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Mate choice copying and conspecific cueing in Japanese quail, *Coturnix coturnix japonica*

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In four experiments, we examined the effects on the affiliative preferences of 'focal' female Japanese quail given the opportunity to watch a conspecific male interact with a 'model' female. Experiments were conducted in three, 10-min phases: (1) a pretest, during which a 'focal' female chose between two males; (2) an observation phase, when each focal female watched the male she had spent less time near during the pretest (her 'nonpreferred' male) interact with a 'model' quail; and (3) a post-test, during which each focal female again chose between her nonpreferred and preferred males. Focal females increased their preferences for nonpreferred males after seeing them together with a model female (but not a model male), even if the nonpreferred male and model female were separated by an opaque barrier that prevented them from interacting. A focal female's preference for the end of the enclosure containing her nonpreferred male was not increased when she either watched him court a concealed model female or watched a model female that was being courted by him. Taken together, the present results suggest that a simple tendency for females to approach areas where they have previously seen a male and female quail, in preference to locations where they have seen only a male quail, can explain some of the effect of watching a nonpreferred male mate on a female's tendency to affiliate with him. However, focal females also showed enhanced preferences for nonpreferred males they had seen mating after we both moved those males and controlled for effects of transposition. Thus, processes akin to both 'mate choice copying' and 'conspecific cueing' remain viable explanations for the increase in a focal female quail's tendency to affiliate with a male she watched mate with another female.

The results of recent experiments examining social influences on preferences of female Japanese quail, *Coturnix coturnix japonica* (Galef & White 1998) demonstrate that a 'focal' female's tendency to remain near a previously nonpreferred male increases significantly after she has watched that male mate with another female (a model). Focal females often reverse their preference after watching the nonpreferred member of a pair of males mate with a model female (Galef & White 1998, experiment 1).

Such findings are consistent with the hypothesis that female quail copy one another's mate choices. However, as Pruett-Jones (1992) and others have indicated, the fact that females increase their tendency to remain near males they have seen mating is not, in itself, sufficient to show that they copy one another's mate choices. The important characteristic of copying behaviour that separates it from other similar processes is that the change in the probability of choice is strictly because of the actions of other females and not the consequences of those actions. Heyes (1993) has made a parallel distinction between imitative and nonimitative forms of social learning of motor acts, defining imitation as involving learning about behaviour (responses, actions, etc.), and nonimitative social learning as resulting from observers' learning socially about stimuli, objects, or events in the environment.

On Pruett-Jones's (1992) definition of mate choice copying, if mating changed the appearance or behaviour of males, thus increasing their attractiveness to females (Goldschmidt et al. 1993), or if females preferred males they had seen courting other females (Grant & Green 1996), such increase in attractiveness would not be a result of mate choice copying. Similarly, if females tended to move about in groups (a tendency that has been labelled conspecific cueing; Keister 1979), a solitary female might move into an area where she had previously seen a female consorting with a male, although she would not be copying the behaviour of the other female.

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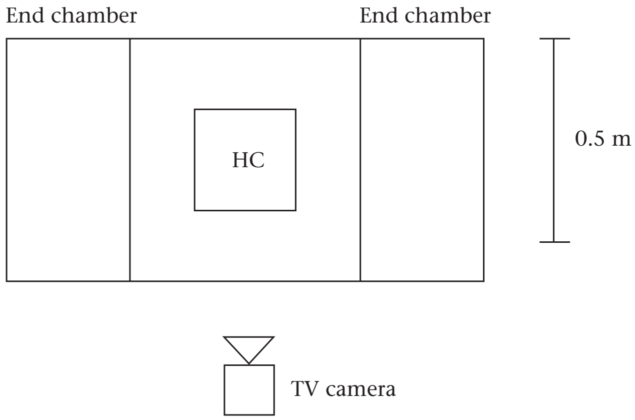

Figure 1. Overhead schematic of the apparatus. TV: closed-circuit television camera; HC: holding cage.

The results of our previous experiments on social influences on affiliative tendencies of female quail (Galef & White 1998) were not consistent with the hypotheses that either enhanced male attractiveness following mating or a tendency to stay near other females produced the observed increases in preferences of female quail for males seen courting and mating since (1) female quail showed increased preferences for males they had seen mating, but not for males that had mated while out of sight, and (2) female quail preferred a male they had seen mating even after his location was exchanged with that of another male that a female had not seen mating (Galef & White 1998, experiments 4 and 3, respectively). While these results suggest that female Japanese quail do copy one another's mate choices, they are obviously not sufficient to exclude alternative explanations of the observed increase in the tendency of female quails to affiliate with males seen courting and mating.

We undertook the present series of experiments to define further the stimuli that alter female quails' preferences for conspecific males they have seen engage in courtship. We hoped to determine whether 'copying' need be invoked to explain observed increases in the tendency of female quail to affiliate with males they have seen engage in reproductive behaviour.

GENERAL METHODS

Apparatus

We conducted all experiments in an enclosure, measuring 122.0 × 61.0 × 30.5 cm, constructed of painted plywood, transparent Plexiglas, and hardware cloth (Fig. 1). The enclosure rested on an aluminium tray covered with disposable, absorbant paper pads (Tray Liners, Lilo Products, Hamilton, Ontario, Canada).

