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Differences between the sexes in direction and duration of response to seeing a potential sex partner mate with another

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We have shown previously that: (1) female Japanese quail, *Coturnix japonica*, increase and male Japanese quail decrease their tendencies to affiliate with potential sex partners after seeing them mate, and (2) in both sexes of quail, affiliative preferences and choice of a sex partner are highly correlated. Here we predict that because effects of a prior male's sperm on a second male's probability of fertilizing a female are relatively brief, a male's avoidance of whichever member of a pair of females he has seen mating should be transitory. Conversely, because female quail seek high-quality males as mates and quality is a relatively permanent characteristic, females' preferences between males should remain constant over time. We found, as predicted, that the durations of effects on affiliation of seeing a potential sex partner mate differed in male and female quail. Forty-eight hours after male quail saw a female mate, they no longer avoided her, whereas 48 h after female quail saw a male mate, his attractiveness remained enhanced. We conclude by suggesting that both the direction and the duration of responses of male and female Japanese quail to seeing a member of the other sex mating enhance the fitness of members of each sex.

Seeing a member of the other sex mate changes the behaviour of both male and female Japanese quail, *Coturnix japonica*, towards the individual seen mating: female Japanese quail increase (Galef & White 1998; White & Galef 1999b; White & Galef 2000) and male Japanese quail decrease (White & Galef 1999c) their tendencies to affiliate with potential sex partners that they have seen mating. In both sexes of quail, affiliative preference predicts choice of a sex partner (White & Galef 1999a).

Because of the relatively greater investment of female than of male quail in production of offspring, females should have evolved to choose male mates that provide either greater direct (e.g. Downhower et al. 1983; Gwynne 1984) or indirect benefits (e.g. Fisher 1930; Zahavi 1975) than their competitors. If, as we assume below, the relative quality of members of a pair of males remains stable, then a female's preference between those males should not change over time.

Male Japanese quail, unlike females of their species, make only a small investment in offspring. Consequently, unlike conspecific females, they will pay no great cost if they are indifferent to both the genetic quality of potential mates and their mates' likelihood of providing direct benefits to young. However, in order to avoid possible reproductive costs associated with sperm depletion (Birkhead & Fletcher 1995), exposure to sexually transmitted diseases (Sheldon 1993), lost opportunities to mate with other females, and so forth, males choosing between a pair of females should prefer to mate with that female whose ova they have the greater chance of fertilizing.

After a domestic hen, *Gallus gallus domesticus*, has been inseminated by a rooster, the probability that a second male that mates with her will inseminate her eggs is initially low, but increases with time (Birkhead 1988; Birkhead & Fletcher 1995; Birkhead & Moller 1998). In general, a male that has seen a hen mate should wait before mating with her, especially if he is in a position to choose between females and mating with one female reduces his probability of mating with another.

Rate of inactivation of sperm in a female's oviduct varies among avian species (Birkhead 1988). It is, therefore, impossible to know a priori how long a male Japanese quail should wait, when choosing between females, before ceasing to avoid a female he has seen mating. However, because Japanese quail and domestic chickens are members of the same family, Phasianidae, it is not unreasonable to assume that in Japanese quail, as in domestic hens, the probability of a male fertilizing a female's eggs increases with time since the female mated, and the longer it has been since a male quail saw a female

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mate, the less her previous mating should affect his choice of sex partner.

In this experiment, we examined the effects on affiliative preferences of 'focal' male and female Japanese quail of imposing a delay between when a focal animal saw a member of the other sex mate and when the focal animal chose between the individual seen mating and another. It was our prediction that, across days, male quail would abandon and female quail would maintain changes in their tendencies to affiliate with individuals of the other sex that they had seen mate.

EXPERIMENT 1: EFFECTS OF DELAY ON MALES' PREFERENCES

In previous experiments we have found that a male Japanese quail shows a reduced tendency to affiliate with a female immediately after seeing her mate (White & Galef 1999c). In this experiment we examined the effect on a focal male's affiliative behaviour of imposing a 48-h delay between when he saw a female mate and when he had an opportunity to choose between females. The methods used here and in experiments 2 and 3 (below) resemble closely those used in Galef & White (1998) and White & Galef (1999c).

Methods

Subjects

We used as subjects 24 male and 33 female 48-day-old Japanese quail acquired from a local commercial breeder (Speck's Poultry Farm, Vineland, Ontario). After we transported subjects to our laboratory (Hamilton, Ontario), we placed each in a stainless-steel cage, measuring 45.7 × 61.0 × 40.6 cm, situated in a colony room illuminated for 16 h/day.

