward the males' own mates was low initially and virtually absent after the first day of testing. This was in marked contrast to the behavior directed at nonmates. All males attacked the unfamiliar animals, and in many instances the entire test period was occupied by the male chasing, slapping, and pecking at the test female. A similar pattern emerged with regard to bow-cooing. All four males directed more bow-cooing to nonmates than mates. In fact only one male was observed bow-cooing to his own mate after the initial test on day 1 of cycle 1. This single exception showed a brief bout of this activity on day 33 of cycle 1 and day 1 of cycle 2. On the other hand, three males bow-

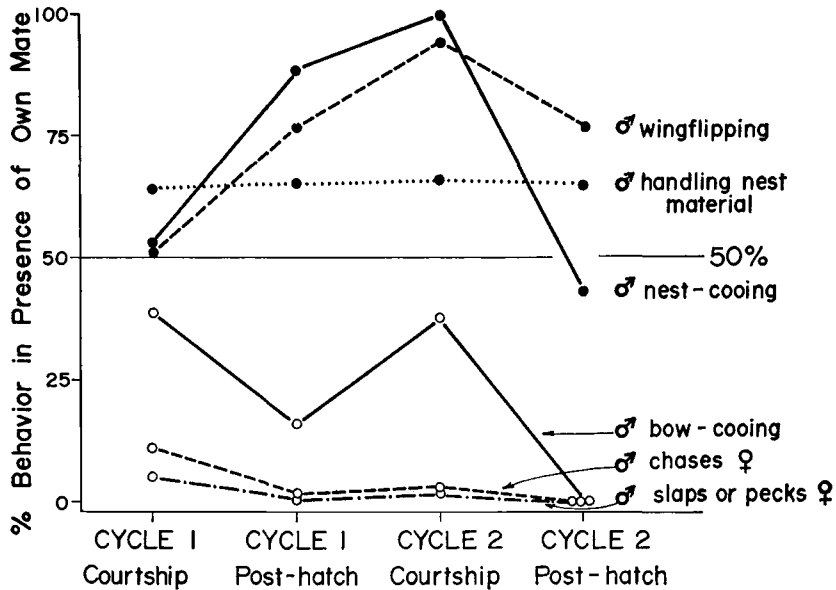


Figure 9. Percentage of each activity that males performed with their own mates when tested in neutral cages.

cooed extensively to nonmates throughout both cycles. The single exception was a male that did nothing but continuously attack any strange female placed in the test cage.

In the preincubation courtship stage of cycle 1 males nest solicited about equally to familiar and unfamiliar females, but in subsequent periods nest soliciting was performed predominantly with the mate. In cycle 2 three of the four males showed a total absence of nest soliciting to nonmates. The exception, male NY10, nest solicited to a nonmate on only one occasion, but on that test he did so almost continuously. This one animal made the sharp reversal in the percentage distributions for wingflipping and nest-cooing in Figure 9. With the exception of this single odd performance, behavior of males in this experiment was very similar to those in Experiment I (compare Figures 2 and 9).

DISCUSSION

The results confirm and extend previous observations in our laboratory. Particularly noteworthy are the differences in aggression that males directed toward mates and nonmates. Even though removed from the presence of their own mate and tested away from their home cage, males were highly aggressive to nonmate females. In several instances

had the tests continued for longer than 15 minutes, these females might have been badly injured. Marked differences in aggression were apparent early in the first cycle and these differences continued to increase subsequently. In contrast, clear differences in bow-cooing emerged only in the post-hatch phase of cycle 1, and nest soliciting differences were not significant until cycle 2. In short, the rate of divergence varied according to the behavior pattern observed, but in general the process was continued through the second cycle.

The functional significance, if any, of quantitative changes in the performance of male Ringed Turtle Doves remains somewhat obscure as the functions of many of the behavior patterns themselves are not clearly known. In a previous report (Erickson and Morris 1972) we suggested that the bow-coo might operate in reproductive isolation. The suggestion is supported by the fact that this behavior pattern is most frequently displayed immediately upon meeting another bird and seems to vary quite sharply from bowing displays in other dove species. We suggested that in previously established pairs, behavior that is instrumental in reproductive isolation is superfluous and possibly disadvantageous and that some mechanism might dampen the bow-cooing display to a mate once pair formation had been accomplished. The present study does not support this hypothesis of a dampening effect. Although we confirmed our previous finding of differences in bow-cooing to familiar and unfamiliar females, the differences were produced, not by a dampening of performance to familiar females, but by an enhancement of bow-cooing in the presence of other females. Actually mates as well showed a slight (but statistically insignificant) increase in bow-cooing from cycle 1 to cycle 2. It is likely that any convincing clarification of the significance of these changes in behavior must await further investigation in the context of field observations.

