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Social effects on mate choices of male Japanese quail, *Coturnix japonica*

DAVID J. WHITE & BENNETT G. GALEF, JR
Department of Psychology, McMaster University

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In four experiments, we examined effects on affiliative preferences of 'focal' male Japanese quail of seeing a conspecific female interact with another male. Each experiment was conducted in three 10-min phases: (1) a pretest during which a focal male chose between two females; (2) an observation phase, when each focal male watched the female he had spent more time near during the pretest (his 'preferred' female) interact with another male (referred to as a 'model' male); and (3) a post-test, during which each focal male again chose between his nonpreferred and preferred females. Focal males decreased their preferences for preferred females after seeing them together with a model male, even when preferred females and model males were separated by a transparent barrier that prevented them from mating, but allowed them to court. A focal male's preference for his preferred female did not decrease when the female mated with a model male out of sight of the focal male. These first results could reflect a tendency for males simply to avoid areas where they saw conspecifics courting. However, focal males also showed reduced preferences for preferred females they had seen mate when the locations of preferred and nonpreferred females were reversed between observation and post-test phases of the experiment and the effects of transposition were controlled for. We concluded that male quail tend to avoid areas that recently contained courting pairs, as well as particular females, seen courting.

Results of recent experiments have shown that mate choices of female Japanese quail can be influenced by their observation of the behaviour of conspecific females (Galef & White 1998; White & Galef 1999). When given a choice between males, female quail spend more time affiliating with males they have seen standing near, courting, or mating with other females. Such use of social information in selecting a sex partner could, under some circumstances, reduce the cost to females of identifying desirable partners (for review, see Gibson & Hoglund 1992; Dugatkin 1996).

In most species, females incur the preponderance of costs of reproduction, and reproductive failure is less costly for males than for females. Consequently, males would, in general, be expected to be less discriminating than females when choosing sexual partners. Still, as Andersson (1994) has argued, one might expect males to be selective in choosing mates whenever: (1) there is predictable variation in the reproductive potential of females; (2) males have the opportunity to mate with more than one female; and (3) mating with any one female reduces a male's chances of fertilizing other females. Indeed, there are several species of vertebrate in which males are known to be choosy (Erickson & Zenone 1976; Berven 1981; Sargent et al. 1986; van den Berghe & Warner 1989; Grant et al. 1995). In avian species examined to date (unfortunately, there are no *Corturnix* species among them), the first of two males to mate within a brief period with a female fertilizes the majority of her eggs (Birkhead 1988; Birkhead & Moller 1992), although this first-male advantage is gradually reversed over hours or days. Males of such species might be expected to show a brief decrease in interest in females seen mating with other males. Predicting the effects of observation of females mating on mate preference of male Japanese quail is complicated by females' ability to exert some control over fertilization of their eggs (Adkins-Regan 1995), and it is not known how this active sperm selection interacts with effects of sperm precedence.

In the present experiments, we asked whether the affiliative preference of male Japanese quail, like those of females of their species, might be influenced by seeing potential mates engage in sexual behaviour.

GENERAL METHODS

Subjects

Groups of 10 male and 10 female Japanese quail purchased from a commercial breeder (Speck's Poultry Farm, St Mary's, Ontario, Canada) when 48 days of age served as subjects in each of the experiments reported below. After

Correspondence: B. G. Galef, Jr, Department of Psychology, McMaster University, Hamilton, Ontario L8S 4K1, Canada (email: galef@mcmaster.ca).

transport to our laboratory in Hamilton, Ontario, we placed each bird in an individual, stainless-steel cage, measuring 45.7 × 61.0 × 40.6 cm, housed in a colony room illuminated for 16 h/day, with light onset at 0600 hours.

We maintained all birds on ad libitum Mazuri Pheasant Starter 5637 (PMI Feeds, St Louis, Missouri) and water and, at the insistence of our University veterinarian, gave each bird biweekly access to a handful of autoclaved hay that was intended to 'enrich' their maintenance environment.

We did not start experiments for 30 days, waiting until the birds had come into breeding condition in response to exposure to light for 16 h/day. We considered females ready to breed when they started to lay eggs once every 2 days.

