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Female Japanese quail that 'eavesdrop' on fighting males prefer losers to winners

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In a series of four experiments, we examined the relationship between male dominance and female preference in Japanese quail, *Coturnix japonica*. Female quail that had watched an aggressive interaction between a pair of males preferred the loser of an encounter to its winner. This superficially perverse female preference for losers may be explained by the strong correlation between the success of a male in aggressive interactions with other males and the frequency with which he engages in courtship behaviours that appear potentially injurious to females. By choosing to affiliate with less dominant male quail, female quail may lose direct and indirect benefits that would accrue from pairing with dominant males. However, they also avoid the cost of interacting with potentially harmful, more aggressive males.

In a series of papers, McGregor and his coworkers explored effects on a nonparticipant 'eavesdropper' of monitoring interactions between others of its species (reviewed in McGregor & Peake 2000). Eavesdroppers can use information extracted from observed interactions to evaluate both potential opponents in future aggressive encounters (e.g. Naguib & Todt 1997) or, more relevant to the present studies, to select a future mate. For example, female Siamese fighting fish, *Betta splendens*, eavesdropping on an aggressive interaction between a pair of conspecific males subsequently spent more time near the winner than the loser of the interaction that they observed (Doutrelant & McGregor 2000). After eavesdropping on a similar interaction, male Siamese fighting fish took longer to display to the winner than to the loser (Oliveira et al. 1998).

As suggested by the preceding examples, studies of eavesdropping have focused on the consequences of observing aggressive interactions between males, although eavesdropping on other sorts of interaction might also affect the subsequent behaviour of eavesdroppers (McGregor & Peake 2000). In particular, results of studies of aftereffects of eavesdropping on sexual encounters between male and female Japanese quail, *Coturnix japonica*, indicate that female quail prefer a male that they have watched court another female, whereas males avoid a female that they see with another male (Galef & White 1998; White & Galef 2000b). In the studies described below, we extended previous work on the effects of eavesdropping on subsequent sexual interactions in Japanese quail to examine the effects on preferences of female quail of observing conspecific males win or lose an aggressive interaction.

Otis (1972) suggested that male Japanese quail live in dominance hierarchies (Boag & Alway 1981) that give dominant individuals priority of access to resources. Consequently, females might be expected to prefer to affiliate and mate with winners of aggressive interactions to increase access both to resources and to the potentially superior genetic material of dominant individuals (Qvarnström & Forsgren 1998).

EXPERIMENT 1: DO FEMALE QUAIL PREFER MALE 'WINNERS'?

We undertook experiment 1 to determine the effects on affiliative preferences of female Japanese quail of observing an aggressive encounter between two conspecific males. In Japanese quail, affiliative preference is an excellent predictor of choice of a partner for copulation (White & Galef 1999).

To provide evidence that any effects on females' preferences resulted from observing males interact rather than from changes in appearance of males after winning or losing an aggressive encounter, we also examined females choosing between winners and losers of fights that had taken place out of sight of choosing females.

Methods

Subjects

Subjects were 37 female and 34 male Japanese quail, acquired from Speck's Poultry Farm (Vineland, Ontario,

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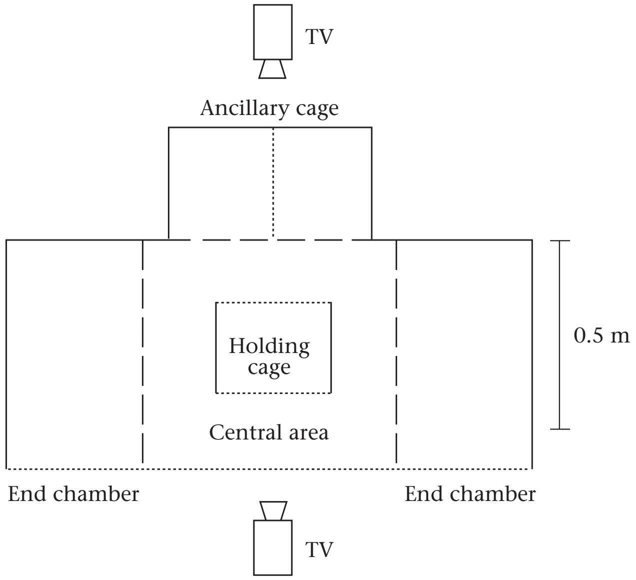

Figure 1. Overhead schematic of the apparatus used in all experiments. Solid lines: Opaque walls; dotted lines: transparent Plexiglas; dashed lines: wire mesh. The camera viewing the ancillary cage was mounted directly above its midpoint, facing down, and the camera viewing the central area was located at its midpoint and oriented horizontally.

