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Effects of Enclosure Size on Sexual Behavior of Japanese Quail (*Coturnix japonica*)

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The authors determined whether results of experiments on copulatory and affiliative behavior of pairs of Japanese quail (*Coturnix japonica*) conducted in a closely confining apparatus would predict behavior in a large enclosure in which female quail could avoid contact with male quail. As found previously in studies of closely confined quail, in a large enclosure containing numerous barriers, both unmated female quail and mated female quail laying unfertilized eggs were more likely to remain near a confined male quail than were mated female quail laying fertilized eggs. Furthermore, the number of copulations that a pair engaged in when closely confined predicted the number of copulations that they engaged in when they were in the large enclosure. Patterns of affiliation and of mating in a confining laboratory apparatus thus predicted behavior in a larger enclosure that provided female quail with opportunity to avoid contact with male quail.

Keywords: sexual behavior, affiliation, Japanese quail

Results of recent studies of effects of reproductive status on the affiliative behavior of female Japanese quail (*Coturnix japonica*) have found that while female quail are laying fertilized eggs, and are therefore not in need of male gametes, they are less likely to remain near male quail than are either female quail that have copulated but are not laying fertilized eggs or unmated female quail (Persaud & Galef, 2004). However, the relevance of such laboratory findings to the behavior of wild, free-living birds can be questioned on at least two grounds. First, since the 11th or 12th century (Crawford, 1990; Howes, 1964), Japanese quail have been domesticated, maintained first as songbirds by the Japanese court and subsequently for production of meat and eggs. It seems reasonable to suppose that centuries of artificial selection have modified both the physiology and behavior of the Japanese quail. Although the long history of domestication of these birds makes them less than perfect subjects for behavioral studies, the reliability and frequency with which they mate in the laboratory (Domjan, Mahometa, & Mills, 2003) has resulted in their frequent use in laboratory studies of reproductive physiology (e.g., Birkhead & Fletcher, 1994) and mating behavior (e.g., Adkins-Regan, 1995; Domjan et al., 2003). Second, in laboratory experiments, reproductive behaviors may be distorted by confinement of mating pairs in small, barren enclosures that force male and female quail to remain within sight of one another and prevent female quail from avoiding interaction with male quail if they are so motivated.

Despite the presence of a feral population of Japanese quail in Hawaii (Mills, Crawford, Domjan, & Faure, 1997), their preference for dense habitat (Nichols, 1991; Wetherbee, 1961) has precluded direct comparison of behaviors of free-living and domesticated strains. However, successful radio-tracking and trapping studies of the closely related common quail (*Coturnix coturnix*; e.g., Rodriguez-Teijeiro, Puigerver, Gallego, Cordero, & Parkin, 2003) suggest much could be done to describe behavior of *Coturnix japonica* in natural circumstances.

In the two experiments reported here, we observed pairs of Japanese quail in a large room that provided female quail with places of concealment. Comparison of affiliative and copulatory behaviors of subjects in such an enclosure with that of subjects observed in more confining standard laboratory apparatus provided an opportunity to begin to assess the generality of previous results obtained in restrictive laboratory environments.

Experiment 1

When we tested female quail in a laboratory apparatus confining them within 50 cm of an unfamiliar conspecific male quail, both unmated and mated female quail laying unfertilized eggs spent more time near the male quail than did female quail laying fertilized eggs (Persaud & Galef, 2004). In the present experiment, we again examined effects of fertilization on female quail's tendency to affiliate with male quail. However, here we observed female quail's behavior in a large enclosure that both allowed female quail to remove themselves from visual contact with male quail and provided them with cover. Our goal was to determine whether results obtained in a confining apparatus generalized to a more natural situation.