To determine when males were ready to breed, we placed each male with females in breeding condition in the apparatus we subsequently used for experiments. We paired each male with a randomly selected female each day until he either mounted the female on 2 successive days or 2 weeks passed without his mounting the female. We, thus, accustomed both males and females to mating in the experimental apparatus before we started the experiments. We used as subjects only those males that reliably mounted females. Males that reached criterion sexual performance were kept in isolation for 7–10 days before we started the experiments.

Testing Schedule

To be sure that we did not repeatedly use the same males with the same females, before beginning each experiment, we assigned males and females to quartets with the restriction that no male was in more than one quartet with any female. We then randomly assigned one of the two males in each quartet to serve as a 'focal' male and the other to serve as a 'model' male (i.e. a mate for one of the females) in that quartet. Although it would have been preferable if no animal ever participated twice in our experiments, practical constraints made it impossible to maintain the hundred or more sexually active quail needed to do so. We did ensure that in each experiment: (1) no focal male ever saw any female twice; (2) no two focal males ever chose between the same pair of females; (3) no male ever served twice as the model male for the same focal male; and (4) on those days when scheduling required that a male participate in the experiment twice on the same day, he never served twice as a model male or twice as a focal male and always served as a focal male before serving as a model male.

Each male served as a focal male once and only once in each condition in an experiment, and within each experiment, we counterbalanced the order in which males served in conditions.

Apparatus

We conducted all experiments in an enclosure, measuring 121.9 × 61.0 × 30.5 cm, constructed of painted

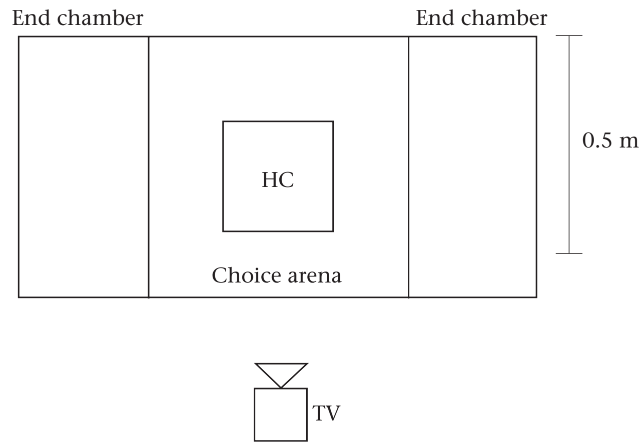

Figure 1. Overhead schematic of the apparatus. TV: Closed-circuit television; HC: holding cage.

plywood (Fig. 1). The enclosure had a Plexiglas roof and front wall, two hardware-cloth partitions, and rested on an aluminium tray covered with disposable, absorbent paper pads (Tray Liners, Lilo Products, Hamilton, Ontario, Canada).

The two hardware-cloth (0.5-in (1.27-cm) mesh) partitions, placed 30.5 cm from opposite ends of the enclosure, divided it into three compartments. We cut a 25.4 × 25.4 cm opening in the centre of the transparent Plexiglas roof of the central compartment through which we could raise or lower a transparent Plexiglas holding cage measuring 25.2 × 25.2 × 40.6 (Fig. 1) using a pulley system operated from a room adjacent to that housing the enclosure.

We also drew a line from top to bottom on the front wall of the enclosure, at the midpoint of the central compartment. This line enabled us to determine reliably, at any time, the end of the enclosure to which a male was closest.

A colour CCTV video camera (Panasonic WV-CP412) attached to a video-cassette recorder (Panasonic AG-1240) and colour video monitor (CT 1331Y) faced the transparent Plexiglas front wall of the enclosure permitting us both to observe in real time all behaviour occurring within the enclosure and to record that behaviour for later scoring.

Procedure

Each of the experiments described below consisted of three 10-min phases. Phase 1 was a pretest we used to determine a 'focal' male's initial preference between two females. Phase 2 was an observation period during which each focal male had the opportunity to observe one of the two females that he had seen during the pretest together with another male. Phase 3 was a post-test used to again determine a focal male's preference between the same two females that he had seen during the pretest.

Experiments differed only in manipulations carried out during phase 2, the observation phase of the experiment.

Phase 1: pretest

To begin an experiment, we placed a reproductively active female quail in each of the two end chambers of the apparatus and a focal male in the holding cage in the centre of the apparatus and left all three animals undisturbed for 30 s. We then raised the holding cage approximately 15 cm, thus permitting the focal male to move freely about the central compartment of the enclosure.