Two hardware-cloth partitions, placed 30.5 cm from each end of the enclosure, divided the enclosure into three compartments: two end compartments and a central compartment. During experiments, each end compartment of the apparatus, measuring 30.5 × 61.0 × 30.5 cm, held a male quail, while the central compartment, measuring 61 × 61.0 × 30.5 cm, held a female quail.

We cut a 25.42-cm opening in the centre of the Plexiglas roof of the central compartment through which we could raise and lower a holding cage, measuring 25.2 × 25.2 × 40.6 cm, that we had constructed of transparent Plexiglas. A pulley system, operated from a room adjacent to that housing the enclosure, allowed us to raise the holding cage and release a female from under it without entering the room containing the enclosure.

We drew a line from top to bottom on the Plexiglas front wall of the enclosure, at its midpoint, so that, at all times, we could reliably determine the end of the enclosure to which a female was closer. A television camera (connected to a VHS video-cassette recorder and video monitor) faced the front wall of the enclosure and permitted us (1) to observe in real time all behaviour occurring within the enclosure, and (2) to determine the location of focal females throughout the pre- and post-test.

Results of tests of interobserver reliabilities in scoring videotapes (Galef & White 1998) revealed a high level of agreement between independent observers (r_{10}=0.99, P<0.001).

Subjects

Six groups, each consisting of 10 male and 10 female Japanese quail that we purchased from a commercial breeder (Speck's Poultry Farm, Vineland, Ontario, Canada) when 48 days old, served as subjects. Groups of 20 subjects were randomly selected from a barn containing several thousand quail of similar age. Selected quail were very unlikely to have been either close relatives or social companions.

After we transported each group of 20 subjects to the laboratory, we placed them in individual stainless-steel cages, measuring 45.7 × 61.0 × 40.6 cm, and gave them ad libitum access to water and Purina Game Bird Startena no. 5419 (Ralston-Purina Canada, Woodstock, Ontario, Canada).

Before we started experiments, we brought all subjects into breeding condition by keeping them for 30 days on a 16:8 h light:dark cycle. We considered females to be ready to breed when they began to lay eggs once every 2 or 3 days.

To establish the readiness of males to breed, we repeatedly placed each male together with a female in breeding condition in one end chamber of the apparatus we subsequently used for experiments (Fig. 1). We thus accustomed subjects to mating in the experimental apparatus at the same time that we determined when males were ready to breed. We paired each male with a different, randomly selected female in breeding condition twice per day until he either mounted two females in succession or 2 weeks passed without his showing interest in the females.

We did not use as subjects any males that failed to mount females 6 weeks after arrival in the laboratory.

Procedure

Each of the experiments described below consisted of three, distinct, 10-min phases: (1) a pretest used to determine a 'focal' female's initial preference between two males; (2) an observation period, during which a focal female could observe one of the two males she had chosen between during the pretest interact with a female and the other remain alone; and (3) a post-test that determined for a second time each focal female's preference between the same two males she had seen during the pretest. Experiments differed only in manipulations carried out during the observation phase.

Pretest

To begin an experiment, we placed a sexually proven male in each end chamber of the apparatus and a focal female in the holding cage in the centre of the apparatus and left them undisturbed for 30 s. We then raised the holding cage approximately 20 cm to allow the focal female to leave the holding cage.

During the 10 min following the first step that a focal female took after we had raised the holding cage, we recorded the time that she spent on each side of the midline of the enclosure. We considered the male on the side of the enclosure where a focal female spent the majority of the 10-min pretest to be her 'preferred' male and the other male to be her 'nonpreferred' male.

Observation

To begin the observation phase, we again placed the focal female in the holding cage, then placed a second female (a model female) in the end compartment that held the focal female's nonpreferred male. We then left the four birds undisturbed for 10 min so that the focal female could observe: (1) her nonpreferred male court and mate with the model female, and (2) her preferred male remaining alone. While in the holding cage, focal females could both see and hear both males.

Post-test

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

Testing schedule

To be sure that we were not repeatedly using the same males and females in any experiment, before beginning each experiment, we randomly assigned two females to each of the combinations of males that we could create using the sexually active male subjects in each group. We then randomly assigned one of the two females in each quartet to serve as a focal female and the other to serve as a model female within that quartet. No two focal females ever chose between the same pair of males, no focal female ever saw any male twice, and no female ever served twice as the model female for the same focal female.

We conducted five trials per day, and allowed no female or male to participate in more than two trials on the same day. On those days when a female participated in the experiment twice, she never served twice as either a focal or model female and always served as a focal female before she served as a model female.

EXPERIMENT 1: EFFECTS OF OBSERVATION OF MATING ON MATE CHOICE

To establish the reliability of social influences on preference for males in Japanese quail, in experiment 1 of the present series, we simply repeated our basic experiment (Galef & White 1998, experiment 1), in which, during the observation phase, nonpreferred males of focal females assigned to the experimental group courted and mated with model females, while nonpreferred males of focal females assigned to the control group did not interact with a model female.