Canada) when 52 days of age. After transporting subjects to our laboratory (Hamilton, Ontario), we placed them in individual cages (55 × 55 × 110 cm), housed in a single temperature- and humidity-controlled colony room illuminated on a 16:8 h light:dark cycle, with light onset at 0700 hours. All subjects had ad libitum access to water and Mazuri Pheasant Breeder (PMI Feeds, St Louis, Missouri, U.S.A.) for the duration of their stay in the laboratory. All procedures were approved by the McMaster University Animal Research Ethics Board (Animal Utilization Proposal No. 99-05-26).

Experiments began only after subjects had achieved sexual maturity. We considered females to be sexually mature when they began to lay at least one egg every other day. To determine whether a male was mature, when he started to call regularly (at about 70 days of age), we placed him together with a succession of sexually mature females, for 5 min/day for 7 consecutive days, in alternating end chambers of the apparatus (Fig. 1). We observed the behaviour of pairs on closed-circuit television, and when a male mounted and made cloacal contact with females on 2 successive days, we considered him to be sexually mature.

Apparatus

We performed the experiment in an apparatus constructed of painted plywood, Plexiglas and wire mesh (Fig. 1; White & Galef 2000a). In brief, the apparatus consisted of a main enclosure and an ancillary cage. The main enclosure was divided into three segments (two end chambers and a central area) by two wire-mesh partitions. A holding cage, with two transparent Plexiglas and two opaque walls, placed in the middle of the central area, could be raised through the roof of the central area to release a restrained subject.

The ancillary cage was divided into two compartments of equal size by both a permanent transparent Plexiglas partition and a removable opaque partition. A wire-mesh barrier separated the ancillary cage from the main enclosure.

Procedure

Group assignment. We assigned subjects to trios each composed of a ‘focal’ female and two ‘target’ males. To construct trios, we first assigned males to 37 unique pairs and then randomly assigned a focal female to each pair. We then assigned 19 trios to ‘eavesdrop’ (E) and 18 trios to ‘not-eavesdrop’ (Not-E) conditions.

Fight phase. To begin the fight phase of the experiment, we placed a focal female in the holding cage and one target male on each side of the barrier dividing the ancillary cage. We then lifted the opaque partition separating the males, leaving the transparent Plexiglas partition in place. For the next 10 min, we used a closed-circuit television camera suspended directly above the midpoint of the ancillary cage and a video-cassette recorder to make a permanent record of the behaviour of the two target males. Two independent observers subsequently scored these videotapes to determine the number of times that each target male pecked the transparent Plexiglas partition during the 10-min fight phase.

Throughout the fight phase, focal females assigned to the E condition had one transparent wall of the holding cage facing the ancillary cage. Focal females assigned to the Not-E condition had an opaque wall of the holding cage facing the ancillary cage blocking their view of the ancillary cage and the target males it contained.

We considered the target male in each trio that pecked the transparent partition more frequently during the fight phase the ‘winner’ of the fight and the male that pecked it less frequently the ‘loser’ of that fight. Schlinger et al. (1987) staged direct aggressive encounters between eight pairs of males and found in all eight cases that the male that had previously pecked more at a Plexiglas barrier separating him from a conspecific target won the aggressive encounter. Because of ethical problems associated with staging aggressive interactions, we used Schlinger et al.’s indirect measure of male aggression.

Choice phase. As soon as the fight phase ended, we placed each target male in the end chamber of the main enclosure that was closer to the side of the ancillary cage he had occupied during the fight phase. We then lifted the holding cage, waited until the released focal female took her first step, and allowed the focal female to move freely about the central area for 10 min, recording her behaviour using a video camera in front of the central area (Fig. 1). We considered a female to ‘prefer’ whichever target male she spent nearer to for more than half of the 10-min choice phase. We excluded data from four trios in which focal females either failed to take a first step within 3 min of our lifting of the holding cage or failed to enter

