

Female Japanese Quail (*Coturnix japonica*) Mated With Males That Harassed Them Are Unlikely to Lay Fertilized Eggs

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Results of previous studies of courtship and mating in Japanese quail (*Coturnix japonica*) suggest that females avoid conspecific males because, while courting and mating, males engage in behaviors that are potentially injurious to females. However, prior experiments provided no direct evidence that females avoided harassing males. Here the authors show that a female quail choosing between a previous sex partner and an unfamiliar male avoids the former if he engaged in relatively many potentially injurious acts while courting and mating, (Experiments 1 and 2) and that males behaving aggressively toward mates are less likely than are gentler males to fertilize the females' eggs (Experiment 3). Male sexual harassment appears to be a tactic both aversive to female quail and relatively ineffective in fertilizing them.

Japanese quail (*Coturnix japonica*), the subject species in the experiments reported here, have been domesticated for centuries (Mills, Crawford, Domjan, & Faure, 1997). Consequently, little information is available concerning the behavior of their wild forebears in the concealing habitat that they prefer (Wetherbee, 1961).

Perhaps because of the difficulty observing free-living Japanese quail, descriptions of their mating system are inconsistent. Some describe Japanese quail as socially monogamous, though with frequent mate switching (Nichols, 1991). Others describe them as polygamous (Domjan & Hall, 1986), as are some closely related quail species (Rodríguez-Teijeiro, Puigcerver, Gallego, Cordero, & Parkin, 2003).

Despite the paucity of information concerning the natural history of Japanese quail, they are useful subjects for laboratory studies of sexual behavior and mate choice. In captivity, Japanese quail mate reliably and the stereotypic behaviors of males during courtship and mating are easy to categorize (Bateson, 1982; Gutierrez & Domjan, 1997; Hagelin & Ligon, 2001; Ruscio & Adkins-Regan, 2003). A male quail attempting to mate chases and pecks at a female, seizes feathers at the back of her head in his beak, and often drags her around by her head feathers before pinning her down, jumping onto her back, and pulling her head backward while attempting to achieve cloacal contact (Mills et al., 1997).

Courtship and mating of Japanese quail appear to a human observer to be both potentially physically harmful to females (Persaud & Galef, 2004) and coercive (Adkins-Regan, 1995). Consequently, we see the experiments presented here as relevant to studies of sexual coercion in general, and in particular, relevant to studies of "harassment," defined by Clutton-Brock and Parker (1995) as involving "repeated attempts to copulate by males [that] have costs to females which induce them to mate immediately" (p. 1345).

Traditionally, sexual selection has been considered to reflect both active mate choice of members of one sex (usually males) by members of the other and competition within a sex (usually between males; Clutton-Brock & Parker, 1995). However, sexually coercive males can force copulations without either winning competitions with other males or being chosen as mates by females (Bro-Jørgensen, 2003; Clutton-Brock & Parker, 1995; Smuts & Smuts, 1993). Because a coerced female is both prevented from mating with males she chooses and may suffer physical harm (McComb & Clutton-Brock, 1994; Linklater, Cameron, Minot, & Stafford, 1999), harassment and coercion by males is costly to females (Censky, 1997; Le Boeuf & Mesnick, 1991; McLain & Pratt, 1999; Schlupp, McKnab, & Ryan, 2001).

That male courtship and copulation can be aversive to female quail can be inferred not only from direct observation of mating behavior (described above) but also from results of experimental studies of the responses of the females to the advances of conspecific males: (a) Female quail more frequently aggregate in the presence than in the absence of a male (Persaud & Galef, 2003), possibly as a selfish-herd defense against sexually harassing males (Deutsch & Nefdt, 1992; Pilastro, Benetton, & Bisazzi, 2003); (b) fertilized females, for whom reproductive benefits of additional matings are relatively low, are more likely to both aggregate in the presence of a male and avoid contact with males than are unfertilized females for whom benefits of further mating are relatively high (Persaud & Galef, 2004); and (c) sexually experienced females that have observed two males interact prefer the less aggressive male of the pair, possibly reflecting the fact that male quail that are relatively aggressive in male-male competitions are

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also more aggressive when courting and mating with conspecific females (Ophir & Galef, 2003).