We began to take data as soon as the focal male took his first step after we had raised the holding cage that had restrained him. For the next 10 min, we recorded the amount of time the focal male spent on each side of the midline of the enclosure. During the pretest, males moved between the two ends of the central compartment, often orienting towards females and occasionally displaying to them. We labelled the female held on the side of the enclosure where the male spent the majority of the 10-min pretest as that male's 'preferred' female and the other female as his 'nonpreferred' female.

Phase 2: observation

To begin the observation phase, we returned the focal male to the holding cage and then placed a second 'model' male in the end compartment that held the focal male's preferred female. We then left the four birds undisturbed for 10 min so that the focal male could observe his preferred female with the model male and his nonpreferred female alone in her end of the enclosure. We recorded whether the preferred female mated with the model male.

Phase 3: post-test

At the end of the observation phase, we removed the model male from the enclosure and repeated the procedure we had used during the pretest (i.e. we released the focal male from the holding cage and, once he had started to walk, recorded the time that he spent on each side of the midline of the enclosure).

Interobserver reliability

To measure the reliability of our scoring methods, we gave two independent observers videotapes of 10 30-min experimental sessions and asked each observer to determine the difference in the time that the 10 focal males in the tapes spent during pretest and post-test with their respective preferred females. A Pearson's product-moment correlation of the 10 difference scores awarded by the two observers was significant (r_{10}=0.99, P<0.001).

Data Analysis

To control for each male's serving as a focal male in each condition in an experiment, we analysed the data using either paired *t* tests (when there were only two conditions in an experiment) or repeated measures ANOVAs (when there were more than two conditions in an experiment).

EXPERIMENT 1: EFFECTS ON FOCAL MALE MATE CHOICE OF OBSERVING A PREFERRED FEMALE MATE WITH A MODEL MALE

We undertook experiment 1 to determine whether, during the post-test, a focal male Japanese quail would spend less time near the female he preferred during the pretest, if he had seen her mate with a model male during the observation period.

Methods

Subjects

First, we randomly assigned 15 males and 18 females from two shipments to 30 quartets. Then we assigned each quartet to either mating or control conditions (N=15 quartets/condition) with the restriction that each male serve only once in each condition.

Procedure

We treated focal males when assigned to the mating condition as described in General Methods. They first chose between two females, then saw their preferred female mate with a model male, and during the post-test, chose between the same two females that they had chosen between during the pretest.

We treated focal males when assigned to the control condition exactly as we treated focal males when they were assigned to the mating condition except that we did not place a model male in the apparatus during the observation phase of the experiment.

Results

Pretest

During the pretest, male subjects while in the mating condition spent a mean ± SE of 7.31 ± 0.42 min near their respective preferred females. When the same subjects were in the control condition, they spent 6.42 ± 0.31 min near their respective preferred females (paired *t* test: t_{14}=1.64, NS).

Observation phase

All model males mounted females when given the opportunity to do so.

Post-test

When in the mating condition (i.e. when they had the opportunity to see their respective preferred females mate during the observation phase of the experiment), focal males spent significantly less time with their preferred females than they had during the pretest (paired *t* test: t_{14}=3.34, P<0.005; Fig. 2). In contrast, focal males when in the control condition (i.e. when their preferred females did not mate with model males during the observation phase), did not show a change between pretest and post-test in the time that they spent on the side of the enclosure containing their respective preferred females (t_{14}= − 1.78, NS; Fig. 2).