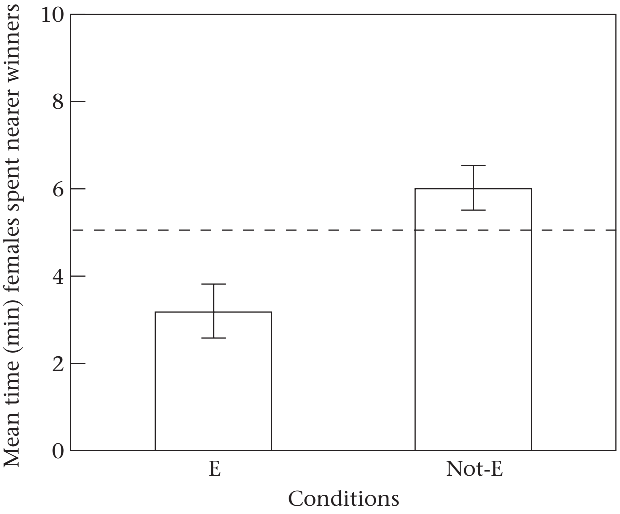

Figure 2. Mean±SE time during the choice phase that focal females in experiment 1 spent closer to the member of a pair of males that won during the fight phase.

both sides of the central area during the 10-min choice phase.

Results and Discussion

Interobserver reliability

There was considerable agreement between independent observers' scoring a random selection of videotapes for both number of pecks delivered by each target male during the fight phase (Pearson's correlation: $r_{22}=0.98$, $P<0.001$) and amount of time focal females spent nearer to each target male during the choice phase ($r_8=0.99$, $P<0.001$).

Fight phase

Winning and losing target males assigned to E and Not-E conditions pecked the Plexiglas partition separating them for a mean ± SE of 597.0 ± 88.5 times (winners assigned to the E-condition), 224.9 ± 36.1 times (losers assigned to the E condition), 378.4 ± 71.7 times (winners assigned to the Not-E condition), and 184.2 ± 48.5 times (losers assigned to the Not-E condition). Winners assigned to both E and Not-E conditions thus pecked the Plexiglas partition more than twice as often as did the losers with whom they interacted. There was, however, no statistically reliable difference in number of pecks delivered by winners (two-sample Student's *t* test: $t_{31}=1.94$, $P=0.07$) or losers (two-sample Student's *t* test: $t_{31}=0.70$, NS) assigned to E and Not-E conditions, or by both members of pairs assigned to E and Not-E conditions ($t_{31}=1.62$, $P=0.11$).

Choice phase

We found a significant effect of group assignment on focal females' preferences for males that won and lost during the fight phase (two-sample *t* test: $t_{31}=3.57$, $P<0.01$; Fig. 2). During the choice phase, focal females assigned to the E condition spent more time nearer losers than winners (one-sample *t* test: $t_{14}=3.01$, $P<0.01$; Fig. 2). In contrast, focal females assigned to the Not-E condition showed a marginal tendency to remain closer to winners than to losers (one-sample *t* test: $t_{17}=1.91$, $P=0.07$), and might best be considered indifferent between winners and losers (see Results of experiments 2 and 3).

Of course, the finding that females that have eavesdropped on a pair of fighting males subsequently prefer to affiliate with the loser of the fight that they observed may have nothing to do with information that females acquired about the relative fighting ability of males they observed engaged in an aggressive interaction. For example, losers (which spent less time pecking at their opponents during the fight phase than did winners) may have spent more time than winners interacting with observing females, and may have become preferred as a consequence.

To determine whether differences in males' interactions with females during the fight phase might explain female preferences during the choice phase, an observer, unaware of group assignment of males, determined the time that each male spent with his beak pointed within the 45 degrees of arc centred on the holding cage. We found no difference in the time that winners ($\bar{X} \pm \text{SE}=279.8 \pm 31.9$ s) and losers (328.7 ± 34.8 s) assigned to the E-condition or winners (190.7 ± 30.1 s) and losers (204.7 ± 25.2 s) assigned to the Not-E conditions directed their gaze towards the holding cage containing the focal female (E condition, paired *t* test: $t_{13}=1.61$, $P=0.13$; Not-E condition: $t_{17}=0.33$, $P=0.75$). The former finding is not consistent with the hypothesis that, during the fight phase, losers interacted more with focal females than did winners.

EXPERIMENT 2: DO MALES INTERACT DIFFERENTLY WHEN WATCHED BY A FEMALE?

The difference between preferences for winning males shown by focal females assigned to E and Not-E conditions in experiment 1 is open to yet another interpretation. During the fight phase, target males assigned to E and Not-E conditions may have behaved differently depending on whether they could see a female while interacting with one another. For example, target males assigned to the E condition (which saw a female during the fight phase) might have interacted more vigorously than did target males assigned to the Not-E condition (which could not see a female during the fight phase). If so, the difference in behaviour during the fight phase of males assigned to E and Not-E conditions might have affected their subsequent relative attractiveness to focal females during the choice phase. If so, focal females' preferences during the choice phase may have reflected their response to the appearance of males during the choice phase, not information acquired during the fight phase.