Although such findings suggest that females attempt to avoid harassment by males, they provide no evidence that females avoid males that are most likely to cause them physical harm. We first examined directly the relationship between a male's harassment of a female during a sexual encounter and her subsequent affiliative response to him (Experiments 1 and 2). Then, we compared the success of relatively coercive and benign males in fertilizing females' eggs (Experiment 3).

Experiment 1: Does Male Sexual Harassment Affect Subsequent Female Mate Choice?

In the present experiment, we first paired a female quail with a randomly selected male and recorded the pair's behavior on videotape while they courted and mated. We then gave each female a choice between the male with whom she had just mated and a randomly selected, unfamiliar, sexually experienced male from our colony. If a female's experience of a male's behavior during courtship and mating influenced her subsequent response to him, then females should have been more likely to avoid males whose courtship and mating were relatively harmful than males whose courtship and mating were relatively benign.

Method

Subjects

We obtained 26 female and 26 male 56-day-old Japanese quail (Pharaoh breed) from a local farm (Cro-quail Farms Inc., Vineland, Ontario) where they are raised for meat and for egg production. At Cro-quail Farms, groups of 5 male and 10 female adults are randomly selected and placed together to breed, so paternity of individuals is not known. The population is not inbred because, once each year, eggs are imported from the Quail Genetic Resource Centre at the University of British Columbia and their issue is used to maintain genetic variability of the population at Cro-quail Farms. Genetic relationships among individuals selected as subjects were not known. However, because subjects were selected haphazardly from a flock of 15,000 individual birds, it is extremely unlikely that subjects were closely related.

After we transported subjects to our laboratory (Hamilton, Ontario), we placed them in individual commercial quail cages (Berry Hill Farms, St. Thomas, Ontario), measuring 55 × 55 × 110 cm, separated by opaque barriers. Cages were housed in a temperature- and humidity-controlled colony room illuminated for 16 hr/day with light onset at 7:00 a.m.

All subjects had ad libitum access to Mazuri Pheasant Starter 5637 (PMI Feeds, St. Louis, Missouri) and water. Twice each week, for environmental enrichment, we provided each bird with a handful of autoclaved hay. When females started to lay one egg/day (at approximately 70 days of age), we considered them to be in breeding condition and ready to use to test males for their sexual maturity. To conduct such a test, we paired a male for 5 min/day for several days in succession with a series of sexually mature females. Pairing took place in alternating end chambers of the experimental apparatus (see Figure 1) and thus served to habituate subjects to the testing environment while establishing that males were mature and ready to participate in the experiment. We considered a male sexually mature 1 week after he had mounted and made cloacal contact with females on 2 successive days.

We randomly assigned subjects to 26 trios, each consisting of one female and two males. Each female served only once in the experiment and each male served twice, first as a "subject" and later as an "unfamiliar" male. No

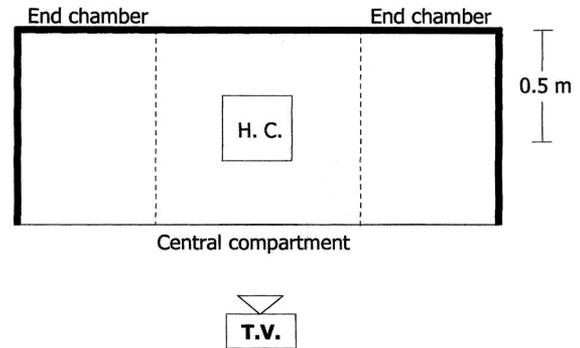


Figure 1. Overhead view of the apparatus. Heavy lines indicate opaque walls, light lines transparent Plexiglas walls, and dashed lines hardware cloth. T.V. = closed-circuit TV. H.C. = holding cage.

two males participated together in more than one trio, and no male participated in two trios on the same day.