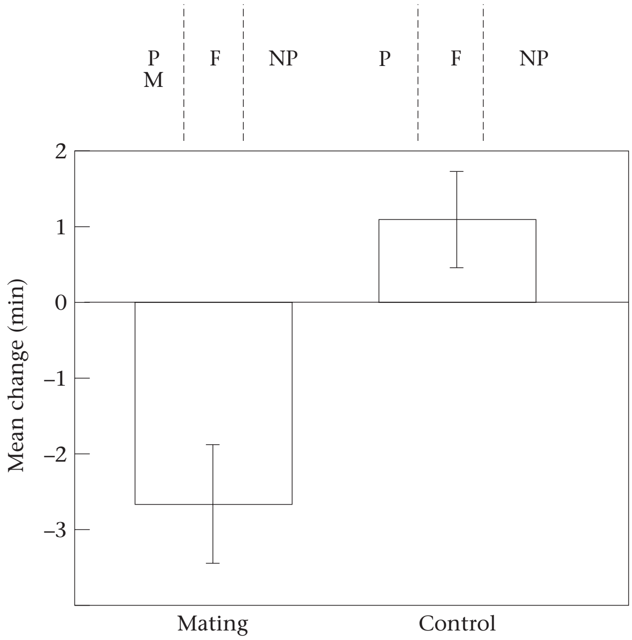

Figure 2. Mean (±SE) change from pre- to post-test in min that focal males in experiment 1 spent on the side of the apparatus containing their respective preferred females when assigned to mating and control conditions. P: Preferred female; F: focal male; M: model male; NP: nonpreferred female.

Furthermore, when males were focal subjects in the mating condition, they showed a significantly greater change from pretest to post-test in the time they spent near their preferred female than when they were focal subjects in the control condition (paired *t* test: t_{14}=3.45, P<0.01).

Also, when we examined each male's first experience as a focal subject, we found that five of the eight focal males assigned first to the mating condition spent less than half of the 10-min post-test on the side of the enclosure containing the female that they had preferred during the pretest, while none of the seven focal males assigned first to the control condition showed a similar change in affiliative behaviour between pretest and post-test (Fisher's exact test: P<0.05). This finding, like the results of the paired *t* tests, is consistent with the hypothesis that focal males showed a decrease in their tendency to affiliate with females after seeing them mate with another male.

When, for symmetry, we repeated experiment 1 with a new set of subjects but placed the model male with each focal male's nonpreferred female, rather than with his preferred female, we found a nonsignificant change between pretest and post-test in the time focal males affiliated with their respective nonpreferred females (-0.58 ± 1.10 min; paired *t* test: t_8=0.53, NS). During the pretest, focal males spent 7.66 ± 0.51 min in contact with their preferred females, and it therefore seems likely that a ceiling effect prevented us from seeing any statistically significant effect of focal males' observation of their respective nonpreferred females mating with model males.

Discussion

The results of experiment 1 are consistent with the hypothesis that male Japanese quail tend to avoid affiliating with females that they have seen mating. The proximal cause of this change in preference remains to be determined.

EXPERIMENT 2: DOES MATING CHANGE A FEMALE'S ATTRACTIVENESS TO MALES?

The changes in males' behaviour towards preferred females seen in experiment 1 may not have been a result of focal males seeing their respective preferred females mate, but of changes in the behaviour or appearance of females after mating. In the present experiment, we compared the behaviour of focal males towards their respective preferred females when those females mated during the observation phase of the experiment and focal males either saw (visible condition) or did not see (blind condition) their preferred females in the act of mating.

Methods

Subjects

First, we randomly assigned nine male and 11 female quail to 18 quartets as described in General Methods. We then randomly assigned these quartets to visible and blind conditions (N=9 quartets/condition).

Procedure

The procedure was identical to that described in General Methods except that we modified the holding cage in which we placed focal males during the observation phase of the experiment. We made two opposite walls of the holding cage opaque by attaching to them pieces of white Bristol board measuring 30 × 30 cm.

During the observation phase, we placed focal males when assigned to the 'visible' condition in the holding cage with the opaque walls facing the front and back of the enclosure; thus, the focal males could see both their preferred and nonpreferred females. When the same males were in the 'blind' condition, we treated them as we treated them when they were in the visible condition, except that, during the observation phase, we oriented the holding cage so that the opaque walls of the cage prevented the focal males from seeing either their preferred or nonpreferred females.

Results

Pretest

During the pretest, focal males when in the visible and blind conditions spent, respectively, a mean ± SE of 7.77 ± 0.62 min and 7.81 ± 0.56 min closer to their preferred than to their nonpreferred females. There was no statistical difference between groups in the time focal males spent near their respective preferred females (paired *t* test: t_8=0.06, NS).