We undertook experiment 2 to determine whether differences in the behaviour of males seeing and not seeing females during the fight phase were responsible for differences in the affiliative preferences of females assigned to E and Not-E conditions during the choice phase in experiment 1. In experiment 2, during the fight phase, a one-way mirror either blocked or did not block the females' views of males, without blocking the males' views of the females (e.g. Doutrelant & McGregor 2000). Keeping the conditions under which males interacted constant while providing or denying females visual access to males provided an opportunity to examine the hypothesis that differences in aggressive interactions of males that either could or could not see a female while fighting were responsible for the outcome of experiment 1.

Methods

Subjects

Subjects were 47 male and 33 female, sexually mature Japanese quail acquired from Speck's Poultry Farm. We randomly assigned trios of subjects to mirror (N=18) and no-mirror conditions (N=15).

Apparatus

We modified the apparatus used in experiment 1 in the following ways. First, we removed the wire-mesh screen separating the ancillary cage and central area and replaced it with a one-way mirror that completely covered the 35 × 40-cm opening between the ancillary cage and central area (Fig. 1). Second, we changed the illumination of the experimental room during the fight phase depending on the condition to which a trio of subjects had been assigned.

When subjects assigned to the mirror condition were in the apparatus, we turned off the room lights and illuminated the central area of the main enclosure with 150-W halogen lights. When subjects assigned to the no-mirror condition were in the apparatus, we turned the halogen lights off and turned the house lights on. Consequently, during the fight phase, focal females and target males assigned to the no-mirror condition could see one another, whereas target males assigned to the mirror condition could see focal females, but focal females assigned to the mirror condition could not see target males.

Procedure

Fight phase. We treated subjects assigned to the mirror and no-mirror conditions exactly as we treated subjects assigned to the E condition of experiment 1 except for illumination of the apparatus during the fight phase when subjects assigned to the mirror condition were in the apparatus.

Choice phase. During the choice phase, we treated subjects assigned to both mirror and no-mirror conditions exactly as we treated subjects during the choice phase in experiment 1.

Results

Interobserver reliability

As in experiment 1, independent observers agreed significantly in their scores of a random sample of videotapes for both number of pecks delivered by each target male during the fight phase (Pearson's correlation: r_{18}=0.91, P<0.001) and time focal females spent nearer to each target male during the choice phase (r_{18}=0.99, P<0.001).

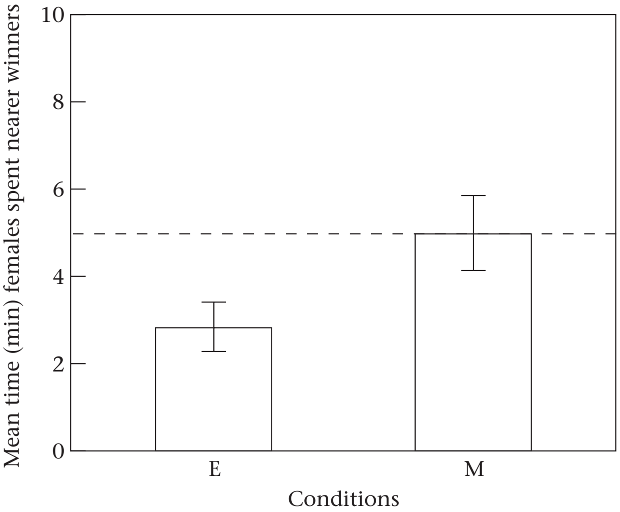

Figure 3. Mean±SE time during the choice phase that focal females in experiment 2 spent closer to the member of a pair of males that won during the fight phase.

Fight phase

Winning and losing target males assigned to mirror and no-mirror conditions pecked the Plexiglas partition separating them for a mean ± SE of 488.9 ± 74.5 times (winners assigned to the mirror condition), 227.9 ± 41.6 times (losers assigned to the mirror condition), 608.4 ± 33.2 times (winners assigned to the no-mirror condition) and 335.6 ± 81.7 times (losers assigned to the no-mirror condition). Taken together, winners assigned to mirror and no-mirror conditions pecked more than twice as often as did the losers with whom they interacted. As in experiment 1, we found no difference in the number of pecks delivered to the Plexiglas partition by winners (two-sample Student's t test: t_{27}=1.11, P=0.28), losers (t_{27}=1.20, P=0.24), or pairs of subjects (t_{27}=1.24, P=0.26), as a function of the condition to which we had assigned subjects.

