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Avoidance of Relatively Aggressive Male Japanese Quail (*Coturnix japonica*) by Sexually Experienced Conspecific Females

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Sexually experienced female Japanese quail (*Coturnix japonica*) that are offered a choice between 2 conspecific males previously observed engaging in an aggressive encounter prefer to affiliate with the less aggressive male. The authors determined whether this apparent preference for less aggressive males results from females approaching less aggressive individuals or avoiding more aggressive individuals. The authors found that females that had seen 2 males fight before choosing, in counterbalanced order, between each of them and a neutral stimulus were indifferent to less aggressive males but avoided more aggressive males. The results are consistent with the view that in species in which male courtship and mating are potentially harmful to females, females keep away from relatively aggressive males in order to avoid the physical punishment that can result from contact with them.

Japanese quail have become an important species in laboratory studies of sexual behavior in general (e.g., Adkins-Regan, 1995; Balthazar, Tlemcani, & Ball, 1996; Domjan, Mahometa, & Mills, 2003) and in studies of the role of social experience in the development of females' mate preferences in particular. Recent studies have shown that the mate choices of female quail are influenced by prior observations of males interacting with either females (for review, see Galef & White, 2000) or other males (Ophir & Galef, 2003) as well as by direct interaction with males (Guitierrez & Domjan, 1997; Ophir & Galef, in press; Persaud & Galef, 2003).

We are concerned with the finding that a sexually experienced female Japanese quail that observes an aggressive interaction between two males and then chooses between them remains closer to the less aggressive of the two males (Ophir & Galef, 2003, in press). In previous experiments examining the affiliative behavior of female quail, Ophir and Galef (in press) offered females a choice between two males, one known to her to be more aggressive than the other. Consequently, the authors could not determine whether the female was choosing to approach the less aggressive or to avoid the more aggressive male.

In general, such ambiguity in interpretation of the motivation underlying a choice between two items can be resolved only by examining separately the response to each item when individuals choose between that item and a neutral situation (Irwin, 1958). In the present study, we determined whether female quail tend to avoid aggressive males or to approach less aggressive males by examining separately the responses of female quail to each member of a pair of males that they had previously observed engaging in an aggressive interaction.

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Experiment 1

In Experiment 1, each female subject first observed a pair of conspecific males engage in an aggressive interaction. She then chose between an empty compartment and a compartment containing first one and then the other member of the pair of males she had just seen engaging in aggressive interaction. If female quail avoid relatively aggressive males, then females should remain closer to an empty compartment than to a compartment containing the more aggressive member of a pair. If, to the contrary, female quail are motivated to remain near less aggressive males, then they should spend the majority of a choice test closer to a compartment containing the relatively less aggressive member of a pair of males than to an empty compartment.

Method

Subjects

We acquired 25 male and 20 female sexually mature Japanese quail (*Coturnix japonica*) from Cro-Quail Poultry Farm (Vineland, Ontario, Canada) to serve as subjects. After we transported the subjects to our laboratory (Hamilton, Ontario, Canada), we placed them in individual commercial quail-breeding cages (Berry Hill, St. Thomas, Ontario, Canada) measuring $55 \times 55 \times 110$ cm. Cage racks were kept in a temperature- and humidity-controlled colony room illuminated on a 16:8 light–dark cycle, with light onset at 0700. All subjects had ad-lib access to water and Mazuri Pheasant Breeder (PMI Feeds, St. Louis, MO).

Experiments began after males were sexually mature. To determine when a male was ready to mate, we waited until he was 70 to 75 days old. Then, each day for 10 min/day for 7 consecutive days we placed him in one end chamber of the apparatus illustrated in Figure 1 together with an unfamiliar, sexually mature female quail. We observed pairs on closed-circuit television, and after a male had mounted and made cloacal contact with females on 2 successive days, we considered him sexually mature. All female subjects had engaged in numerous sexual encounters before the start of the present experiments. After the present experiment was completed, all subjects were kept for use in future studies.