Methods

Subjects

We randomly assigned each of 24 quartets of quail to experimental ($N=14$ quartets) and control ($N=10$ quartets) conditions.

Procedure

At the end of the pretest, we placed a model female in the end chamber of the enclosure containing the nonpreferred male of each focal female that we had assigned to the experimental condition. We treated each focal female assigned to the control condition exactly as we treated focal females assigned to the experimental condition except that we did not place a model female in the apparatus during the observation phase of the experiment.

Results and Discussion

Pretest

During the pretest, focal females assigned to the experimental group spent an average (±SE) of 7.32±0.44 min on the side of the cage containing their preferred males. Focal females assigned to the control group did not differ from those assigned to the experimental group in the time (7.38±0.51 min) that they spent close to their respective preferred males ($t_{22}=0.08$, NS).

Observation

During the observation phase, all 14 males assigned to the experimental group mounted their respective model females.

Post-test

Focal females in the experimental group spent significantly more time with their nonpreferred males during the post-test than during the pretest (paired *t* test, $t_{13}=5.59$, $P<0.001$; Fig. 2). On the other hand, there was no change between pre- and post-tests in the time focal females assigned to the control condition spent on the

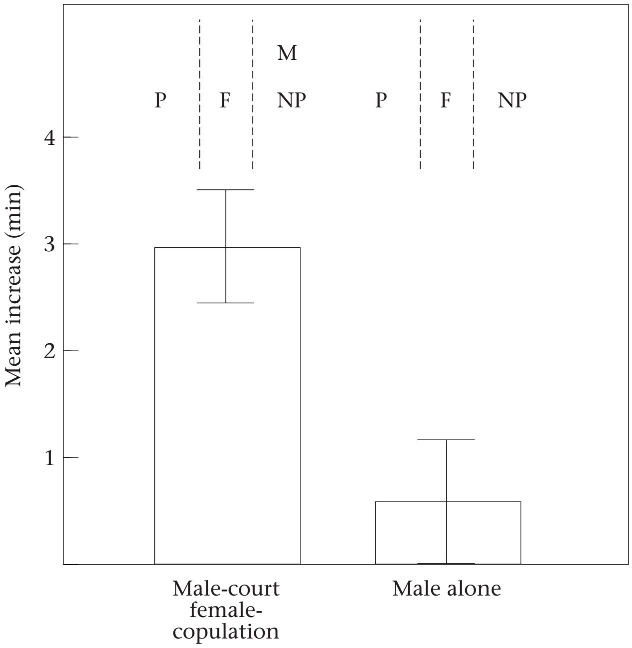

Figure 2. Mean (±SE) change from pre- to post-tests in the number of minutes that focal females spent on the side of the apparatus containing their respective nonpreferred males in experiment 1 after seeing their nonpreferred male court and mate (experimental condition) or not court and mate (control condition). Letters above histograms show the relative positions of the model female (M), the focal female (F), the preferred male (P) and the nonpreferred male (NP) during the observation phase of the experiment.

side of the enclosure containing their respective nonpreferred males (paired *t* test: $t_9=1.03$, NS; Fig. 2).

The change in time spent with nonpreferred males between the pre- and post-tests was significantly greater for focal females assigned to the experimental group than for focal females assigned to the control group (*t* test: $t_{22}=2.98$, $P<0.01$; Fig. 2). During the post-test, nine of the 14 subjects assigned to the experimental group spent more time affiliating with the male they had not preferred during the pretest, while only two of the 10 subjects assigned to the control group did so (Fisher's exact test $P<0.04$).

The results of experiment 1 confirmed the main findings of Galef & White (1998). Female Japanese quail show an enhanced tendency to affiliate with nonpreferred males after seeing nonpreferred males court and mate with model females.

EXPERIMENT 2: DEFINING NECESSARY CONDITIONS FOR CHANGES IN FEMALE PREFERENCE

We undertook experiment 2 to determine whether a focal female had to observe a nonpreferred male actually court and mate with a model female in order for her attraction to that male to increase. If seeing a nonpreferred male court and mate is, in fact, necessary to enhance his attractiveness, then mate choice copying would seem a likely explanation for the changes in preferences of focal females in experiment 1. Copying would seem an unnecessarily elaborate explanation for the effects on focal females of watching males and model females mate if, either seeing a male and model female in the same area without seeing them interact or simply seeing a model female in an area later increased the attractiveness of that area to focal females (Grant & Green 1996). Indeed, in the latter case, 'conspecific cueing' would seem an appropriate explanation for the phenomenon.

Methods

Subjects

We used as subjects 16 male and 20 female Japanese quail assigned to 41 quartets as described in General Methods. We randomly assigned quartets to the 'male-court' (14 quartets), 'male-court-female-no-copulation' (14 quartets) and 'isolate' (13 quartets) conditions.