Apparatus

We conducted experiments in an enclosure measuring 122 × 61 × 30.5 cm (see Figure 1), constructed of painted plywood and transparent Plexiglas (Altuglas International, Philadelphia, Pennsylvania), that rested on an aluminum tray covered with disposable absorbent paper pads (Tray Liners, Lilo Products, Hamilton, Ontario). Partitions of 1/2-in (1.57-cm) hardware cloth 30.5 cm from each end of the enclosure divided it into two end chambers and a central compartment. To facilitate determination of which end chamber of the apparatus a focal subject was nearer, we drew a line from top to bottom of the Plexiglas front wall of the central compartment at its midpoint.

An opening (25.4 × 25.4 cm) in the center of the Plexiglas roof of the central compartment permitted us to raise or lower a transparent Plexiglas holding cage, measuring 25.2 × 25.2 × 40.6 cm high (see Figure 1), using a rope and pulley system. A color closed-circuit TV video camera (Panasonic WV-CP412), attached to a video recorder (Panasonic AG-1240) and color monitor (Panasonic CT 1331Y), faced the Plexiglas front wall of the enclosure and allowed observation and recording of all behavior in the apparatus.

Procedure

Each trial consisted of two 10-min phases: a mating phase and a choice phase. To begin the mating phase of a trial, we removed the holding cage from the apparatus and placed a female in the central compartment together with the subject male member of that female's trio and recorded their courtship and mating on videotape for later scoring.

At the end of the mating phase, we lowered the holding cage and placed the female inside it. We then removed the subject male from the central compartment, placed him in a randomly selected end chamber of the apparatus, and placed the unfamiliar male member of the female's trio in the other end chamber.

After allowing 1 min for the trio members to settle, we raised the holding cage, thus permitting the female to move about the central compartment. For 10 min after the female took her first step, we determined how much time she spent closer to each end chamber of the apparatus. If a female spent more than 5 min of the choice phase nearer the end chamber containing the subject male, we considered him "preferred." If she spent less than half the choice phase nearer the end chamber containing the subject male, we considered him "nonpreferred."

Behavioral analysis. On completion of both phases of the experiment, an observer, blind to the preferences that females had exhibited during the choice phase, scored the video recording of each 10-min mating phase for frequencies of the first eight male behaviors described in Table 1. As indicated in Table 1, we considered five of these eight behaviors potentially harmful to females.

Statistical analysis. Because the behavioral frequencies were not normally distributed, we used nonparametric Mann-Whitney *U* tests to compare groups (Wekowitz, Ewen & Cohen, 1982).

Presenting data describing all eight of the behaviors scored provides the most complete picture of the interaction of males with females. However, because it is unlikely that the frequencies of occurrence of these behaviors are independent of one another; repeated significance testing of group differences in individual behaviors requires Bonferroni corrections. If such corrections were made, none of the observed differences between groups was statistically significant, although there were obvious differences in the behavior of preferred and nonpreferred subject males during the mating phase. Those concerned about this statistical problem can choose whichever index of potentially harmful behavior (either feather pulling or pecking would have the highest face validity) they prefer and disregard the rest of the data that we have made available. Further, we created a "total aggression score" by simply adding the frequencies of each potentially harmful behavior to one another as an additional indicator of the level of a male's aggressive sexual behavior.

Results and Discussion

During the 10-min choice phase, the 26 females spent a mean \pm SE of 316.8 ± 43.0 sec nearer subject males than unfamiliar males, and 13 of the 26 females preferred the subject male with whom they had previously mated. The 13 subject males that females preferred during the choice phase had performed significantly fewer chases, pecks, feather pulls, and back mounts during the mating phase than had the 13 subject males that females did not prefer during the choice phase (Mann-Whitney *U* tests performed for all four behaviors; *U*s = 43.0, 44.0, 36.5, and 35.0, respectively; $N_1 = N_2 = 13$; *P*s = .03, .04, .01 and .01, respectively; Figure 2). The only behavior that we considered potentially harmful that nonpreferred subject males did not perform significantly