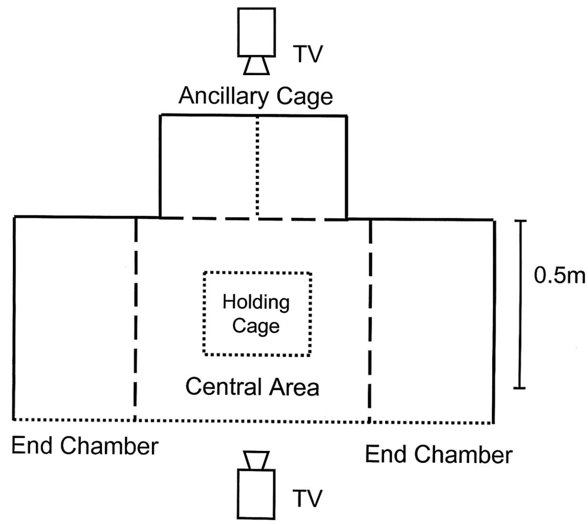

Figure 1. Diagram of the apparatus. The camera viewing the ancillary cage was mounted directly above its midpoint, facing down, and the camera viewing the central area was located at its midpoint and was oriented horizontally. Solid lines = opaque walls; dotted lines = transparent Plexiglas; dashed lines = wire mesh.

Apparatus

We performed the experiment in the apparatus, consisting of a main enclosure and ancillary cage, described in detail in Ophir and Galef (2003, in press) and illustrated in Figure 1. Wire mesh partitions divided the main enclosure into two end chambers and a central area. A transparent holding cage located in the middle of the central area could be raised through a hole in its roof to release a restrained subject. The ancillary cage, located adjacent to the central area and separated from it by a wire mesh partition, was divided into two compartments of equal size by both a permanent transparent Plexiglas partition and a removable opaque partition. Two closed-circuit television cameras, one located in front of the midpoint of the central area and the other directly above the midpoint of the ancillary cage, permitted us to observe subjects without disturbing them.

Procedure

Group assignment. We first randomly assigned 15 male and 10 female subjects to the experimental condition and 10 males and 10 females to the control condition. Subjects in the experimental condition were then assigned to 10 trios, each of which consisted of 2 males and 1 female. To compose such trios, we first assigned the males to 10 pairs constructed so that no 2 males served together in more than one pair. We then added a randomly selected female to each pair of males. We randomly assigned 1 male and 1 female subject from the control condition to each of 10 pairs. During the experiment, each female served in only one trio and some males served in two trios.

Fight phase. To begin the experiment, we placed 1 of the 10 females assigned to the experimental condition in the holding cage and the 2 male members of her trio on opposite sides of the partitions that bisected the ancillary cage. We then removed the opaque partition from the ancillary cage, leaving the 2 males separated by the transparent partition. For the next 10 min, we used the closed-circuit television camera suspended directly above the ancillary cage to videotape the males' behavior.

First choice phase. Immediately upon completion of the fight phase, we randomly selected the more aggressive members of five male pairs and the less aggressive member of the remaining five male pairs to serve in the first choice phase. We placed that male in the end chamber of the apparatus closer to the side of the ancillary cage that he had occupied during the fight phase and placed the other male pair member of the pair out of sight of both of the other members of his trio. We then lifted the holding cage restraining the female member of the trio, waited until the she took her first step, and for the next 10 min used the video camera located in front of the central area to determine the female's position relative to the two end compartments.

Second choice phase. As soon as the first choice phase ended, we (a) removed the male from the apparatus, (b) placed the 2nd male trio member in the end chamber of the apparatus closer to the side of the ancillary cage that he had occupied during the fight phase, and (c) returned the female to the holding cage. We then conducted a second choice test identical to the first.