We maintained all subjects on ad libitum Mazuri Pheasant Starter 5637 (PMI Feeds, St Louis, Missouri) and tap water, and for environmental enrichment, twice each week, we gave each bird access to a handful of autoclaved hay.

To allow birds to come into breeding condition, we waited 30 days before starting the experiment. We considered a female ready to breed when she started to lay an egg at least once every 2 days. To determine whether males would mate when given access to females, we placed each male with a succession of females in breeding condition in one of the end chambers of the apparatus that we subsequently used for experiments (Fig. 1). We gave each male access to a randomly selected female each day until he either mounted females on 2 successive days or 2 weeks passed without his mounting a female.

After a male had mated with two females in succession, we left him in isolation for 7–10 days, then started the experiment. We first assigned males and females to 24 quartets, each consisting of a single 'focal' male, two 'target' females and a 'model' male.

Although it would have been preferable if each animal participated only once in the experiment, practical constraints made it impossible for us to maintain the number of quail needed to do so. We did, however, ensure that: (1) each male served only once as a focal male; (2) no two males served together in more than one quartet; (3) no two focal males ever chose between the same pair of target females; and (4) no focal male had prior experience with either of his target females.

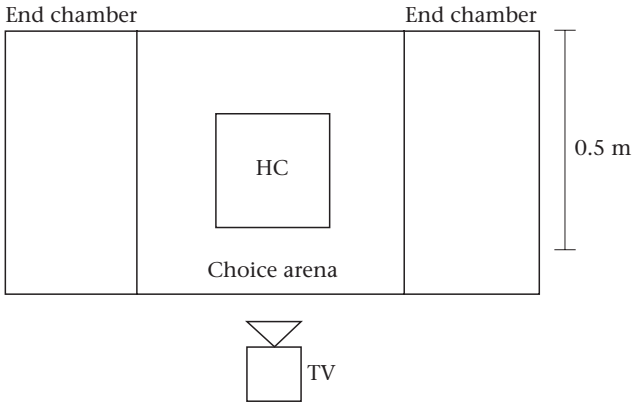

Figure 1. Overhead schematic of the apparatus used in experiments 1–3. TV: Closed-circuit television; HC: holding cage.

We randomly assigned eight focal males to each of no-delay, 48-h delay and control (no model, 48-h delay) conditions.

Apparatus

We conducted all experiments in an enclosure, measuring 121.9 × 61.0 × 30.5 cm, constructed predominantly of painted plywood (Fig. 1). The enclosure had a transparent Plexiglas roof and front wall, and rested on an aluminium tray covered with disposable, absorbant paper pads (Tray Liners, Lilo Products, Hamilton, Ontario, Canada). Hardware-cloth partitions placed 30.5 cm from opposite ends of the enclosure divided it into a choice arena and two end chambers (Fig. 1).

We drew a line from top to bottom of the front wall of the enclosure at the midpoint of the choice arena so that we could determine, at any time, the end of the enclosure to which a focal male was closer.

An opening in the centre of the roof of the choice arena, measuring 25.4 × 25.4 cm, allowed us to lift a transparent Plexiglas holding cage, measuring 25.2 × 25.2 × 40.6 cm (Fig. 1), using a pulley system operated from a room adjacent to that housing the apparatus.

A colour CCD video camera (Panasonic WV-CP412) feeding into a videotape recorder (Panasonic AG-1240) and colour video monitor (Panasonic CT 1331Y) faced the transparent Plexiglas front wall of the apparatus and permitted us to observe all activity occurring in the apparatus and record that activity for later scoring.

Procedure (no-delay and 48-h delay conditions)

Each test consisted of three 10-min phases: a pretest, a delay and a post-test.

Pretest. To begin the experiment, we placed a focal male in the holding cage in the middle of the choice arena and a female target subject in each end

compartment of the apparatus. We then waited for 1 min to let all subjects settle down. At the end of the 1-min period, we started the videotape recorder and raised the holding cage to release the focal male. In the 10 min after the focal male took his first step, we recorded the time he spent closer to each end chamber of the apparatus.

We will refer below to the target female held on the side of the enclosure where a focal male spent more than half the 10-min pretest as that focal male's 'preferred' female and the other target female as that focal male's 'nonpreferred' female.