Apparatus

We used the same apparatus as experiment 1 with the addition of a second holding cage into which we placed model females during the observation phase of the experiment. This second holding cage measured 18.8 × 18.8 × 30 cm and was constructed of transparent Plexiglas. We then made one of the walls opaque by attaching to it a piece of white Bristol board measuring 30 × 30 cm. By confining the model female in her holding cage, placing it in the middle of the end compartment (so that nonpreferred males could not walk around the holding cage), and facing the opaque wall of the cage in various directions, we could change the visual stimuli available both to the focal females and to the nonpreferred males during the observation period, while holding everything else constant.

Procedure

The procedure was identical to that of experiment 1, except that, during the observation phase of the experiment, we confined model females, as well as focal females, in holding cages. We labelled the various experimental groups in terms of what focal females could see during the observation phase. If, during the observation phase of the experiment, the opaque wall of a model female's holding cage faced away from the focal female, she could see her nonpreferred male court but not mate with a model female (the male-court-female-no-copulation group). If the opaque wall was between the model female and the nonpreferred male, the focal female could see both the nonpreferred male and the model female, but the nonpreferred male and model female would not be visible to each other (the isolate group), and thus the male could not court or mate with the model female. If the opaque wall faced the focal female, the focal female could both see and hear a male courting (the male-court group), but she could not see the object of his attention.

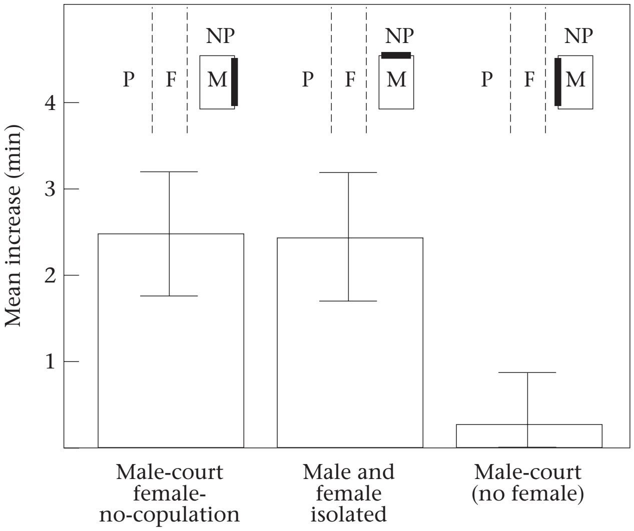

Figure 3. Mean (±SE) change from pre- to post-tests in the number of minutes that focal females spent on the side of the apparatus containing their respective nonpreferred males in experiment 2 for the male-court-female, isolate and male-court groups. See Fig. 2 for letter designations appearing above histograms. Letters enclosed in squares represent subjects confined in a Plexiglas holding cage, and the thick line represents the opaque wall of the cage.

Results and Discussion

Pretest

During the pretest, focal females assigned to male-court, male-court-female-no-copulation and isolate groups spent, respectively, an average (± SE) of 7.49 ± 0.39 min, 7.41 ± 0.43 min and 7.70 ± 0.40 min on the side of the enclosure containing their preferred males. There were no significant differences between groups in the time focal females spent with their preferred males during the pretest ($F_{2,38}$=0.13, NS).

Post-test

A one-way ANOVA performed on the change between pre- and post-tests in the time that each focal female assigned to male-court, male-court-female-no-copulation and isolate groups spent with her nonpreferred male revealed a significant effect of group assignment on affiliation ($F_{2,38}$=3.41, P<0.05; Fig. 3). Focal females assigned to both male-court-female and isolate groups showed a significant increase between the pre- and post-tests in the time they spent with their nonpreferred males (paired t tests: both ts>3.23, both Ps<0.01; Fig. 3), while focal females assigned to the male-court condition did not (t=0.43, NS; Fig. 3).

The finding that focal females were attracted to areas where they had seen nonpreferred males and model females simply standing near one another (isolate group) suggests that much of the apparent increased attractiveness to focal females of nonpreferred males seen courting and mating may have resulted not from ‘copying’ of the behaviour of model females by focal females, but from the focal females’ attraction to areas where they had previously seen either two quail or a male and female quail.

EXPERIMENT 3: TWO QUAIL OR A MALE AND FEMALE QUAIL?

During the observation phase of experiment 2, focal females assigned to the isolate group saw two quail, one male and one female, at one end of the test enclosure. It is impossible to know whether the focal female’s increased attraction to that end of the enclosure during the post-test was the result of her having seen her nonpreferred male in the vicinity of a female quail or of her having seen her nonpreferred male in the company of another quail, whose sex was irrelevant.

In experiment 3, we both repeated the isolate group of experiment 2 and added a new condition (the male-male-isolate group) in which the focal female saw her nonpreferred male standing near a model male during the observation phase of the experiment.

Methods

Subjects

As described in General Methods, we conditioned and assigned eight male and eight female quail to quartets, that we then assigned to two conditions (N=10 quartets/condition).

Apparatus and procedure

The apparatus and procedure were exactly those of experiment 2, except that we examined the behaviour of 10 quartets treated as we had treated quartets assigned to the isolate condition of experiment 2, and an additional 10 quartets, each consisting of three males and a single female, which we assigned to a male-male-isolate condition.