An experimenter, unaware of the outcomes of the choice phase, reviewed videotapes of males engaged in the fight phase and determined the number of times that each member of a pair of males pecked the transparent Plexiglas partition separating them. We considered the male in each pair that pecked the transparent partition more frequently during the fight phase to be the more aggressive member of that pair. Ethical problems associated with staged aggressive interactions led us to use an indirect measure of male aggression rather than to allow males to engage in unrestrained fights.

Schlinger, Palter, and Callard (1987) reported that when male Japanese quail pecked at conspecifics through a glass partition separating them, males that pecked more frequently also won subsequent unrestrained fights with males that pecked less frequently. We have found repeatedly that female quail respond differently to males that they previously observed pecking more or less frequently during an aggressive interaction (Ophir & Galef, 2003, in press).

Control group. We tested females assigned to the control group as we had tested females assigned to the experimental group during the first choice phase. However, females assigned to the control group chose between an empty end chamber and a randomly selected end chamber containing an unfamiliar male.

Data Analysis

All data were analyzed by using paired and unpaired *t* tests as appropriate.

Results and Discussion

Fight Phase

More and less aggressive members of each pair pecked the Plexiglas partition separating them an average ($\pm$ *SE*) of 468.1 $\pm$ 96.5 and 250.0 $\pm$ 79.8 times, respectively.

First and Second Choice Phases

Figure 2 shows the mean number of minutes that females assigned to control and experimental conditions spent nearer to the end chamber containing a male during 10-min choice phases. As can be seen in Figure 2, when the male in one end chamber of the apparatus was either unfamiliar to a female (i.e., she had been assigned to the control group) or the less aggressive of the pair of males that she had seen interact during the fight phase, the female was indifferent to his presence: one-sample *t* tests, both $t(9) < 0.76$, *ns*. In contrast, and as can also be seen in Figure 2, females spent significantly less than 5 min nearer to the end chamber containing the more aggressive of a pair of males that they had observed during the fight phase, $t(9) = 4.78$, $p < .001$.

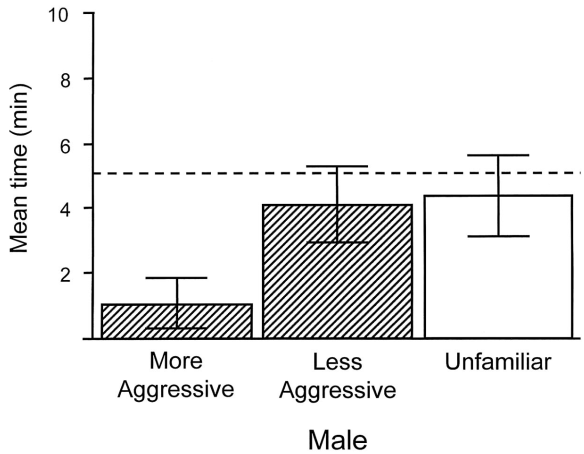

Figure 2. Mean (± *SE*) number of minutes out of 10 during choice phases that females in Experiment 1 spent closer to the end chamber containing a more or less aggressive male or an unfamiliar male. All females chose between end chambers containing a male and an empty end chamber. Dashed line = indifference; hatched bars = experimental group; open bar = control group.

As in our previous experiments (Ophir & Galef, 2003), during choice tests, females assigned to the experimental condition spent significantly more time close to the end chamber containing the less aggressive male than to that containing the more aggressive male member of the pair they had observed during the fight phase: paired *t* test, $t(9) = 2.43$, $p < .05$. Further, females spent an equal amount of time near unfamiliar and less aggressive males, Student's *t* test, $t(18) = 0.14$, *ns*, and more time closer to unfamiliar males than to more aggressive males, $t(18) = 2.13$, $p < .05$.