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Method

Subjects

Fifty-nine sexually experienced male and female Japanese quail (*Coturnix japonica*) obtained from Croquail Farms (Vineland, Ontario, Canada) participated in the experiment. We transported subjects to the vivarium of the McMaster University's Department of Psychology (Hamilton, Ontario, Canada) and placed them in individual commercial, quail-breeding cages (Berry Hill Ltd., St. Thomas, Ontario, Canada), measuring 51 cm × 25.5 cm × 22.5 cm. All subjects had ad libitum access to Mazuri Pheasant Starter (PMI Feeds, St. Louis, MO) and water, and they lived in a temperature- and humidity-controlled colony room that was illuminated for 16 hr per day.

Apparatus

We tested subjects in a room (2.8 m × 3.0 m) that contained 32 L-shaped, painted wooden barriers, 30 cm high and 32 cm on a side, which we used to create a maze-like environment through which a female subject could move freely. Each male subject was restrained in a transparent Plexiglas holding cage, measuring 25 cm × 25 cm × 50 cm, placed in the center of the maze (see Figure 1).

Absorbent paper toweling (Tray Liners, Lilo Products, Hamilton, Ontario, Canada) covered the floor of the experimental room, and black electricians tape delineated an area—measuring 80 cm × 100 cm—that was centered on the Plexiglas holding cage and within which a free-moving female and confined male quail could see one another. Two closed-circuit television cameras and associated videocassette recorders permitted us to observe subjects anywhere in the room and to score their behavior without disturbing them.

Procedure

Pretreatment. To ensure that the reproductive condition of all female quail was identical at the start of the experiment, we removed each female quail from contact with male quail for 14 days before the start of the experiment, thus emptying her sperm-storage tubules of any viable sperm (Birkhead & Moller, 1992).

Habituation. To ensure that female subjects moved about the experimental room during testing, we habituated them for 3 days before testing them. During habituation, we placed two female quail in the maze with an empty Plexiglas holding cage in the center of the room and left the female quail undisturbed for 3 hr.

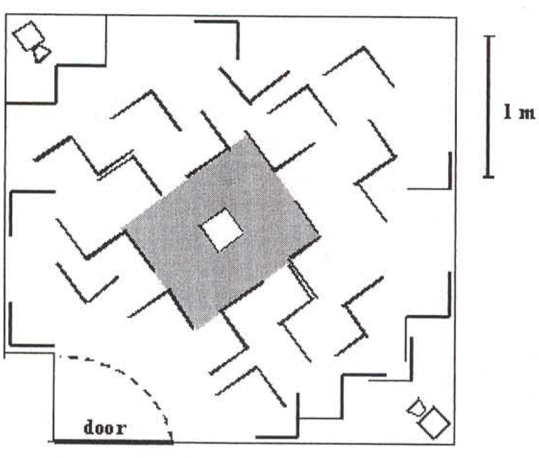

Figure 1. Overhead schematic of the test room indicating the holding cage for male quail and the 80 cm × 100 cm area in which female quail were considered to be near the male quail in Experiment 1.

Mating. The day after we finished habituating a female quail, we randomly assigned her to one of two groups whose members we either mated (n = 42) or did not mate (n = 17) with sexually experienced male quail. We placed a female quail to be mated together with a male quail in an enclosure that was 46 cm × 65 cm in area, and we left the pair undisturbed for 10 min while we observed via closed-circuit television to ensure that each female quail assigned to the mated group participated in at least one successful copulation. Female quail assigned to the unmated condition remained in their home cages.

Determining fertilization. For 5 days after a female quail mated, we collected all eggs that she laid (~1 per day), and for 5 days, we incubated the eggs at 37.5 °C in an incubator that rotated them once every 2 hr (Hova-Bator Model, 2362N, G.Q.J. Manufacturing, Savannah, GA). We then opened and inspected each egg to determine whether it had been fertilized. Mated female quail laid three to four (n = 23) or no (n = 19) fertilized eggs. In previous studies, we have found nearly perfect interobserver agreement as to whether an egg was fertilized (99 cases of 100), and because in the present experiment the examiner of the eggs did not know how the subject that had laid an egg had behaved in the test of affiliative preference, and could not inadvertently bias the results, we did not determine interobserver reliabilities.