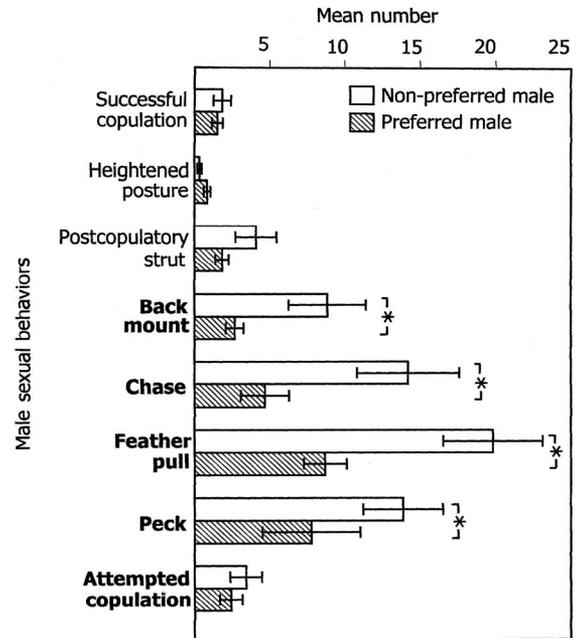


Figure 2. Mean number of times nonpreferred (open bars) and preferred (striped bars) males engaged in five potentially injurious behaviors (bold type) and three noninjurious behaviors during the mating phase of Experiment 1. Error bars = \pm 1 SEM, **p* < .05 (Mann-Whitney *U* tests).

more frequently than preferred subject males during the mating phase was attempted copulation ($U = 75.5$; $N_1 = N_2 = 13$, $p = .64$; Figure 2). The total aggression score for preferred and not preferred males (mean \pm 1 SEM = 24.12 ± 5.11 and 55.39 ± 9.84 , respectively) differed significantly (Mann-Whitney *U* test, $U = 36.5$, $p = .01$).

Subject males that were preferred and not preferred by females during the choice phase did not differ in the frequency with which

Table 1
Descriptions of Scored Male Japanese Quail Behaviors

Behavior ^a	Description	Potentially harmful
1. Heightened posture	Male stands in one spot, with back arched, neck stretched out, and wings spread slightly away from the body.	No
2. Post copulatory strut	Stance is similar to "heightened posture" except male exhibits behavior while walking, usually after a successful copulation.	No
3. Successful copulation	Perched on female's back, male lowers his posterior under hers, and the pair pauses, making cloacal contact.	No
4. Chase/charge	Male rushes toward female, often while she runs away.	Yes
5. Peck	Male makes forceful contact with beak tip on some part of female's body.	Yes
6. Feather pull	Male grasps a female's feathers in beak and tugs.	Yes
7. Back mount	Male restrains female by climbing onto her back, lifting both his feet off the ground, and holding female's head feathers in his beak. No lowering of posterior is observed.	Yes
8. Attempted copulation	Maneuver is similar to back mount except male tries to lower his posterior under female's. No pause indicating cloacal contact is made, often because female dislodges male.	Yes
9. Drag	Maneuver is similar to "feather pull" but occurs while pair is moving. Either male pulls female around by her head/neck feathers, or she runs around while he has her feathers grasped in his beak.	Yes
10. One-foot mount	Attempting to climb onto a female, male succeeds in getting only one foot off the ground and onto female's back before being dislodged.	Yes

^a In Experiment 1, only behaviors 1–8 were scored whereas all 10 behaviors were scored in Experiments 2 and 3.

they exhibited nonaggressive behaviors (heightened posture, postcopulatory strut, and successful copulation; all Mann–Whitney U tests, $U_s = 54.5, 66.5,$ and $84.0,$ respectively; $N_1 = N_2 = 13;$ $P_s = .12, .36,$ and $.98,$ respectively; Figure 2), indicating that the not preferred subject males were not simply generally more active than preferred subject males.

The results of the first experiment are consistent with the hypothesis that females avoid males with whom they have had relatively more distressing sexual contact (Persaud & Galef, 2003, 2004). The design of Experiment 1, however, does not preclude the possibility that males that behaved aggressively during the mating phase also engaged in behaviors that were unattractive to females during the choice phase. If so, females might have chosen males solely on the basis of their behavior during the choice phase and still have provided data consistent with the hypothesis that females avoid males that have harassed them. Unfortunately, we have no way of determining whether male harassment of females during the mating phase or some male trait correlated with such harassment and exhibited during the choice phase caused the pattern of female choice found in Experiment 1. Experiment 2, though not conclusive, does however provide additional evidence suggesting that female quail tend to avoid harassing males.