During the observation phase of experiment 3, focal females assigned to the male-male-isolate condition were treated exactly like those assigned to the isolate condition of experiment 2, except that they saw their nonpreferred male in the vicinity of a caged model male, rather than a caged model female. During the observation phase, nonpreferred males assigned to the isolate and male-male-isolate conditions were separated from the caged model by an opaque partition.

Results and Discussion

Pretest

During the pretest, focal females assigned to the isolate condition spent an average (± SE) of 7.85 ± 0.51 min on the side of the cage containing their preferred males. Focal females assigned to the male-male-isolate condition did not differ from those assigned to the isolate condition in the time (7.34 ± 0.37 min) that they spent close to their respective preferred males (t_{18}=0.81, NS).

Post-test

Focal females in the isolate condition spent significantly more time with their nonpreferred males during the post-test than they had during the pretest (paired t test: t_9=4.48, P<0.01; Fig. 4). On the other hand, focal

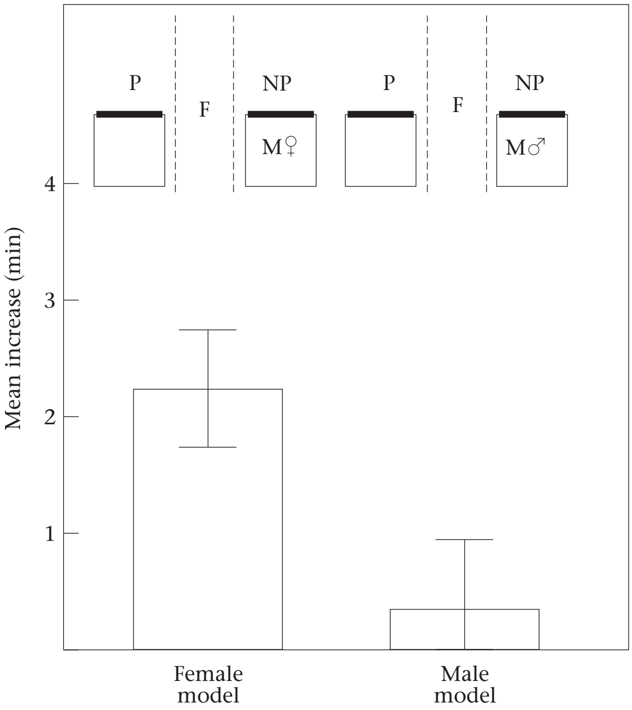

Figure 4. Mean (±SE) change from pre to post-tests in the number of minutes that focal females spent on the side of the apparatus containing their respective nonpreferred males in experiment 3 for the isolate (female model) and male-male-isolate (male model) groups. See Figs 2 and 3 for letter designations appearing above histograms.

females assigned to the male-male-isolate condition did not show a change between pre- and post-tests in the amount of time they spent on the side of the enclosure containing their respective nonpreferred males (paired *t* test: t_9=0.57, NS; Fig. 4).

The change in the time spent with nonpreferred males between pre- and post-tests, was significantly greater for focal females assigned to the isolate condition than for focal females assigned to the male-male-isolate condition (*t* test: t_{18}=2.43, $P<0.05$; Fig. 4). Clearly, a focal female's preference for her nonpreferred male increased after she saw him in the vicinity of a model female, not after she saw him in the vicinity of a model male. Consequently, the socially induced change in time that focal females assigned to the isolate condition in experiment 2 spent with their nonpreferred males cannot be attributed to a simple tendency of females to prefer areas where they had recently seen two quail over those areas where they had seen only one quail. The presence of a female in the end of the enclosure occupied by a nonpreferred male was necessary to increase a focal female's preference for that male.

EXPERIMENT 4: A MALE AND FEMALE QUAIL OR JUST A FEMALE QUAIL?

Of course it is possible, as the conspecific cueing hypothesis suggests, that focal females in experiment 3 were simply attracted to areas of the cage where they had seen a fellow female. In experiment 4, we determined whether simply seeing a female in an area previously occupied by a nonpreferred male increased the subsequent attractiveness of that area to focal females.

Methods

Subjects

We used as subjects 20 female and 16 male Japanese quail, conditioned and assigned to 42 quartets as described in General Methods.

Apparatus

The apparatus used was that used in experiment 1, with the addition of two holding cages into which we placed each male during the observation phase of the experiment. We made these two holding cages, each measuring 17.8 × 17.8 × 30.0 cm, of transparent Plexiglas, and then made one wall of each opaque by attaching a piece of white Bristol board, measuring 30 × 30 cm, to it.

Procedure

The procedure was as described in General Methods except that during the observation phase of the experiment, we confined both preferred and nonpreferred males assigned to experimental conditions in holding cages.

As in experiment 2, we labelled the groups to which we assigned subjects in terms of the view available to focal females during the observation phase of the experiment. If, during the observation phase, the opaque wall of each male's holding cage faced the focal female, she could see only the model female in the area where the nonpreferred male was held (model female group). If the opaque wall of the cages confining preferred and nonpreferred males faced away from the focal female, she could see the model female and the nonpreferred male courting the model female, but not mating with her (male-court-female group). We treated members of a control group (male-alone group) exactly as we treated members of the male-court-female group except that we did not place a model female in the enclosure with the nonpreferred male during the observation phase of the experiment.