It might be argued that during the choice phase of the present experiment, females' choices were influenced not by the behavior that they had observed during the fight phase, but by the behavior of more and less aggressive males during the choice phase itself. There are two reasons to reject the hypothesis that females' choices were influenced primarily by the behavior of males during the choice phase. First, female participants in experiments very similar in design to the present one that chose between pairs of males that they had not observed while the males engaged in an aggressive interaction tended to prefer more aggressive males (Ophir & Galef, 2003, Experiments 1 and 3). Consequently, if females in the present experiment were deciding whether to remain near males on the basis of the males' behavior during the choice phase, females should have either preferred or been indifferent to aggressive males. To the contrary, females in the present experiment avoided more aggressive males. Second, the group of randomly selected unfamiliar males presented to females assigned to the control condition should have been a mix of more and less aggressive individuals. If females were attending to male behavior during the choice phase, then their responses to unfamiliar males should have been intermediate to their responses to more and less aggressive males. To the contrary, females' responses to unfamiliar males and less aggressive males were identical. The results of Experiment 1 are thus most readily interpreted as indicating that female quail use information obtained from observing males interact aggressively to identify and avoid aggressive males rather than to identify and approach less aggressive males.

Experiment 2

The results of Experiment 1 indicate that female quail observing male conspecifics interact aggressively subsequently avoid aggressive males and are indifferent to less aggressive males. If so, then female quail that watch two males interact before choosing between a more aggressive or a less aggressive male and an unfamiliar male should (a) prefer unfamiliar to more aggressive males and (b) be indifferent when choosing between unfamiliar and less aggressive males.

Method

Subjects

Twelve female and 10 male sexually mature Japanese quail, different from those used in Experiment 1 but obtained from the same source and maintained under the same conditions, served as subjects. At the end of the experiment, all subjects were killed by exposure to carbon dioxide.

Apparatus

We used the same apparatus as in Experiment 1.

Procedure

Group assignment. We assigned subjects to 1 of 12 quartets, each composed of a female, an "unfamiliar" male, and two "interacting" males. We first assigned 3 males to each of 12 trios so that no 2 males were together in more than one trio, and then randomly assigned a female to each trio.

Fight phase. As in Experiment 1, a pair of males interacted in the ancillary cage for 10 min while the female observed them from the holding cage.

First and second choice phases. The two 10-min choice phases were identical to the corresponding phases of Experiment 1, with one exception: Instead of leaving one end chamber of the apparatus empty during each choice phase, we placed the unfamiliar male member of each quartet in the end chamber opposite that in which we placed a male that the female had seen interacting aggressively.

Data Analysis

Because we had strong directional predictions based on the results of Experiment 1 (i.e., females should prefer unfamiliar males to more aggressive males and be indifferent when choosing between less aggressive males and unfamiliar males), we used one-tailed tests of significance. One-tailed tests both increased our probability of finding support for the prediction that females would avoid more aggressive males and decreased our probability of finding support for the prediction that females would be indifferent when choosing between less aggressive males and unfamiliar males.

Results and Discussion

Fight Phase

More and less aggressive interacting males pecked the Plexiglas partition separating them an average (± *SE*) of 377.4 ± 59.9 and 176.7 ± 44.1 times, respectively.

First and Second Choice Phases

As can be seen in Figure 3, and consistent with the results of Experiment 1, when choosing between an unfamiliar male and

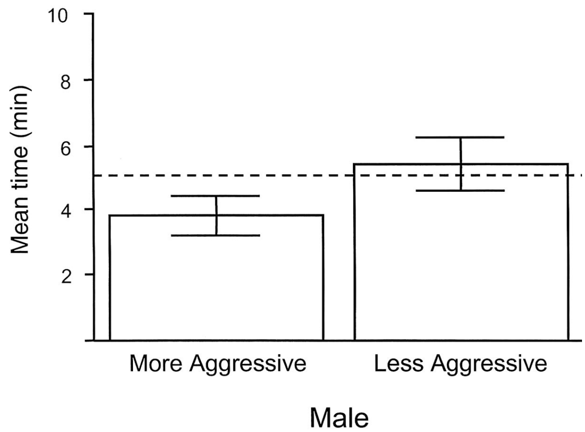

Figure 3. Mean (± *SE*) number of minutes out of 10 during choice phases that females in Experiment 2 spent closer to the end chamber containing a more or less aggressive male. Females chose between end chambers containing a male that each female observed during the fight phase and a male that was unfamiliar to her. Dashed line = indifference.