Choice phase

We discarded data from four trios when females failed to move within 3 min of release from the holding cage.

We found a significant effect of group assignment on focal females' preferences for males that won and lost during the fight phase (two-sample t test: t_{27}=2.05, P<0.05; Fig. 3). During the choice phase, focal females assigned to the no-mirror condition spent significantly more time nearer the loser than the winner (one-sample t test: t_{13}=3.92, P<0.01; Fig. 3). In contrast, focal females assigned to the mirror condition were indifferent to winning and losing males (one-sample t test: t_{14}=0.01, P=0.99).

Discussion

The results of experiment 2 are consistent with the prediction that whether focal females can see target males is important and whether target males can see focal females is not important in determining whether focal females prefer to affiliate with losers of aggressive encounters. However, using a one-way mirror to allow males to see females without permitting females to see males turned out to be a less than ideal procedure. The mirror degraded visual stimuli passing between the ancillary cage and the central area throughout both phases of the experiment and, during the fight phase, required use of potentially distracting bright lights and provided the focal female with a mirror image of herself.

EXPERIMENT 3: DO MALES INTERACT DIFFERENTLY WHEN WATCHED BY A FEMALE REVISITED?

Rather than persevere with one-way mirrors, we took an alternative approach to determining the effects of seeing a focal female on the males' behaviour during the fight phase. We repeated experiment 1, but added a substitute-female (S-F) condition in which, during the fight phase, target males interacted while seeing an observing female, as did target males assigned to both the E condition of experiment 1 and to the no-mirror condition of experiment 2. However, in the S-F condition, a female other than the female that had observed the fight phase chose between target males during the choice phase. If, seeing a female during the fight phase caused males to interact so as to enhance subsequent attractiveness of losers to females, then females assigned to the S-F condition that chose between males, like focal females assigned to the E condition in experiment 1 and the no-mirror condition in experiment 2, should prefer losers to winners during the choice phase.

Methods

Subjects and apparatus

Subjects were 66 male and 68 female sexually mature Japanese quail acquired from Speck's Poultry Farm. Nine females served only as models in the S-F condition. We used the same apparatus that we had used in experiment 1 (Fig. 1).

Procedure

We first randomly assigned males to 59 unique pairs, then randomly assigned one female to each of 19 pairs of target males that we assigned to the E condition and each of 20 pairs of target males that we assigned to the Not-E condition. We then assigned a unique pair of females to each of the 20 pairs of target males that we assigned to the S-F condition.

Fight phase. During the fight phase, we treated both female subjects and target males assigned to E and Not-E conditions just as we had treated subjects assigned to those conditions in experiment 1. We treated subjects assigned to the S-F condition exactly as we treated those assigned to the E condition, except that we removed the female that had observed target males during the fight phase (the model female) and replaced her with a female that had not observed target males interacting (the focal female). Thus, target males assigned to the S-F condition fought in the presence of a female, as had target males assigned to the E condition. However, focal females assigned to the S-F condition, like focal females assigned to the Not-E condition, had not seen a fight before choosing between target males.

Choice phase. During the choice phase, we removed model females from the experiment and treated both their replacement focal females and target males exactly as we had during the choice phases of experiments 1 and 2.

Results and Discussion

Interobserver reliability

As in experiments 1 and 2, independent observers agreed significantly on scores from a random sample of videotapes for both number of pecks delivered by each target male during the fight phase (Pearson's correlation: $r_{16}=0.88$, $P<0.001$) and time focal females spent nearer to each target male during the choice phase ($r_{14}=0.97$, $P<0.001$).

Fight phase

Winners assigned to E, Not-E and S-F conditions pecked at the partition separating them from losers a mean ± SE of, respectively, 495.9 ± 60.5, 511.0 ± 80.9 and 506.22 ± 62.07 times. Losers in the same three groups pecked, respectively, 201.7 ± 40.0, 224.0 ± 27.4 and 153.7 ± 42.7 times. As in experiment 1, group assignment had no effect on pecking rates of winners, losers (one-way ANOVAs: both $Fs_{2,47}<0.90$, both NS), or pairs (one-way ANOVA: $Fs_{2,47}=0.18$, $P=0.83$). As in experiments 1 and 2, because we consistently assigned subjects that pecked more frequently to the group of winners, the pecking rates of winners was greater than that of losers.