Results and Discussion

Pretest

During the pretest, focal females assigned to male-alone, male-court-female and model-female groups spent, respectively, an average (±SE) of 6.81±0.37 min, 7.19±0.36 min and 7.40±0.36 min on the side of the enclosure containing their preferred males. There was no difference between groups in the time that focal females spent near their preferred males during the pretest ($F_{2,39}$=0.67, NS).

Post-test

A one-way ANOVA performed on the change in the time each focal female spent with her nonpreferred male

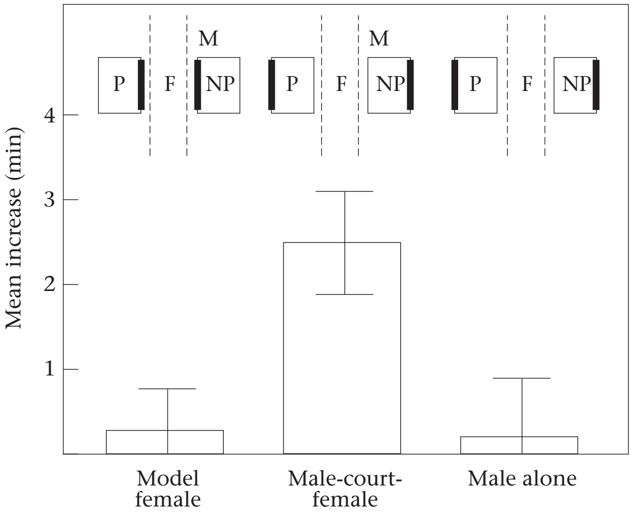

Figure 5. Mean (±SE) change from pre- to post-tests in the number of minutes that focal females spent on the side of the apparatus containing their respective nonpreferred males for the model-female, male-court-female and male-alone groups in experiment 4. See Figs 2 and 3 for letter designations appearing above histograms.

during the pre- and post-tests revealed a significant effect of group assignment ($F_{2,39}=4.75$, $P<0.02$; Fig. 5) on affiliation. Tukey's multiple-comparison post hoc tests revealed that focal females assigned to the male-court-female group showed a significantly greater increase in their tendency to affiliate with their respective nonpreferred males than did focal females assigned to either the model-female or male-alone groups (both Ps<0.04). Furthermore, focal females assigned to the male-court-female group also showed a significant increase between pre- and post-tests in the time they spent with their nonpreferred males (paired t test: $t_{13}=4.07$, $P<0.005$; Fig. 5), whereas focal females assigned to the model-female and male-alone groups did not (paired t tests: both t_{13}s<0.55, both NS; Fig. 5).

These results show that confined, nonpreferred males seen courting model females, like unconfined, nonpreferred males seen courting females (experiments 1, 2 and 3) increase in attractiveness to focal females. The results also show that focal females do not show an increase in their tendency to spend time near an area where they have simply seen a female being courted by a male that is invisible to them. Thus, a simple tendency for females to aggregate in the same area cannot explain the effects of seeing model females near males on the affiliative behaviour of focal females.

Taken together the results of experiments 2, 3 and 4 indicate that much of the change in the behaviour of focal females that results from watching a male court and mate with a model female (experiment 1) may have been the result of a tendency for focal females to show an enhanced attraction to areas where they had seen both a male and female quail relative to areas where they had seen only a male quail.

EXPERIMENT 5: THE SWITCH EXPERIMENT

We undertook the final experiment in the present series to determine whether female quail are attracted not only to areas where they have seen a male and female quail, but also to an individual male that they have seen mating.

The standard laboratory technique for disassociating a focal female's attraction to an area where a male and female were seen mating and her attraction to the mating male per se is to move the male to a new area prior to testing the preference of the focal female (Galef & White 1988; Dugatkin 1992, 1996; Dugatkin & Godin 1992; Schlupp et al. 1994).

There is, however, a problem in interpreting results of experiments in which: (1) a focal female watches one male consort with a model female and a second male not consort with a female, (2) the positions of the two males are reversed before testing the preference of the focal female, and (3) it is found that the female prefers the male she saw consorting with the female, not the place where the pair was observed together. In such an experiment, there is no control for the possibility that the disturbance caused by reversing the position of the two males affects the females' preferences. We would not mention such an inherently unlikely possibility except that, as shown below, at least in Japanese quail, such effects of disturbance on mate choice are surprisingly robust.

We have reported (Galef & White 1988, experiment 4) results of an experiment in which: (1) focal female quail watched their respective nonpreferred males court and mate with model females during the observation phase of the experiment, (2) the positions of nonpreferred and preferred males were reversed, and focal females showed a substantially enhanced preference for their respective nonpreferred males, not for the areas that those nonpreferred males and model females had previously occupied. Here, we repeat that experiment with appropriate controls.

Methods

Subjects

We used as subjects 10 female and eight male Japanese quail, conditioned and assigned to 28 quartets as described in the General Methods.