Affiliation testing. Two days after mating (or not mating), an observer, unaware of group assignment of individual female quail, tested each female quail to determine her tendency to remain near a conspecific male quail. To begin an affiliation test, we placed a male quail (other than the male quail with which a female quail had mated) in the transparent holding cage and a female quail in the maze adjacent to the holding cage. We then waited 2 min to let the pair settle down. For the immediately following 10 min, we recorded the time that the female quail spent inside the marked area surrounding the holding cage containing the male quail.

Data analysis. Heterogeneity of variance made parametric statistics inappropriate.

Results and Discussion

We did not determine the reliability of the sole observer to score the time that individual female quail spent within the marked area surrounding the male quail because she did not know the experimental condition to which individuals had been assigned and, consequently, could not inadvertently bias the results.

As can be seen in Figure 2, the reproductive state of female quail had a significant effect on the time that they spent in the marked area surrounding the holding cage that contained the male quail (Kruskal–Wallis one-way analysis of variance, H = 8.44, $p < .02$), with fertilized female quail spending significantly less time in the area immediately surrounding the confined male quail than either unfertilized female quail (Mann–Whitney U test), $U(23, 19) = 128$, $p < .02$, or unmated female quail, $U(23, 17) = 108$, $p < .02$. Furthermore, on the assumption that a female quail was equally likely to spend time in all portions of the experimental room, mated female quail laying fertilized eggs spent significantly less time than would be expected by chance (57 s) in the marked area surrounding the holding cage (Fisher's Exact Test, $p < .01$), whereas neither mated female quail laying unfertilized eggs (p = .49) nor unmated female quail (p = 1.00) did so, suggesting that fertilized female quail avoided male quail, but unfertilized and unmated female quail did not. Results of the present experi-

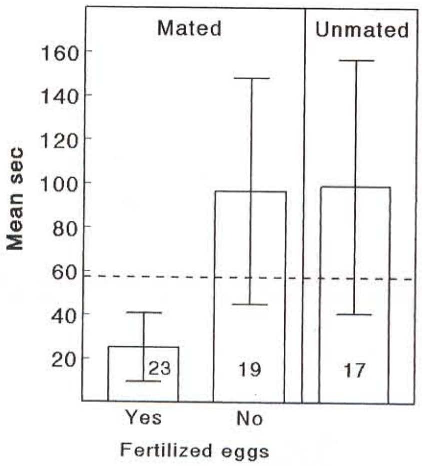

Figure 2. Mean number of seconds that unmated female and mated female quail laying either fertilized or unfertilized eggs in Experiment 1 spent in the 80 cm × 100 cm area surrounding a confined male quail. Bars = 95% confidence intervals. Numbers within histograms = number of female quail per group. Dotted line = number of seconds that female quail would be expected to spend in the 80 cm × 100 cm area surrounding the restrained male quail on the assumption that female quail were equally likely to spend time in all areas of the enclosure.

ment, conducted in an enclosure permitting female quail to avoid visual contact with male quail, precisely parallel those of Persaud and Galef (2004). Fertilized female quail avoided male quail; unfertilized female quail and unmated female quail did not.

Experiment 2

While carrying out experiments in which mature male and female quail interacted in close confinement, we were struck by the variability in quail copulatory behavior. In 10 min, male quail in some pairs mounted partners 20 times or more and achieved cloacal contact 6 or 7 times. Others mounted their partners only once.

Such individual differences in courtship and mating behaviors provided another opportunity to examine the relationship behavior in subjects confined in small and large enclosures. In the first study, we measured consistency in the number of attempted and successful copulations in pairs of quail mated twice in a confined space. In the second study, we looked for consistency in the frequency of copulatory behavior of pairs of quail observed first in a confined space, then in a large enclosure.