Choice phase

Data from nine focal females were discarded when they either failed to take a first step during the first 3 min of the choice phase or failed to enter both halves of the central area during the choice phase.

We found a significant effect of group assignment on the affiliative behaviour of focal females during the choice phase (one-way ANOVA: $F_{2,47}=3.48$, $P<0.05$; Fig. 4). Focal females assigned to the E condition, who saw a pair of males fight before choosing between them, preferred losers more than did focal females assigned to either Not-E or S-F conditions (Fisher's positive least significant difference (PLSD) tests, both Ps<0.05; Fig. 4).

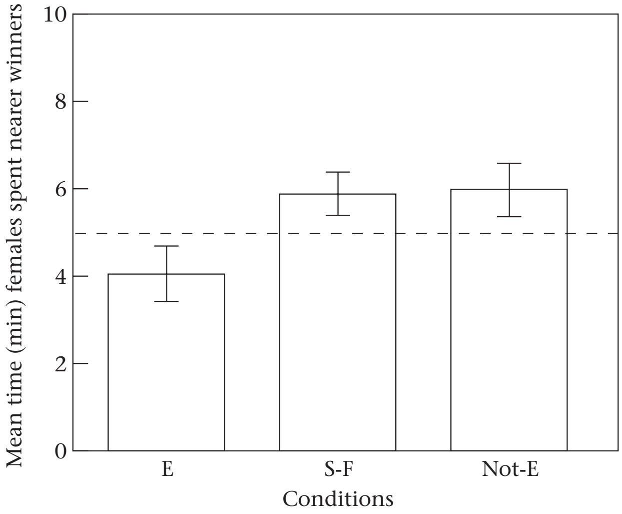

Figure 4. Mean±SE time during the choice phase that focal females in experiment 3 spent closer to the member of a pair of males that won during the fight phase.

On the other hand, focal females assigned to S-F and Not-E conditions, who had not seen a pair of males fight before choosing between them, did not differ from one another (Fisher's PLSD test: P=0.92; Fig. 4). Although none of the three groups showed a statistically significant preference for either winners or losers (one-sample *t* tests: group E: t_{16}=1.52, P=0.15; group S-F: t_{17}=1.79, P=0.09; group Not-E: t_{14}=1.52, P=0.15), both groups E and Not-E deviated from chance in the same direction as in our previous experiments.

The results of experiment 3 replicate the finding in experiment 1 showing that focal females that have watched two males fight prefer the loser of the fight to the winner. The present results, like those of experiment 2, suggest that information garnered by females watching a fight between males determines their subsequent choice of a male with whom to affiliate.

EXPERIMENT 4: WHY MIGHT FEMALES PREFER LOSERS?

As discussed briefly in the introduction, on general theoretical grounds, a female quail might be expected to favour the more aggressive or dominant member of a pair of males that she has seen interact (Qvarnström & Forsgen 1998). Dominant males are generally assumed to have superior access to resources and to be bearers of better genes than submissive males. Consequently, the reproductive success of females mating with dominant males should generally be greater than that of females mating with submissive individuals (Qvarnström & Forsgen 1998). In fact, females of several species have been shown to prefer dominant to submissive males (e.g. Brown et al. 1988; Rich & Hurst 1998; Doutrelant & McGregor 2000). However, results of experiments 1, 2 and 3 above indicate that female Japanese quail, like females of several other species (reviewed in Qvarnström & Forsgren 1998), show the opposite effect and prefer to affiliate with submissive rather than dominant males. Why might female Japanese quail prefer losers to winners?

To a human observer, the courting behaviour of male Japanese quail, like that of male horses, *Equus caballus* (Linklater et al. 1999), fallow deer, *Dama dama* (Clutton-Brock et al. 1989) and elephant seals, *Mirounga angustirostris* (Le Boeuf & Mesnick 1990) seems able to physically damage females of their species. Consistent with this view, results of recent studies in our laboratory show that female Japanese quail find the attentions of at least some male suitors unpleasant and form aggregations in the presence of male conspecifics to reduce the probability of sexual harassment (Persaud & Galef 2003).

We saw considerable variability in the frequency with which males engaged in potentially injurious behaviours while courting females. However, most courting males chased females, pecked vigorously at their heads and bodies, seized the feathers at the back of females' heads, dragged them around by their feathers and repeatedly jumped onto females' backs while attempting to achieve cloacal contact. If relatively dominant males are more violent when courting females than are relatively submissive males, then females might gain by foregoing whatever benefits might accrue from mating with a dominant male to escape the cost of being courted by him.