Apparatus

The apparatus was the same as that used in experiment 1.

Procedure

The method was essentially the same as that we used in experiment 1 except that, as described below, we reversed the position of preferred and nonpreferred males assigned to experimental groups at the end of the observation phase and before starting the post-test. We treated the subjects we assigned to the 'mating' condition ($N=9$ quartets) exactly as we had treated subjects in the experimental condition of experiment 1 (i.e. during the observation phase, the nonpreferred male courted and mated

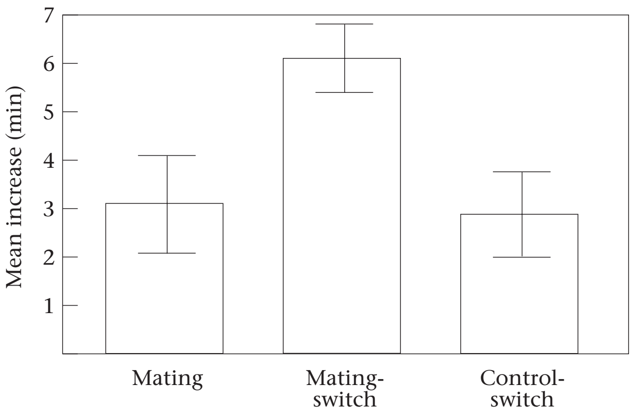

Figure 6. Mean (±SE) change from pre- to post-tests in the number of minutes that focal females spent on the side of the apparatus containing their respective nonpreferred males for the mating, mating-switch and control-switch groups in experiment 5.

with a model female). We treated subjects assigned to the 'mating-switch' condition (N=9 quartets) as we treated subjects assigned to the mating condition except that we reversed the positions of preferred and nonpreferred males after the observation phase of the experiment and before the post-test. We treated subjects assigned to the 'control-switch' condition (N=10 quartets) exactly as we treated subjects assigned to the mating-switch condition except that we did not introduce a model female into the enclosure containing the nonpreferred male during the observation period before we reversed the positions of preferred and nonpreferred males.

In all three groups, in order to reduce the disturbance resulting from the switch process to a minimum, at the end of the observation phase, we placed an opaque shell around the holding cage containing the focal female for approximately 1 min (while we reversed the position of males assigned to mating-switch and control-switch groups), and then waited 5 min before releasing the focal female from her holding cage to start the post-test.

Results and Discussion

Pretest

During the pretest, focal females assigned to control-switch, mating-switch and mating groups spent, respectively, an average (±SE) of 7.54±0.52 min, 7.67±0.37 min and 7.64±0.44 min on the side of the enclosure containing their preferred males. There was no significant difference between groups in the time that focal females spent near their preferred males during the pretest ($F_{2,25}$=0.03, NS).

Post-test

Focal females in all three groups spent more time affiliating with their nonpreferred male during the post-test than during the pretest (paired t tests: all $t_{8 \text{ or } 9}$ values >3.09, all Ps<0.02; Fig. 6). A one-way ANOVA performed on the change in the time between pre- and post-tests that focal females spent with their nonpreferred male revealed a significant effect of group assignment on the dependent variable ($F_{2,25}$=4.25, P<0.03; Fig. 6). Tukey's multiple-comparison post hoc tests revealed that focal females assigned to the mating-switch group showed a significantly greater increase in the time that they spent affiliating with their nonpreferred male than did focal females assigned to the control-switch group (P<0.04; Fig. 6), while focal females in mating and control-switch groups showed virtually identical changes between pre- and post-tests in their responses to nonpreferred males (P<0.99; Fig. 6).

The results suggest three conclusions: first, and for reasons unknown, the simple act of switching the positions of two male quail caused an increase in the focal females' preferences for nonpreferred males as large as that induced by seeing a nonpreferred male court and mate with a model female. This change in female preference for males following reversal of their positions was not a chance outcome. We repeated experiment 5 twice: once without the 5-min delay at the end of the observation phase before releasing the focal female from her holding cage and once with the lights in the experimental room extinguished while we reversed the positions of preferred and nonpreferred males. In both repetitions, switching the position of preferred and nonpreferred males reversed the females' preferences.

Second, the finding that simply reversing the positions of males can change females' preferences between those males indicates that experiments in which positions of males are reversed and no controls are used for effects of this reversal on female preference do not provide compelling evidence of mate choice copying.

Third, although some of the increase in focal females' preferences for nonpreferred males in the present experiment could be explained as a result of simple disturbance, the opportunity for focal females to see their nonpreferred males court and mate with model females before they were moved induced a further, significant increase in the nonpreferred males' attractiveness to their respective focal females. Consequently, the entire observed effect on the mate preferences of female quail of seeing males mate with model females cannot be attributed to a tendency for females to spend time near locations where they have seen a male and model female mate. Focal females increased their preference for nonpreferred males they had seen courting and mating.