Method

Subjects

Thirty pairs of sexually experienced quail participated in the experiment, 14 in Study 1 and 16 in Study 2. We conducted Study 2 immediately after Study 1.

Apparatus

We used both the large enclosure used in Experiment 1 and a small mating enclosure constructed of Plexiglas, which was 58 cm × 65 cm in area. A Plexiglas holding cage, identical to that placed in the center of the large cage, was located in the middle of the mating enclosure.

Data Collected

We did not attempt to quantify details of the behavior of the quail (e.g., Adkins-Regan, 1995) because the relatively poor quality of the video images of quail moving about a large room made detailed observation of behavior unreliable. We focused on the most biologically relevant and easily quantified behaviors, the frequencies with which male quail mounted female quail and succeeded in achieving cloacal contact with them.

Procedure

Test 1. The first test of subjects assigned to Studies 1 and 2 was identical. We (a) placed the male member of a pair in the Plexiglas holding cage in the small mating enclosure and a female quail outside the holding cage, (b) waited 2 min for the pair to settle down, (c) raised the holding cage to release the male quail, and (d) left the pair undisturbed for 10 min. Two observers independently scored videotapes of each mating pair, determining the number of both attempted and successful copulations during the 10-min mating period. We identified successful copulations by the distinct pause that occurs while sperm transfer takes place following mounting of a female quail by a male quail (Mills et al., 1997). An attempted copulation was identical to a successful copulation except that no pause in male activity during which sperm transfer may have occurred was discerned (Persaud & Galef, 2005).

Test 2. The first and second tests of subjects assigned to Study 1 were identical. The second test of subjects assigned to Study 2 was the same as that of subjects assigned to Study 1 except that we carried out Test 2 for subjects assigned to Study 2 in the large enclosure used in Experiment 1.

We first placed a male quail in the holding cage in the middle of the maze, then placed the female quail adjacent to the holding cage, waited 2 min, entered the room, and removed the holding cage. We determined whether the female quail was in sight of the male quail when we removed the holding cage and videotaped the mating behavior of the members of each pair for 10 min for subsequent scoring by two independent observers.

Results and Discussion

In Study 1, interobserver reliabilities were excellent for successful copulations (linear correlation), $r(28) = .95$, $p < .0001$; attempted copulations, $r(28) = .94$, $p < .0001$; and total number of copulations, $r(28) = .96$, $p < .0001$. Interobserver reliabilities for successful copulations in the second test of Study 2 were lower. The quality of video images recorded in the larger room was relatively poor, and it was more difficult to distinguish successful from attempted copulations: successful, $r(16) = .73$, $p < .002$; attempted, $r(16) = .82$, $p < .001$; and total copulations, $r(16) = .77$, $p < .001$. Data analyses reported below are based on scoring by the first of the two observers of each tape.

Study 1

The total of attempted and unsuccessful copulations engaged in by pairs of subjects in Test 1 predicted the number that they engaged in Test 2 (linear correlation), $r(14) = .65$, $p < .02$ (see Figure 3). If one excludes the outlier (see Figure 3), $r(13)$ rises to $.81$, $p < .001$. Similarly, the number of attempted copulations that a pair engaged in during Tests 1 and 2 were significantly