Experiment 2: Do Reluctant Female Quail Incite Male Harassment?

Although the results of Experiment 1 demonstrate a correlation between the aggressiveness of male quail toward conspecific females and the subsequent affiliative preference of females for males with whom they have interacted, the data are not sufficient to permit the inference that features of males' courtship and mating cause females' subsequent preferences. Possibly, female Japanese quail are more likely to resist advances of males that they dislike, thus provoking rejected males to harass them.

In Experiment 2, we first gave each female a choice between two males. We then paired her with either her preferred or non-preferred male and monitored the behavior of the courting and mating pair. If a female that does not like a male when she first encounters him resists his advances and if resistant females elicit harassment from males, then males paired with females that did not prefer them should engage more frequently in coercive behaviors than males paired with females that did prefer them.

Method

Subjects

Thirty-nine female and 39 male Japanese quail that were obtained, housed, and habituated as described in Method of Experiment 1 served as subjects. We randomly assigned subjects to 39 trios, each consisting of one female and two males. As in Experiment 1, each female served only once, and each male served twice. Again, no two males participated together in more than one trio and no male participated in two trios on the same day.

Apparatus

We used the same experimental apparatus as in Experiment 1 (see Figure 1).

Procedure

As in Experiment 1, the procedure involved two phases, a choice phase and a mating phase. There were, however, three differences between the

procedure of Experiment 1 and that of the present experiment. First, we reversed the order in which we conducted the two phases, completing the choice phase before, rather than after, the mating phase. Second, we randomly determined whether each female was paired with her preferred male ("p.m. condition," $n = 18$) or her nonpreferred male ("N-p.m. condition," $n = 21$). Third, pairing of females with males took place in the end chamber where the randomly selected male with which a female was to be paired had been confined during the choice phase.

After completion of both phases of the experiment, an observer, blind to the experimental condition to which each pair had been assigned, scored video recordings of their courtship and mating for frequency of occurrence of male sexual behaviors (see Table 1). We added two more potentially harmful behaviors (drag and one-foot mount) to the repertoire of male behaviors that we scored after these behaviors were identified by Ophir and Galef (2003) as indices of male aggressiveness toward females. Thus, we tallied 10 behaviors, 7 that we considered potentially harmful and 3 deemed nonaggressive. Again, because behaviors were not normally distributed, we used nonparametric Mann–Whitney U tests to assess differences between groups.

Results and Discussion

As in Experiment 1, males assigned to p.m. and N-p.m. conditions did not differ in the frequency with which they performed nonaggressive behaviors (heightened posture, postcopulatory strut, and successful copulation, all Mann–Whitney U tests, $U_s = 176.5, 159.5,$ and $155.0,$ respectively; $N_1 = 18, N_2 = 21;$ $P_s = .72, .41,$ and $.34,$ respectively; Figure 3). However, unlike Experiment 1, males assigned to p.m. and N-p.m. conditions in the present experiment also did not differ significantly in the frequency with which they exhibited potentially harmful behaviors (pecking, feather pulling, attempted copulation, chasing, back mounting,

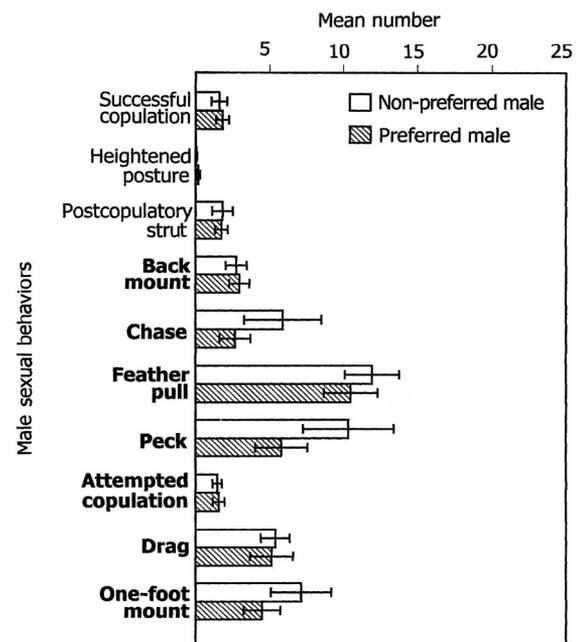


Figure 3. Mean number of times nonpreferred (open bars) and preferred (striped bars) males engaged in seven potentially injurious behaviors (bold type) and three noninjurious behaviors during the mating phase of Experiment 2. Error bars = ± 1 SEM.