GENERAL DISCUSSION

Taken together, the results of experiments 2, 3 and 4 are consistent with the view that the increase in attractiveness of nonpreferred male quail to focal females that observe them court and mate with model females (experiment 1) may be attributable to a simple tendency of focal females to approach locations where they have seen a male and female quail in preference to locations where they have seen a male quail alone. The results of experiment 5 indicate that female quail increase their tendency to affiliate with nonpreferred males after watching such males court and mate with other females.

Of course, it cannot be concluded from the present experiments that the increased attractiveness of nonpreferred males seen courting and mating in experiment 5 resulted from females seeing those males actually court and mate. A male might become more attractive to a female that saw him simply standing near another female, but whether this increase in male attractiveness is an example of 'mate choice copying' is open to debate.

Determining the stimuli sufficient to change a female's attraction either to a given area or to a given male is a relatively straightforward matter. One can define such stimuli to whatever degree of precision one desires. Determining the underlying psychological process that produces the observed change in behaviour is more difficult. Unfortunately, terms such as 'mate choice copying' and 'conspecific cueing' refer to psychological processes occurring within the observer, as well as to stimuli in the environment.

Those familiar with the 100-year history of experiments to determine whether animals can learn by imitation (Galef 1988, 1998) will be aware of how difficult it is to of establish that any change in behaviour results from one animal copying the behaviour of another, as Pruett-Jones (1992) has suggested is critical to the definition of mate choice copying. There are experimental outcomes that might permit the conclusion that imitation or copying of behaviour occurs, if for example, as in the present experiments, focal females showed an enhanced tendency to affiliate with nonpreferred males only after they see these males actually court and mate with model females. However, such clear experimental outcomes are rare.

The same 100-year history also demonstrates the limited heuristic value of taxonomies of psychological processes that might underlie social influences on behaviour (e.g. Galef 1976, 1988; Whiten & Ham 1992).

Studies of social influences on behaviour in domains other than mate choice suggest that experiments undertaken to discover the necessary and sufficient conditions for social interactions to affect affiliative behaviour and subsequent choice of a mate are more likely to be informative than are experiments undertaken to demonstrate 'mate choice copying', or other hypothetical types of social influence on mating behaviour. The results of the present experiments suggest the same conclusion.

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References

Dugatkin, L. A. 1992. Sexual selection and imitation: females copy the mate choices of others. *American Naturalist*, **139,** 1384–1389.

Dugatkin, L. A. 1996. Copying and mate choice. In: *Social Learning in Animals: The Roots of Culture* (Ed. by C. M. Heyes & B. G. Galef, Jr), pp. 85–106. San Diego: Academic Press.

Dugatkin, L. A. & Godin, J.-G. 1992. Reversal of female mate choice by copying in the guppy (*Poecilia reticulata*). *Proceedings of the Royal Society of London, Series B*, **249,** 179–184.

Galef, B. G., Jr. 1976. Social transmission of acquired behavior: a discussion of tradition and social learning in vertebrates. In: *Advances in the Study of Behavior*. Vol. 6 (Ed. by J. S. Rosenblatt, R. A. Hinde & C. Beer), pp. 77–100. New York: Academic Press.

Galef, B. G., Jr. 1988. Imitation in animals: History, definition and interpretation of data from the psychological laboratory. In: *Social Learning: Psychological and Biological Perspectives* (Ed. by T. R. Zentall & B. G. Galef, Jr), pp. 3–28. Hillsdale, New Jersey: Lawrence Erlbaum.

Galef, B. G., Jr. 1998. Recent progress in the study of imitation and social learning in animals. In: *Advances in Psychological Science:* Vol. 1. *Biological and Cognitive Aspects* (Ed. by M. Sabourin, F. I. M. Craik & M. Robert), pp. 275–300. London: Psychology Press.

Galef, B. G., Jr & White, D. J. 1998. Mate choice copying in Japanese quail. *Animal Behaviour*, **55,** 545–552.

Goldschmidt, T., Bakker, T. C. M. & Feuth-De Bruijn, E. 1993. Selective copying in mate choice of female sticklebacks. *Animal Behaviour*, **45,** 541–547.

Grant, J. W. A. & Green, L. D. 1991. Mate copying versus preference for actively courting males by female Japanese medaka (*Oryzias latipes*). *Behavioral Ecology*, **7,** 165–167.

Heyes, C. M. 1993. Imitation, culture and cognition. *Animal Behaviour*, **46,** 999–1010.

Keister, R. 1979. Conspecifics as cues: a mechanism for habitat selection in the panamanian grass anole (*Anolis auratus*). *Behavioral Ecology and Sociobiology*, **5,** 323–330.

Pruett-Jones, S. 1992. Independent versus nonindependent mate choice: do females copy each other? *American Naturalist*, **140,** 1000–1009.

Schlupp, I., Marler, C. & Ryan, M. J. 1994. Benefit to male sailfin mollies of mating with heterospecific females. *Science*, **263,** 373–374.

Whiten, A. & Ham, R. 1992. On the nature of imitation in the animal kingdom: a reappraisal of a century of research. In: *Advances in the Study of Behavior.* Vol. 21. (Ed. by P. J. B. Slater, J. S. Rosenblatt, C. Beer & M. Milinski), pp. 239–283. New York: Academic Press.