either a more or less aggressive male, (a) females avoided more aggressive males—one-sample *t* test, $t(11) = 1.86$, $p < .05$—and (b) females showed no preference between an unfamiliar male and a less aggressive male: one-sample *t* test, $t(11) = 0.57$, *ns*. As can also be seen in Figure 3, and consistent with the finding in Experiment 1 that females avoid more aggressive males, females spent significantly more time closer to the end chamber of the apparatus containing a less aggressive male than to the end compartment containing a more aggressive male: paired *t* test, $t(11) = 2.22$, $p < .05$.

General Discussion

The results of the present experiments indicate that female Japanese quail observing aggressive interactions between conspecific males acquired information that they subsequently used primarily to avoid further contact with more aggressive males. Female quail appeared to make little use of whatever information they obtained from observing less aggressive males.

The tendency of females to avoid more aggressive, presumably relatively dominant males is potentially problematic. Females would, in general, seem to gain both direct benefits (those that increase a female's own survival and reproduction) and indirect benefits (those that increase the fitness of a female's offspring) by consorting and mating with relatively aggressive males.

Male quail are territorial (Schwartz & Schwartz, 1949), and dominant males tend to defend preferred mating and feeding sites (Edens, Bursian, & Holladay, 1983; Otis, 1972). Consequently, female quail should gain direct benefits by associating with more aggressive males. Further, aggressiveness is heritable in male quail (Boag & Alway, 1981), so the sons of relatively aggressive males should inherit from their fathers a tendency toward dominance and consequent increased access to resources.

However, in species like Japanese quail in which encounters between the sexes are potentially harmful to females (e.g., Anguillian ground lizard, *Ameiva plei*, Censky, 1997; sailfin molly, *Poecilia latipinna*, Schlupp, McKnab, & Ryan, 2001; mosquitofish, *Gambusia holbrooki*, Pilastro, Benetton, & Bisazza, 2003; fallow deer, *Dama dama*, Clutton-Brock, Price, & MacColl, 1992; wild horse, *Equus caballus*, Linklater, Cameron, Minot, & Stafford, 1999), females may need to consider potential costs as well as potential benefits of consorting with dominant males (Qvarnström & Forsgren, 1998). Males that are relatively aggressive when interacting with other males may also engage relatively frequently in courtship behaviors that are potentially harmful to females (Ophir & Galef, 2003). Consequently, females that avoid contact with males they observe behaving aggressively during competitions between males could reduce their probability of suffering physical damage while mating.

In fact, female quail appear to consider both potential costs and potential benefits when deciding whether to affiliate with males. Unfertilized females are indifferent to conspecifics of both sexes, whereas female quail with male gametes in their sperm-storage vesicles, who would experience fewer benefits from additional sexual contact than would unfertilized females, both avoid males and aggregate with other females, presumably to reduce physical harassment by males (Persaud & Galef, in press).

In quail, preference for less aggressive males is a result of prior experience of male courtship and mating behavior. Only sexually experienced females avoid the more aggressive member of a pair of males that they have previously observed interacting aggressively. Sexually naïve females actually prefer such males (Ophir & Galef, in press).

Thus, the present data, together with results of previous studies of mate choice in quail, suggest that when male patterns of courtship and mating are potentially harmful to their partners, females may learn to avoid males that they have previously observed behaving relatively aggressively. Such learned avoidance of aggressive males could serve to reduce the probability that females will suffer physical damage while acquiring the male gametes they need to reproduce.

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