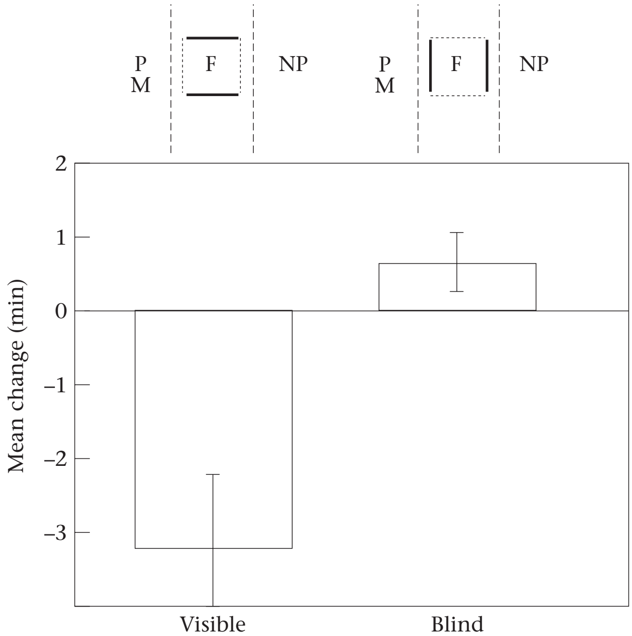

Figure 3. Mean (±SE) change from pre- to post-test in min that focal males in experiment 2 spent on the side of the apparatus containing their respective preferred females when in the visible and the blind conditions. See caption of Fig. 2 for explanation of the cartoons above histograms.

Observation phase

All model males mounted females when given the opportunity to do so.

Post-test

Focal males when in the visible condition showed a significantly greater decrease between pretest and post-test in the time that they spent near their preferred female than they did when in the blind condition (t_8=3.42, P<0.01; Fig. 3). Only when focal males were in the visible condition did they show a significant decrease between pretest and post-test in the time that they spent on the side of the enclosure that held their preferred female (paired *t* tests: visible group, t_8=3.23, P<0.02; blind group: $t_8 = -1.57$, NS; Fig. 3).

Discussion

The results indicate that males are less attracted to females they have seen mating because they saw mating occur, not because of some change in the appearance or behaviour of females that resulted from mating.

EXPERIMENT 3: WHAT DO MALES HAVE TO SEE PREFERRED FEMALES DO IN ORDER TO LOSE INTEREST IN THEM?

In experiment 3, we determined the type of interaction between the model male and the preferred female that a focal male had to observe, if he were to show a reduced tendency to affiliate with a preferred female. Perhaps a focal male had to see his preferred female actually copulate with another male, if his preference for her was to be reduced. Perhaps seeing a preferred female simply standing near another male would reduce her attractiveness.

Methods

Subjects

First, we assigned 10 male and 10 female quail to 30 quartets, and then assigned each quartet to one of the three groups described in Procedure (N=10/group).

Apparatus

The apparatus that we used in experiment 3 was identical to that described in General Methods except that during the observation phase of the experiment we confined the model male in a transparent Plexiglas holding cage, measuring 25.2 × 25.2 × 40.5 cm, with one wall made opaque by attaching to it a piece of white Bristol board measuring 30 × 30 cm. To control for effects of presence of a holding cage in the end compartment of the enclosure containing a focal male's preferred female, we placed an identical holding cage, in the same orientation, in the end compartment of the enclosure containing each focal male's nonpreferred female, but placed no model male in it.

Procedure

The procedure of experiment 3 was identical to that described in General Methods except that, during the observation phase, we confined model males, as well as focal males, in holding cages. The only difference in treatment of focal males when assigned to the different conditions was in the orientation during the observation phase of the experiment of the opaque wall of the holding cage containing the model male. When focal males were assigned to the 'female-alone condition', the opaque wall of the cage holding the model male was situated between the focal male and the model male so that, during the observation phase, the focal male saw his preferred female standing alone. When focal males were assigned to the 'male-female-isolated condition', during the observation phase of the experiment, we placed the opaque wall of the cage holding the model male between the model male and the focal male's preferred female, so that each focal male saw his preferred female and a strange male standing near one another, but not interacting. Last, when we assigned males to the 'male-court condition' we placed the model male in the holding cage with the opaque wall of the cage facing away from the focal male. Consequently, during the observation phase of the experiment, each focal male when in the male-court condition saw a model male actively courting, but not mating with, his preferred female.