Observation. At the end of the 10-min pretest, we returned the focal male to the holding cage, placed a 'model' male in the end chamber of the apparatus together with the focal male's preferred female, and left the preferred female and model male to court and mate for 10 min. We then removed the model male from the experiment, and either immediately conducted the post-test (no-delay condition) or returned the focal male and target females to their respective home cages for 48 h (48-h delay condition).

Post-test. During the post-test each focal male chose between the same two target females that he had chosen between during the pretest. We conducted the post-test exactly as we had conducted the pretest, first raising the holding cage, then waiting for the focal male to take his first step, and subsequently recording, for 10 min, the time that the focal male spent in each half of the choice arena.

Procedure (control condition)

We treated focal males assigned to the control condition exactly as we had treated focal males assigned to the 48-h delay condition except that during the observation phase of the experiment, we did not place a model male in the end chamber containing each focal male's preferred target female.

Results and Discussion

Pretest

During the pretest, focal males assigned to the three conditions spent an average ± SE range of 6.89 ± 0.44–8.12 ± 0.59 min nearer their respective preferred target females ($F_{2,21}$=1.27, NS).

Observation

Each model male courted and mated with the target female with which he was paired.

Post-test

Group assignment had a significant effect on change from pretest to post-test in the time focal males spent with their preferred female subjects ($F_{2,21}$=4.58, P<0.03; Fig. 2). Focal males assigned to the no-delay condition showed a significantly greater decrease from pretest to post-test in the time spent affiliating with their previously preferred target female than did focal males assigned to either the 48-h delay or control conditions (Tukey-Kramer multiple comparisons tests: both P<0.05; Fig. 2). Focal males assigned to 48-h delay and control conditions did not differ from one another.

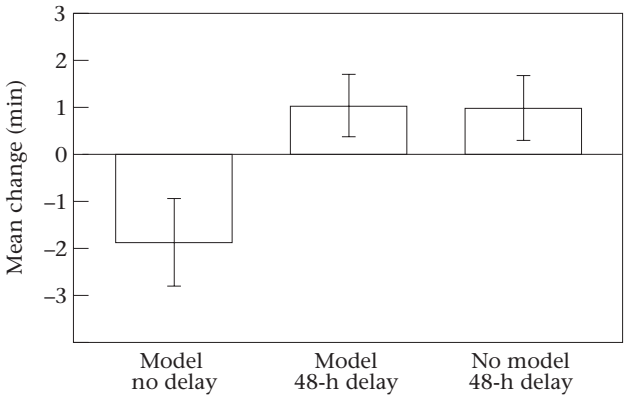

Figure 2. Mean±SE change in time (min) between pre- and post-test that focal male subjects assigned to no-delay, 48-h delay and control (48-h delay, no model) conditions spent nearer the female target subject they had preferred during the pretest.

The tendency of focal male quail to avoid affiliating with preferred females they had seen mating disappeared after 48 h. This result is consistent with White & Galef's (1999c) suggestion that sperm competition underlies male avoidance of contact with females seen mating. The result is not consistent with some other explanations of the avoidance of females seen mating by males. For example, if reduced risk of exposure to sexually transmitted diseases underlies male quails' avoidance of females seen mating, then delay between observation of a female mating and opportunity to affiliate with her should not reduce male avoidance of the female.

EXPERIMENT 2: EFFECTS OF DELAY ON FEMALES' PREFERENCES

In experiment 2 we examined the effect on a focal female's socially enhanced preference for a target male of imposing a 48-h delay between when she saw a previously nonpreferred target male mate and when she had an opportunity to affiliate with him.

Methods

Subjects

Thirty-nine female and 29 male Japanese quail served as subjects that we assigned to quartets in the same manner as experiment 1 except that in this experiment: (1) females served as focal and model subjects; and (2) males served as target subjects. We ensured that: (1) each female served only once as a focal female; (2) no two females served together in more than one quartet; (3) no target males served together as members of more than one quartet; and (4) no focal female had prior experience with either of her target males.

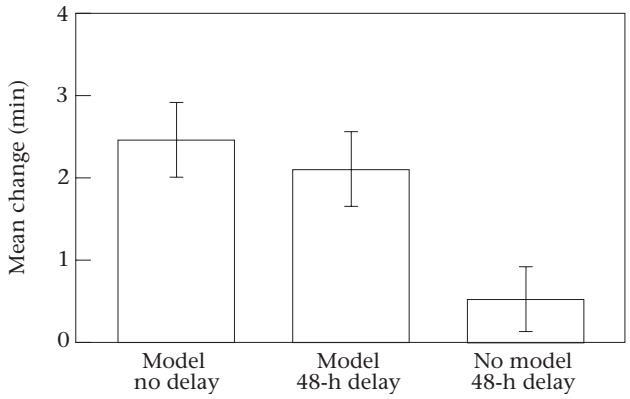

Figure 3. Mean±SE change in time (min) between pre- and post-test that focal female subjects assigned to no-delay, 48-h delay and control (48-h delay, no model) conditions spent nearer the male target subject they had not preferred during the pretest.