one-foot mounting, and dragging, $U_s = 179.5, 173.0, 186.5, 165.0, 174.5, 147.5,$ and $169.5,$ respectively; $N_1 = 18, N_2 = 21;$ $P_s = .79, .65, .94, .50, .68, .24,$ and $.58,$ respectively; Figure 3). The total aggression score for preferred and not preferred males (mean $\pm SEM = 21.60 \pm 4.00$ and $29.80 \pm 6.26,$ respectively) did not differ significantly ($U = 165.5, p = .51$). Failure of males to engage more frequently in potentially harmful behaviors when paired with females that did not prefer them than when paired with females that did prefer them suggests that male sexual harassment is not elicited by female resistance.

Experiment 3: Are Sexually Harassing Males Successful in Fertilizing Females' Eggs?

Taken together, the results of Experiments 1 and 2 indicate that harassment by male Japanese quail is not a reaction of males to reluctant females but is a behavior that males use to secure copulations. However, the results of previous experiments suggest that females avoid harassing males (Experiment 1) and that females are less likely to allow not preferred than preferred males to fertilize their eggs (Persaud & Galef, 2004). Because female quail are less likely to be successfully fertilized by males that they do not like and females do not like males that have harassed them, harassing males should be less likely than relatively benign males to fertilize the eggs of females with whom they interact.

Method

Subjects

Forty-six female and 46 male Japanese quail that were obtained, housed, and habituated as described in Method of Experiment 1 served as subjects. We randomly assigned subjects to 46 pairs, each consisting of one female and one male. Each subject served only once in the experiment.

Apparatus

We used the same experimental apparatus (see Figure 1) as we used in Experiments 1 and 2.

Procedure

Each trial consisted of one 10-min mating phase, conducted as in Experiments 1 and 2. During the mating phase, we placed a female in the central compartment together with a male and recorded their courtship and mating on videotape for later scoring.

Examination of eggs. To determine whether males had been successful in fertilizing the eggs of females with whom they were paired, for 12 days following mating of each female (12 days being the maximum time that female Japanese quail can use sperm stored in their sperm-storage tubules), we collected all the eggs that each female laid (approximately 1 egg/day) and placed them in a humidity-controlled incubator that maintained the eggs at 99 °F and rotated them once every 2 hr (Hova-Bator Incubator, Model 2362N, G.Q.F. Manufacturing; Savannah, Georgia).

After 5 days of incubation, each egg was opened by an experimenter, blind to the nature of the mating experience of the females whose eggs she examined, who determined whether the egg contained a developing embryo, the presence of which indicated that the egg was fertilized (Adkins-Regan, 1995). Each female laid either many fertilized eggs during the 12 days following mating or laid no fertilized eggs at all.

Behavioral analysis. After completion of the experiment, an observer who did not know which females had laid fertilized eggs scored the video

recordings of each pair's courtship and mating for the frequency of occurrence of the 10 male behaviors described in Table 1. As in Experiment 2, we tallied 7 behaviors considered potentially harmful as well as 3 nonaggressive behaviors.

Statistical analysis. Because we had a strong directional prediction (i.e., that males that frequently harassed females would be less likely than relatively benign males to fertilize females' eggs), we used one-tailed tests in analyzing the data. Because of the distributions of data points, we again used nonparametric tests.