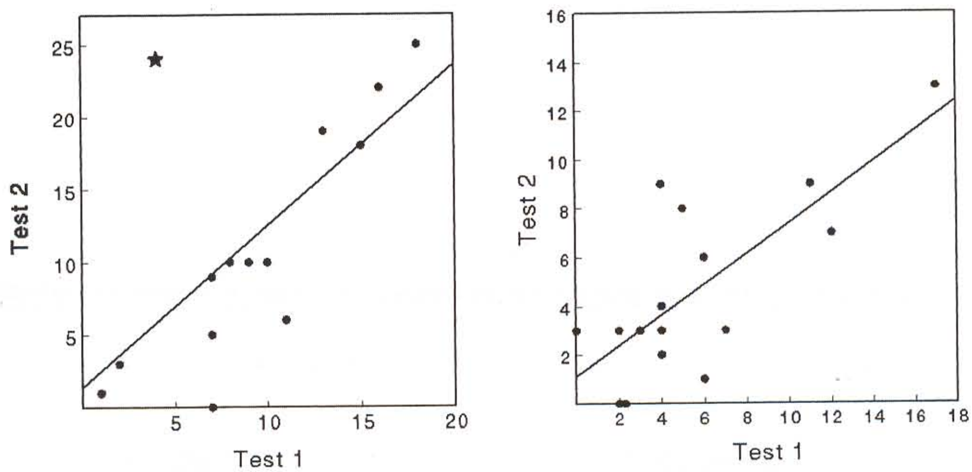

Figure 3. Total number of unsuccessful and successful copulations in which pairs of quail engaged during Test 1 and Test 2. Study 1 is shown in the left-hand panel, and Study 2 is shown in the right-hand panel. The star represents the outlying data point in Study 1.

correlated, $r(14) = .62$, $p < .02$, as were the number of successful copulations, $r(14) = .58$, $p < .04$.

Study 2

Consistent with the hypothesis that female quail tend to avoid conspecific male quail (Persaud & Galef, 2004), not 1 of the 16 female quail in Study 2 was within sight of the male quail when we removed the holding cage, and after male quail were released from the holding cage, they had to seek out female quail and pursue them before mating. Consequently, male quail took longer to make first physical contact with female quail in the maze ($M \pm SEM = 2.3 \pm 2.4$ min) than in the mating apparatus (12.5 ± 6.1 s), although the mean number of attempted and successful copulations occurring in 10 min was only slightly greater in the mating apparatus (6.2 ± 1.3) than in the maze (4.9 ± 0.9).

As in Study 1, the total numbers of successful and unsuccessful copulations that a pair of subjects engaged in during Test 1 and Test 2 were significantly correlated, $r(16) = .77$, $p < .001$—an r value intermediate between those found in Study 1 when the outlier was and was not included in calculations. Also, as in Study 1, correlations between the numbers of successful, $r(16) = .73$, $p < .002$, copulations observed in Tests 1 and 2 were significant. However, in Study 2, the number of unsuccessful copulations in Tests 1 and 2, although positively correlated, did not reach the conventional level of significance, $r(16) = .57$, *ns*. Possibly, the number of successful copulations in which a pair engages during a 10-min test is largely determined by the potency of the male member of the pair and is relatively constant from one situation to another, whereas the number of attempted copulations needed by a male quail to achieve his quota of ejaculations is influenced by female resistance, the effectiveness of which varies from one situation to another.

Observation of the behavior of quail mating in the large enclosure, where female quail could avoid male quail, also suggests that much of the mating behavior of male quail that appears arbitrary and unnecessarily harmful to female quail when observed in a small enclosure is, in fact, instrumental in male quail securing copulations. Feather pulling, head pecking, and dragging of female quail by male quail all appeared to prevent female quail from fleeing when male quail encountered female quail in conditions in which flight was possible.

General Discussion

The results of the present pair of studies suggest that results of laboratory investigations of mating behavior in Japanese quail may have considerable generality beyond the confined conditions in which such laboratory work is usually conducted. The results are consistent with Adkins-Regan's (1995) report of similar reproductive behavior in Japanese quail observed in 0.02-m^3 and 2.00-m^3 barren cages and with Witte and Ryan's (2002) demonstration that the mate-choice copying observed in female sailfin mollies (*Poecilia latipinna*) in confined laboratory conditions also occurs in the wild. The present results thus increase the confidence with which laboratory data providing evidence of effects on mating behavior may be extrapolated to field situations.

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