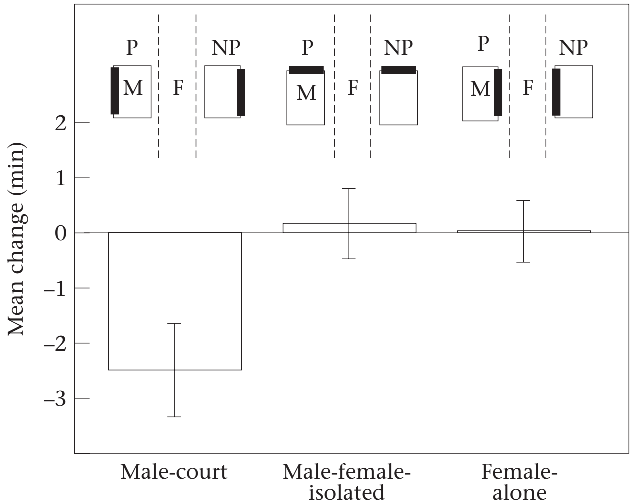

Figure 4. Mean (±SE) change from pre- to post-test in min that focal males in experiment 3 spent on the side of the apparatus containing their respective preferred females when in male-court, male-female-isolated and female-alone conditions. See caption of Fig. 2 for explanation of the cartoons above histograms.

Results and Discussion

Pre-test

During the pretest, when focal males were assigned to female-alone (mean ± SEM=7.43 ± 0.50 min), male-court (7.53 ± 0.42 min) and male-female-isolated conditions (7.59 ± 0.35 min), they did not differ in the time that they spent closer to their preferred females than to their nonpreferred females (repeated measures ANOVA, $F_{2,18}=0.03$, NS).

Post-test

We found a significant effect of condition on the change between pretest and post-test in the time that focal males spent nearer their preferred than nonpreferred females (repeated measures ANOVA: $F_{2,18}=4.76$, $P<0.03$; Fig. 4). Only when focal males were assigned to the male-court condition did they show a significant decrease between pretest and post-test in the time that they spent on the side of the enclosure that held their preferred females (male-court condition: paired *t* test: $t_9=2.98$, $P<0.02$; male-female-isolated and female-alone conditions: both t_9s>0.10, NS; Fig. 4). Post hoc tests revealed that when assigned to the male-court condition, focal males decreased the time that they spent with their respective preferred females significantly more than they did when assigned to either male-female-isolated or female-alone conditions (Tukey's tests, both *P*s<0.05).

The results indicate that a focal male has to see a model male actively court his preferred female, if the focal male's attraction to that female is to be reduced. This result differs from that obtained by White & Galef (1999) in studies of social influences on mate choices of female Japanese quail. Attractiveness of a nonpreferred male quail to a focal female increased when she saw the male simply standing near a model female (White & Galef 1999).

EXPERIMENT 4: CAN FOCAL MALES IDENTIFY AN INDIVIDUAL FEMALE SEEN COPULATING WITH A MODEL MALE?

The results of experiments 1–3, while consistent with the hypothesis that a focal male is less attracted to a female after seeing her mate with another male, can also be interpreted as showing that a focal male tends to avoid areas where he has seen another male. We undertook experiment 4 to determine whether the changes in the affiliation of focal males with preferred females seen in experiments 1–3 might represent changes in response to individual females seen interacting with model males, rather than changes in attractiveness of places where a female has been seen interacting with a male.

Methods

Subjects

Thirteen male and 19 female quail from two shipments served as subjects. We randomly assigned these 32 animals to 39 quartets, and then assigned these quartets to the three groups as described in Procedure.

Apparatus

The apparatus was that used in experiments 1–3.

Procedure

We treated focal males when assigned to the 'mating condition' exactly as we treated focal males when assigned to the mating condition in experiment 1 except that at the end of the observation phase, and before starting the post-test, each female was first removed from, then replaced in, the same end chamber that she had occupied since the start of the pretest. When focal males were assigned to the mating condition, during the observation phase of the experiment, they saw their respective preferred females mate with model males. We treated focal males when assigned to the 'mating-switch condition' exactly as we treated focal males when assigned to the mating condition except that at the end of the observation period, and before starting the post-test, we reversed the position of the two females. We controlled for possible effects of disturbance caused by moving females in the mating-switch condition (experiment 5 in White & Galef 1999), by treating focal males when assigned to the 'control-switch condition' exactly as we treated focal males when assigned to the mating-switch condition with one exception. During the observation phase of the experiment, we did not place a model male with each focal male's preferred female.