Results and Discussion

Eighteen of the 46 females that we paired with males laid fertilized eggs; 28 did not. Females that laid fertilized eggs had experienced significantly fewer pecks, feather pulls, one-foot mounts, and drags than females that did not lay any fertilized eggs (Mann-Whitney U tests, $U_s = 174.0, 172.5, 135.5,$ and $150.5,$ respectively; $N_1 = 18, N_2 = 28;$ $P_s = .04, .04, .004,$ and $.01,$ respectively; Figure 4). Females that laid fertilized eggs did not differ from females that laid no fertilized eggs in the frequency with which their male partner engaged in aggressive chases, back mounts, and attempted copulations ($U_s = 191.5, 207.5,$ and $191.0,$ respectively; $N_1 = 18, N_2 = 28;$ $P_s = .09, .16,$ and $.08,$ respectively; Figure 4). The total aggression score for males successful and unsuccessful at fertilizing females (mean $\pm SEM = 19.61 \pm 2.66$ and $38.18 \pm 5.60,$ respectively) differed significantly ($U = 162.5, p = .04$).

There was also no difference between males who successfully fertilized females' eggs and males who did not successfully fer-

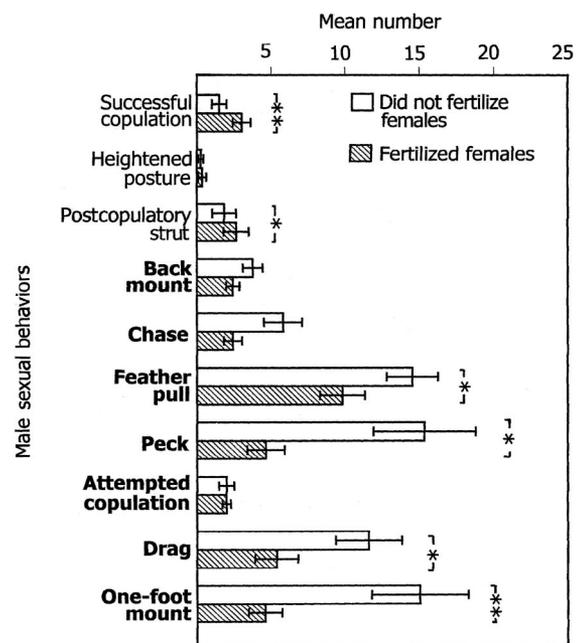


Figure 4. Mean number of times males who fertilized (striped bars) and did not fertilize (open bars) females engaged in seven potentially injurious behaviors (bold type) and three noninjurious behaviors during the mating phase of Experiment 3. Error bars = ± 1 SEM, * $p < .05$, ** $p < .01$ (Mann-Whitney U tests).

tilize females' eggs in their frequency of heightened postures ($U = 246.5$; $N_1 = 18$, $N_2 = 28$; $p = .90$; Figure 4). However, males who fertilized females' eggs engaged in significantly more successful copulations ($U = 130.0$; $N_1 = 18$, $N_2 = 28$; $p < .01$; Figure 4) and postcopulatory struts ($U = 157.0$; $N_1 = 18$, $N_2 = 28$; $p < .02$; Figure 4) than did males that failed to fertilize females' eggs.

In sum, under the experimental conditions imposed, males that frequently engaged in potentially harmful behaviors were relatively unlikely to be reproductively successful. This finding is similar to one reported in zebra finches, *Taeniopygia guttata castanotis*, in which female control of fertilization renders forced extrapair copulations by males less likely to result in offspring than extrapair copulations solicited by females (Burley, Parker, & Lundy, 1996).

General Discussion

Previous studies have shown that fertilized females are more likely than unfertilized females both to aggregate with others of their sex and to move away from males (Persaud & Galef, 2003, 2004). Both these findings suggest that female quail find some aspects of male courtship aversive. The results of Experiment 1 above are consistent with the hypothesis that female Japanese quail tend to avoid males that, in the past, behaved aggressively toward them, and it seems reasonable to propose that the aggressive and potentially harmful nature of male courtship and mating may underlie the aversion toward males exhibited by fertilized females (Persaud & Galef, 2004).

The results of Experiment 2 provide evidence that the frequency with which a male quail behaves aggressively toward a conspecific female is not incited by her rejection of him, as is the case in bearded tits (*Panurus biarmicus*; Hoi, 1997). Rather, in quail, as in cockroaches (*Nauphoeta cinera*; Moore, Gowaty & Moore, 2003; Moore, Gowaty, Wallin, & Moore, 2001), female choice appears to be, at least in part, a response to differences in the potential costs of mating with various males. As in cowbirds (*Molothrus ater*; White, King, & West, 2002), the behavior of courting males appears to determine their attractiveness to females.