We randomly assigned equal numbers of focal females to no-delay, 48-h delay and control (48-h delay no model) conditions.

Apparatus

We used the same apparatus that we had used in experiment 1.

Procedure

The procedure was the same as experiment 1 except that: (1) females, rather than males, served as focal subjects; (2) males rather than females served as target subjects; and (3) we placed a model female in the end chamber containing each focal female's nonpreferred target male.

Results and Discussion

Pretest

During the pretest, focal females assigned to the three conditions spent an average ± SE range of 7.37 ± 0.37–7.90 ± 0.57 min nearer their respective preferred target males ($F_{2,39}$=0.12, NS).

Observation

Each nonpreferred target male courted and mated with the model female placed with him.

Post-test

Group assignment had a significant effect on the change between pretest and post-test in focal females' affiliative behaviour ($F_{2,36}$=5.65, P<0.01; Fig. 3). Post-hoc Tukey–Kramer multiple comparisons tests revealed that focal females assigned to both no-delay and 48-h delay conditions differed significantly from those assigned to the control condition in change in time spent near their nonpreferred target males (both P<0.05; Fig. 3). Females assigned to no-delay and 48-h delay conditions did not differ from one another on this measure. The increase in the tendency of a female quail to affiliate with a nonpreferred male seen with another female was stable over 48 h.

It has been hypothesized that in avian species (e.g. black, *Lyrurus tetrix*, and sage grouse, *Centrocercus urophasianus*) in which females visit a lek before breeding (presumably to evaluate potential mates) and wait 2–3 days before returning to breed, a female's mate choice may be influenced by her prior observations on the lek of the mate choices of others (Hoglund et al. 1990; Gibson et al. 1991). If this is so, effects on the mate preferences of females of observing the mate choices of others must be stable over days (Brooks 1996). The results of the present experiment suggest that social influences on preferences of female birds may, in fact, be of sufficient duration to produce socially mediated, nonindependent female mate choice on leks.

EXPERIMENT 3: EFFECTS OF DELAY ON MALES' PREFERENCES REVISITED

It might be argued that the differing effect on affiliative behaviour of a 48-h delay between the observation and post-test phases of experiment 1 and experiment 2 was not due to differences in the sex of focal subjects, but to our having placed model subjects with preferred target subjects in experiment 1 and with nonpreferred target subjects in experiment 2. In experiment 3 we replicated the procedures of experiment 1 exactly except that we allowed focal males to observe their nonpreferred, rather than their preferred, target females mate with model males during the observation phase of the experiment.

Methods

Subjects

Thirty-one male and 43 female Japanese quail served as subjects. We randomly assigned either 10 or 11 males as focal subjects to each of 48-h delay, no-delay and control (no model, 48-h delay) conditions.

Apparatus

We used the same apparatus that we used in experiments 1 and 2.

Procedure

The procedure was identical to that used in experiment 1, except that during the observation phase of the experiment, we placed a model male in the end chamber containing each focal male's nonpreferred, rather than its preferred, target female.

Results and Discussion

Pretest

During the pretest, focal males assigned to the three conditions spent an average ± SE range of 7.32 ± 0.55–8.70 ± 0.32 min nearer their respective preferred target females ($F_{2,28}$=2.50, NS).

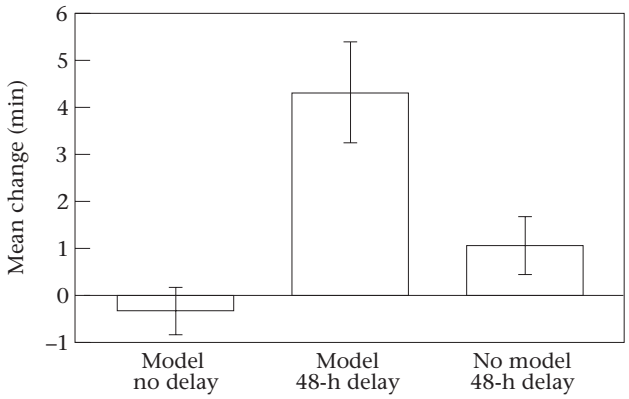

Figure 4. Mean±SE change in time (min) between pre- and post-test that focal male subjects assigned to no-delay, 48-h delay and control (48-h delay, no model) conditions spent nearer the female target subject they had not preferred during the pretest.