Results

Pre-test

During the pretest phase of the experiment, when focal males were assigned to mating, mating-switch and control-switch conditions they spent, respectively, a mean ± SE of 8.41 ± 0.34, 7.51 ± 0.40, and 7.79 ± 0.45 min of the 10-min pretest closer to their respective

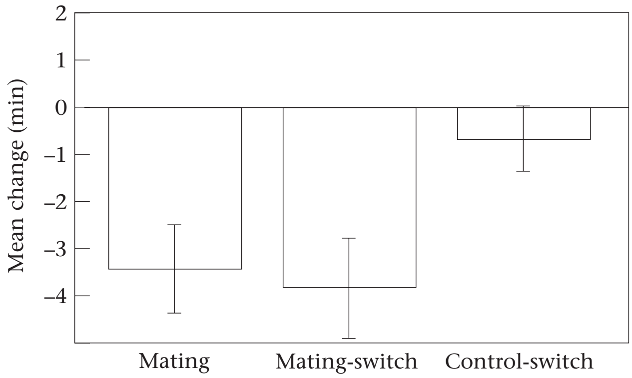

Figure 5. Mean (±SE) change from pre- to post-test in min that focal males in experiment 4 spent on the side of the apparatus containing their respective preferred females when in mating, mating-switch, and control-switch conditions.

preferred than nonpreferred females (repeated measures ANOVA: $F_{2,24}$=1.40, NS).

Post-test

We found a significant effect of condition on the change between pretest and post-test in the time that focal males spent nearer their preferred than nonpreferred females (repeated measures ANOVA: $F_{2,24}$=3.63, P<0.05; Fig. 5); focal males when assigned to both mating and mating-switch conditions showed a significant decrease between pretest and post-test in the time they spent on the side of the enclosure that held their respective preferred females (paired t tests: mating-condition: t_{12}=3.79, P<0.01; mating-switch condition: t_{12}=3.65, P<0.01, Fig. 5), while focal males when assigned to the control-switch condition did not show a change in preference between pre- and post-test (paired t test: t_{12}=0.93, NS).

Discussion

The results of experiment 4 are consistent with the view that male quail can identify individual females they see copulating with other males, and subsequently avoid contact with such females.

GENERAL DISCUSSION

'Mate-choice Copying' by Females and Social Reversal of Males' Mate Choices

Patriquin-Meldrum & Godin (1998, page 570) have proposed that 'A female [should be] considered to have copied the mate choice of another female(s) if the probability of her choosing a specific male as a mate is increased specifically as a result of her observing other females previously choosing that same male, rather than because of any change in that male's behavior due to his prior mating or proximity to females or because of any preference by females for certain sites irrespective of the male or to aggregate with other females' (see also Wade & Pruett-Jones 1990; Dugatkin 1992, 1996; Pruett-Jones 1992). By exchanging the sex of chooser and chosen in Patriquin-Meldrum & Godin's (1998) definition, one could produce a description of 'true' social influence on mate choice in males as well, what we will call 'social reversal of males' mate choices'.

Results of experiment 2 indicate that the change in attractiveness of female quail to conspecific males (like the change in attractiveness of male quail to conspecific females) is not a result of changes in behaviour or appearance caused by mating. Results of experiment 4 indicate that in male, as in female quail (Galef & White 1998; White & Galef 1999), attractiveness of an individual of the opposite sex, not attractiveness of the area that that individual occupies, can change after a member of the opposite sex has been seen copulating. Thus, the behaviour of male Japanese quail meets the criteria for social reversal of male mate choice analogous to the criteria for mate-choice copying by females proposed by Patriquin-Meldrum & Godin (1998) and met by female Japanese quail.

Choice of a Sex Partner by Male and Female Japanese Quail

Taken together, the results of experiments 1–4 provide compelling evidence that male Japanese quail, like females of their species (Galef & White 1998; White & Galef 1999), change their tendency to affiliate with individuals of the opposite sex seen in compromising situations: female Japanese quail show an increased tendency to affiliate with male they have seen with other females (Galef & White 1998; White & Galef 1999), male Japanese quail showed a decreased tendency to affiliate with females they have seen courted by other males. We also now know that, in both sexes of Japanese quail, affiliative preference is a very potent predictor of actual choice of a sex partner (unpublished data). The opposite direction of the response of males and females to observation of sexual behaviour by potential mates interacting is, therefore, consistent with the hypotheses that: (1) female quail experience costs associated with selection of a sex partner; and (2) male quail experience costs associated with copulation with recently inseminated females.

Acknowledgments

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