Many species among the Columbidae are particularly well-known for maintaining fidelity to a single mate (see Morris and Erickson 1971), but various factors are capable of interfering with the maintenance of a pair-bond. Darwin (1874: 467) described Weir's observations of pigeons noting "if a pair which naturally would remain mated for life be separated for a few weeks during the winter, and afterwards matched with other birds, the two, when brought together again, rarely, if ever, recognize each other." In our own laboratory we have shown that after a brief period of isolation from former mates, Ringed Turtle Doves will readily mate with unfamiliar individuals (Erickson and Morris 1972). Craig (1908) noted that pair bonds between Ringed Turtle Doves sometimes dissolved between breeding cycles, and Whitman (1919) observed that although Ringed Turtle Doves usually return to the same mate for each

breeding, females may reject a mate when he has been defeated in a fight. Other reports indicate that in some circumstances male doves and pigeons may readily mate with two or more females simultaneously. Ewers (1942) reports the case of a male Ringed Turtle Dove that mated with two females, participated in the construction of both nests, incubated both sets of eggs, and shared in feeding both sets of young. Ewers cites similar but unpublished observations of Oscar Riddle, and Whitman (1919) quotes Fulton as having observed a male pigeon mated with five females simultaneously.

It has been suggested that lapses of fidelity reported in the above studies are largely artifacts attributable to the birds' confinement. Ewers (1942) concluded that males ordinarily lack the opportunity to take a second mate. In the wild, birds often isolate themselves for nesting. The male spends much of the daytime on the nest, and after the squabs hatch he helps feed them. In an earlier study of pigeons Carpenter (1929) suggested that although the female may remain faithful, the male is ready to mate with other females at any time except for brief periods immediately following copulation. These latter investigators implied that, at least for the male, the maintenance of the pair bond was more a manifestation of various constraints imposed by the demands of breeding than it was an expression of social attachment between the animals. In captivity these constraints were thought to be disrupted and mate fidelity consequently diminished.

Although external constraints may indeed contribute to the preservation of the breeding dyad, quite possibly they are gradually reinforced by developing social attachments; Carpenter (1929) suggested that a "sentiment" develops between members of a pair. In newly formed groups of mixed sexes in captivity no external constraints are available to insulate the dyad prior to pair bond formation. As a result, multiple breeding relationships may occur. If given the opportunity to form social bonds beforehand, confinement in mixed groups may be of little consequence to the pair's fidelity. The present study shows that, with the exception of aggression, mate and nonmates are treated similarly throughout much of the early part of the first cycle, and marked differences in behavior may not emerge until subsequent breeding cycles. It seems not unlikely that other manifestations of social attachment such as resistance to separation and intruder seduction also develop only after a fairly lengthy period of association with one individual.

Undoubtedly the duration of prior association is but one factor among many contributing to the strength of the pair bond. Huxley (1914) emphasized the importance of displays in maintaining mate constancy, and the studies of Adélie Penguins (*Pygoscelis adeliae*) by LeResche

and Sladen (1970) have drawn attention to the age variable. Recently, on the basis of their experiments with Bobwhite Quail, Stettner et al. (1971) have suggested that pair bond strength is a complex product of territory, length of pair bond relationship, and amount and type of exposure to new mates. It is highly probable that Ringed Turtle Dove pair bonds are also the product of many contributing factors.

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SUMMARY

Twelve pairs of Ringed Turtle Doves were mated in laboratory cages and allowed to complete two breeding cycles with the same mate. As these reproductive cycles progressed, the birds were periodically taken from their home cages and observed in neutral cages with either their own mates or other doves of opposite sex. Few differences in responsiveness to mates and nonmates occurred during the early stages of the initial breeding cycle. As association with a mate progressed marked differences in responsiveness developed. Aggressive behavior became intense and was directed almost exclusively to all animals other than the mate. In contrast, nest soliciting displays, nest material handling, and allopreening were increasingly and preferentially performed with the mate. The study suggests that pair formation may be expressed through a broad spectrum of behavioral changes. Some of these changes manifest themselves shortly after introduction to a breeding partner, others may not emerge until the second or subsequent breeding cycles.

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