Observation

Each model male courted and mated with the nonpreferred target female with which he was paired.

Post-test

Group assignment had a significant effect on the change between pretest and post-test in focal males' affiliative behaviour ($F_{2,28}$=8.61, P<0.002; Fig. 4). Focal males assigned to the 48-h delay condition showed a significantly greater increase from pretest to post-test in the time that they affiliated with their respective previously nonpreferred target females than did males assigned to either no-delay or control conditions (Tukey–Kramer multiple comparisons tests: both P<0.05; Fig. 4), which did not differ from one another.

In confirmation of the results of White & Galef (1999a), the mate choices of males assigned to the control condition did not change from pretest to post-test (paired t test: t_{10}=1.70, NS). Mate choices of unmanipulated males remain stable over time.

In confirmation of White & Galef (1999c, Experiment 1) focal males allowed to see their nonpreferred target females mate and tested immediately thereafter (no-delay condition) did not show a change from pretest to post-test in their affiliative behaviour (t_9=0.06, NS). In the present experiment, as in Galef & White (1999c, Experiment 1), focal males spent, on average, less than 2 min of the pretest closer to their nonpreferred than to their preferred target females. Because focal males spent so little time near their nonpreferred target females during the pretest, a significant reduction between pretest and post-test in the time focal males spent nearer their nonpreferred female was unlikely to be observed.

We have no data from earlier experiments that would lead us to predict the change in affiliative behaviour of focal males assigned to the 48-h delay condition. If there is a cost to males of choosing a mate, as their seems to be to females, and if males can avoid this cost by copying the mate choices of others, then focal males might be expected to show an increased preference for females seen mating once sufficient time passed for the fertilizability of such females to regain baseline levels. Alternatively, because the value of information concerning which females have mated depreciates rapidly over time, males might have evolved to forget such observations in a few hours. If so, 48 h after a male saw a focal female mate, we would expect to see no change from pretest to post-test in his affiliative behaviour.

The actual outcome of experiment 3, in which males assigned to the 48-h delay condition showed a significant increase from pretest to post-test in the time they spent nearer to their nonpreferred target females (t_9=4.00, P<0.01) 48 h after seeing them mate suggests two conclusions. First, males do remember for 48 h or more which target female they saw mating during the observation period. Second, and more important for interpretation of the difference in outcomes of experiments 1 and 2, the difference between male and female quail in the stability of their changes in mate preference over 48 h was not an artefact resulting from differences in the initial attractiveness of members of the opposite sex seen mating by focal subjects in the two experiments. In the present experiment, focal males assigned to the model, 48-h delay condition, like males assigned to the same condition in experiment 1, showed a significantly greater enhancement of their preference for a target female than did focal males assigned to the model, no-delay condition.

GENERAL DISCUSSION

Sexual selection theory leads to the prediction that male and female quail should respond differently to seeing a member of the opposite sex mate; and the expected differences in response have been confirmed in previous publications from our laboratory (Galef & White 1998; White & Galef 1999b, c). The same theoretical arguments that predict differences in the immediate response of males and females to seeing a member of the opposite sex mate also lead to the prediction that these acquired responses of male and female quail should differ in duration; females' enhanced preference for males seen mating should be longer lasting than males' avoidance of females seen mating. The results of the present experiments: (1) replicate our previous demonstrations of different effects on the affiliative behaviour of male and female focal subjects of observing a member of the other sex mate; and (2) demonstrate for the first time that the duration of such effects varies between sexes in the direction sexual selection theory would predict.

Rozin & Kalat (1971) first interpreted the special features of taste-toxicosis conditioning as reflecting an adaptive specialization of a learning mechanism. In the intervening 30 years, relatively few other compelling instances of such adaptive specialization have been described in the literature (reviewed in Shettleworth 1998). The present results suggest that observed differences in the direction and duration of the responses of male and female quail to seeing members of the opposite sex mate reflect the action of domain-specific information-processing systems (Cosmides & Tooby 1995). Whether the difference between the sexes in duration of response to the sight of a member of the opposite

sex mating reflects a sex-related difference in affective or cognitive responses remains to be determined.

Acknowledgments

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