Here, we first used a round-robin tournament to establish the relative dominance of a cohort of male quail. We then allowed each male in the cohort to court and mate with three females in succession and scored the potentially punishing aspects of each male's interactions with females that he courted.

Methods

Subjects and apparatus

Subjects were 17 sexually mature male and 17 sexually mature female Japanese quail. We used the same apparatus that we had used in experiments 1 and 3.

Procedure

Dominance phase. We determined the dominance of our 17 male subjects over 8 days by allowing each male to interact through the Plexiglas partition in the ancillary cage (Fig. 1) with each of the other 16 males. Because we had to score 136 aggressive encounters between males, we reduced the duration of each to 2 min. No male participated in more than two encounters on any one day, and a minimum of 20 min separated any male's participation in two encounters.

Two reviewers independently scored videotapes of encounters to determine how many times each member of a pair of males pecked at the Plexiglas barrier separating them. As in previous experiments, we considered whichever member of a pair of males that pecked the Plexiglas barrier the most times to be the winner of an encounter. To create a relative ranking of the 17 males, we determined how many times each male won in the 16 encounters in which he was engaged.

Courtship and mating phase. After we determined the dominance ranking of each male, we allowed him to court and mate for 10 min every third day until he had mated with three females. An experimenter who was unaware of the outcome of the dominance phase scored videotapes of encounters between males and females to determine the number of potentially harmful behaviours and the number of courtship behaviours in which each male engaged. We considered pecks, feather pulls, drags, mounts and single-foot mounts to be potentially damaging to females, and heightened postures, strut/tidbitting, approach, invitations to preen and feather ruffles as courtship behaviours. Each of these behaviours other than 'single-foot mount' has been described in the literature (Adkins & Adler 1972; Wilson & Bermant 1972; Ramenofsky 1984; Schleidt et al. 1984). We defined a 'single-foot mount' as any instance in which a male placed only one foot on a female when attempting to mount.

Results

Interobserver reliabilities

Once again, we found substantial agreement between independent observers scoring videotapes as to the number of pecks delivered by target males during the dominance phase (Pearson's correlation: r_{46}=0.93, P<0.001). Observers also agreed on the number of female-directed pecks (r_{15}=0.83, P<0.001), number of other harmful behaviours males directed towards females (r_{15}=0.86, P<0.001) and number of courting behaviours (r_{15}=0.90, P<0.001) produced by males during the courtship and mating phase.

Main results

We found a strong positive relation between the number of wins that a male achieved during the dominance phase and the number of pecks that he delivered to females with whom he interacted during the courtship and mating phase (r_{15}=0.83, P<0.0001; Fig. 5a). There was a similar strong positive correlation between the number of wins that a male achieved during the dominance phase and the number of potentially harmful behaviours other than pecking that a male engaged in during the courtship and mating phase (r_{15}=0.71, P<0.001; Fig. 5b).

Males winning more encounters during the dominance phase were not just generally more active than males scoring fewer wins during the dominance phase. For example, we found no correlation between the number of wins that a male achieved during the dominance phase and the frequency of his courting behaviours during the courtship and mating phase (r_{15}= − 0.08, P=0.77; Fig. 6).