The results of Experiment 3 suggest that male harassment is not only aversive to females, it is also relatively ineffective in producing fertilization, indicating that female quail have evolved ways to avoid the consequences of unwanted copulations when they occur. How female quail control fertilization is not completely clear. Domjan, Mahometa, and Mills (2003) reported that success of male Japanese quail in fertilizing conspecific females depends on females remaining immobile during copulation. Adkins-Regan (1995) has also provided data indicating that females can affect fertilization via their receptivity to males' advances. Female quail can eject sperm from their cloacae following insemination (Adkins-Regan, 1995) and have multiple sperm-storage tubules that they can fill to varying degrees with sperm from different copulating males (Birkhead & Møller, 1992, as cited in Eberhard, 1996). Although evidence of selective sperm ejection by females has been found in a number of bird species other than quail (Davies, 1983), whether female Japanese quail selectively eject sperm or differentially allocate storage to the sperm of different males is not known.

Female control of reproduction has been reported in several species that, like Japanese quail (Adkins-Regan, 1995), have

mating systems in which male coercion of females occurs frequently. For example, domestic fowl (*Gallus gallus domesticus*) reduce potential sexual coercion by resisting copulation and distress calling (Pizzari, 2001). Female eastern mosquito fish (*Gambusia holbrooki*) control the occurrence of forced copulation by approaching coercive males only when deprived of mates (Bisazza, Vaccari, & Pilastro, 2001). In fruit flies (*Drosophila pseudoobscura*), female approach to, affiliation with, and solicitation of conspecific males may influence male reproductive success (Gowaty, Steinichen, & Anderson, 2002).

That harassment both reduces a male quail's attractiveness to females and causes females to avoid fertilization by males that have copulated with them raises questions as to why male aggression toward females persists. Perhaps, as Gowaty and Buschhaus (1998) have proposed, the function of "aggressive copulation" by males is not to fertilize a female immediately but to create an environment in which she will cooperate in future copulations. In this model, male sexual coercion, rather than resulting in immediate fertilization, assures males continued access to intimidated females.

It is also possible that studies of sexual behavior in domesticated populations of quail in captive conditions do not reflect their behavior under more natural conditions: One thousand or more years of domestication may have resulted in unnaturally aggressive male quail. Perhaps males only harass females when confined with them in a small space. Obviously, caution is required when extrapolating from domesticated to wild populations and from artificial to natural environments (Wolff, 2003). However, a study of Japanese quail in large enclosures has also reported high levels of male aggression toward females (Otis, 1972), and Nichols (1991) has reported that Japanese quail from a domesticated strain are actually slightly less aggressive than feral Japanese quail that have lived wild on Maui since 1921 (Munro, 1960, as cited in Otis, 1972).

Perhaps, in Japanese quail, as in both Ross's (*Chen rossi*) and lesser snow geese (*Chen caerulescens*), coercion is effective only under specific conditions (Dunn, Afton, Gloutney, & Alisauskas, 1999). Alternatively, given the correlation between the aggressiveness that individual males direct toward conspecific males and conspecific females (Ophir & Galef, 2003), benefits associated with heightened male aggression during male-male competition may offset any cost of aggressiveness during contact with members of the opposite sex.

As has been proposed for cockroaches, a species in which a component of male pheromone that makes a male dominant to other males renders dominant males less attractive to females (Moore et al., 2001), male-male competition and female choice in Japanese quail may provide opposing selective forces. Correlation in levels of aggression that individual males exhibit toward conspecific males and females (Ophir & Galef, 2003) may reflect effects of neurological or hormonal substrates that are maintained by success in competition with other males, despite their reducing males' attractiveness to females and success in fertilizing them. In Japanese quail, selecting for increased mating frequency results in increased intermale aggression, suggesting a linkage between the two traits (Bernon & Siegel, 1983; Blohowiak, Zelenka, & Siegel, 1985).

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