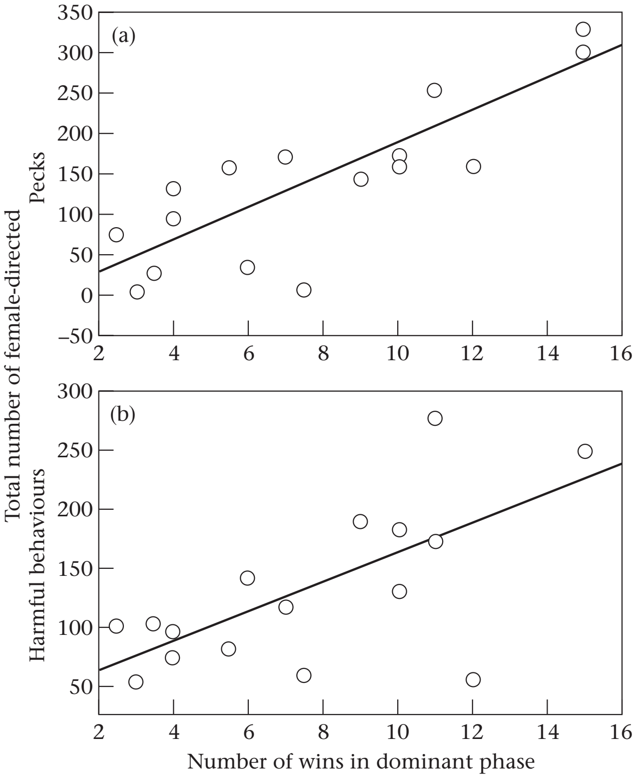

Figure 5. Scatter plots of the number of wins that a male achieved during the dominance phase and the number of (a) pecks and (b) other potentially harmful behaviours that he engaged in during the courtship and mating phase in experiment 4. The solid line represents the best linear fit.

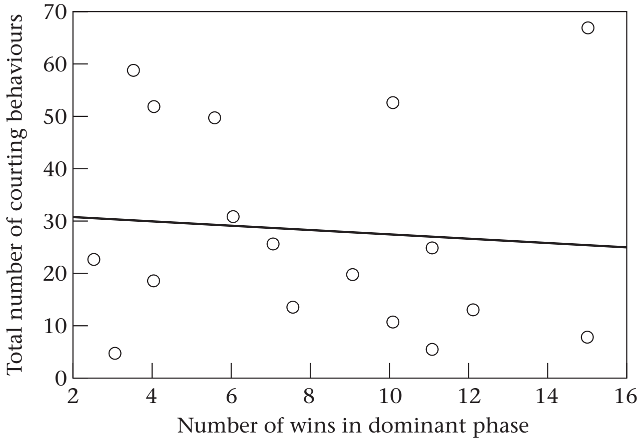

Figure 6. Scatter plots of the number of wins that a male achieved during the dominance phase and the number of courtship behaviours that he engaged in during the courtship and mating phase in experiment 4. The solid line represents the best linear fit.

Discussion

Females eavesdropping on a pair of males engaged in an aggressive interaction could predict which male would be more likely to peck at them and to engage in other potentially harmful behaviours. Consequently, by affiliating with less dominant males, females could avoid contact with males more likely to engage in potentially injurious behaviour when courting and mating.

GENERAL DISCUSSION

Evidence shows that females of many, but not all, species prefer to mate with relatively dominant males (Qvarnström & Forsgren 1998). Female preference for winners of intrasex competitions would be expected on the hypothesis that dominant males have greater access to resources or better genes than do subordinate males, and females could, therefore, acquire direct or indirect benefits from mating with dominant individuals (Qvarnström & Forsgren 1998).

The finding in experiments 1, 2 and 3 indicate that female quail prefer the less aggressive of two males that they have seen interact. The results of experiment 4 suggest that the relatively less dominant males that females prefer as affiliative partners are less likely than are more dominant males to court in ways that could be harmful to females.

Ideally, we would be able relate our laboratory findings to the behaviour of free-living Japanese quail. Unfortunately, Japanese quail are difficult to observe in the wild, and there is contradictory information as to both their social organization and sexual behaviour (Wetherbee 1961; Nichols 1991). Opportunistic observations of mating in wild Japanese quail have produced reports of both monogamy and polygyny (Kawahara 1967, cited in Nichols 1991).

Studies of both domestic and feral quail in large flight cages (Nichols 1991) suggest that females bond with one or two males, but that most engage in extrapair copulations. Most important for studies of female mate choice, Nichols (1991) reported that female Japanese quail solicit copulations from some males by walking in front of them and crouching, thus apparently inviting particular males to mount, and female quail prevent apparently undesired copulations by resisting males or fleeing from them. Nichols (1991, page 62) concluded that 'the female plays an active role in the formation and maintenance of the bond by choosing and remaining close to the male', behaviours quite similar to those that we used in the present studies as indices of female preference. Whether females in natural circumstances would have an opportunity to observe males fighting or defending territories is difficult to know.

Taken together, the results of all four experiments suggest that female quail can use information that they acquire while eavesdropping on males engaged in aggressive interactions to reduce their own probability of sustaining injury while mating. Theoretically, reproductive costs to female Japanese quail of mating with dominant conspecific males should be greater than the direct and indirect reproductive benefits that such males might provide (Qvarnström & Forsgren 1998). Unfortunately, empirical tests of that hypothesis are difficult to envision in a species such as *Coturnix japonica*, where whatever physical damage that males inflict on females is not readily observed.

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