

Mate-choice copying in Japanese quail, *Coturnix coturnix japonica*

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Abstract. We performed four experiments to examine effects on the mate choices of female Japanese quail, *Coturnix coturnix japonica*, of observing a male mate with another female. Each experiment was conducted in three phases: (1) a pre-test during which subject females were allowed to choose between two males with which to affiliate; (2) an observation phase, in which subject females either watched or did not watch the male they had spent less time near during the pre-test (their 'non-preferred' male) copulate with a 'model' female; and (3) a post-test when subject females again chose between non-preferred and preferred males. Only females that had watched their non-preferred male mate with a model female during the observation phase spent significantly more time affiliating with him during the post-test than they had during the pre-test. Watching mating did not change females' criteria for choosing males, and non-preferred males that had mated recently were no more attractive to females than were non-preferred males that had not done so, unless subject females actually observed the mating take place. The results were consistent with the hypothesis that female quail copy one another's mate choices.

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Mate-choice copying requires that several members of both sexes of a species be within view of one another while mate choice takes place. Consequently, field studies of the phenomenon have often focused on lekking species. The frequently observed, highly skewed mating success of males on avian leks has sometimes been explained as a result of strong social influences on female mate choice (e.g. Hoglund et al. 1990, 1995; Gibson et al. 1991). Such dependence on social information in mate selection might be advantageous when costs associated with mate selection are high (e.g. Wade & Pruett-Jones 1990) or the relative abilities of females to identify high-quality males are asymmetrical (e.g. Losey et al. 1986).

Although field data are often consistent with the hypothesis that female birds copy one another's choices of males, it is difficult, under field conditions, to exclude alternative explanations for observed concordance in female selection of mates. For example, some males may simply be more attractive to females or occupy more attractive territories than do their competitors. Or, a tendency of females to move about in groups

(Pruett-Jones 1992), rather than mate-choice copying per se, might be responsible for observed differences in the mating success of males in lekking species (Clutton-Brock & McComb 1993). Alternatively, engaging in mating behaviour may change the appearance or behaviour of males, making them more attractive to females (Goldschmidt et al. 1993).

The strongest experimental evidence of mate-choice copying has been provided by Dugatkin (1992) and co-workers using guppies, *Poecilia reticulata*, as subjects. In a series of experiments, Dugatkin offered a confined female guppy (a 'focal' female) the opportunity to observe two confined males, one of which was courting a second female (the 'model' female). Shortly after the model female was removed from the vicinity of the male that had been courting her, the focal female was released and allowed to choose between males. Focal females spent more time near a male that they had seen courting than near a male that they had seen alone, even if the locations of the two males were reversed before a focal female was released to choose between them. In subsequent studies particularly relevant to the experiments reported here, Dugatkin and his colleagues provided evidence that the tendency

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of female guppies to copy the mate choices of others was sufficiently powerful to reverse prior preferences for one male over another (Dugatkin & Godin 1992; Dugatkin 1996).

We undertook the present series of studies to examine social influences on mate choice in Japanese quail, *Coturnix coturnix japonica*. Our goal was to study, under controlled conditions, social influences on mate choice in a species more closely related than are guppies to the lekking birds that are subjects of most field studies of social influence on mate choice. Our choice of Japanese quail was strongly influenced by the frequency with which these birds mate in the laboratory. Whenever a sexually mature male and female Japanese quail are placed together, the male will attempt to mount the female, and more often than not, the female will acquiesce.

An obvious shortcoming to Japanese quail in studies of mate choice is that there is no reliable information about the social and sexual behaviour of Japanese quail in natural settings (Wetherbee 1961; Nichols 1991). Opportunistic observations of mating in wild Japanese quail have produced contradictory reports of both monogamy and polygamy in the species (Dement'ev et al. 1967 and Kawahara 1967, cited in Nichols 1991). Observation of both domestic and feral Japanese quail in large flight cages (Nichols 1991) suggest that most females bond with one or two males, but that most also engage in extra-pair copulations. According to Nichols, female Japanese quail solicit copulations from males by walking in front of them and crouching, thus inviting the male to mount, and females can prevent undesired copulations either by resisting males or fleeing and hiding from them. Nichols (1991, page 62) concluded that 'the female plays an active role in the formation and maintenance of the bond by choosing and remaining close to a male'. It is thus reasonable to examine female mate choice in the species.

GENERAL METHODS

Subjects

Ten male and 10 female Japanese quail acquired from a commercial breeder (Speck's Poultry Farm, Vineland, Ontario) at 48 days of age served as subjects in all four of the experiments reported here. After we transported

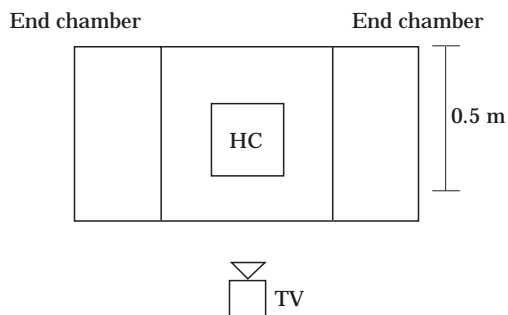


Figure 1. Overhead schematic of the apparatus. HC: holding cage; TV: television camera.

subjects to the laboratory, we placed them in individual, stainless-steel cages ($45.7 \times 61.0 \times 40.6$ cm) and gave them ad libitum access to water and Purina Game Bird Startena 5419 (Ralston-Purina Canada, Woodstock, Ontario).

To bring subjects into breeding condition, we kept them for 30 days on a 16:8 h light:dark cycle before starting experiments. We considered females to be ready to breed when they started to lay eggs regularly (once every 2 or 3 days).

To establish the readiness of males to breed, we repeatedly placed each male with a female in breeding condition into the apparatus that we subsequently used to conduct experiments. Testing males for readiness to breed in the experimental apparatus also acclimated both males and females to mating there.

We continued pairing each male with two randomly selected females per day until he either mounted two females in succession or 2 weeks passed without his showing interest in females. Once a male had shown readiness to mate, we left him in isolation until we started experiments 1–2 weeks later.

Two males failed to court or mate when presented with sexually active females, and we did not use these two males in experiments.

Apparatus

We conducted all experiments in a painted plywood enclosure ($121.9 \times 61.0 \times 30.5$ cm). The enclosure had a Plexiglas roof and front wall, with hardware cloth partitions (Fig. 1). The enclosure had no floor. Instead, it rested on an aluminium tray covered with disposable, absorbent paper pads (Tray Liners, Lilo Products, Hamilton, Ontario, Canada).

The partitions, placed 30.5 cm from opposite ends of the enclosure, divided it into three compartments. During experiments, each of the two end compartments of the apparatus held a single male quail.

We cut a 25.4×25.4 -cm opening in the centre of the transparent Plexiglas roof of the enclosure, through which we could raise or lower a transparent Plexiglas holding cage measuring $25.2 \times 25.2 \times 40.6$ cm (Fig. 1). We could move the holding cage vertically to release a female from under it by using a pulley system that we operated from a room adjacent to that housing the enclosure.

We drew a line from top to bottom of the front wall of the enclosure at its midpoint so that we could reliably score the location of the focal female.

A television camera attached to a VHS videocassette recorder and monitor faced the transparent Plexiglas front wall of the enclosure permitting us (a) to observe in real time all behaviour occurring within the enclosure and (b) to record that behaviour for later scoring.

Procedure

Each of the four experiments described below consisted of three 10-min phases. Phase 1 was a pre-test that we used to determine a female subject's initial preference between two males. Phase 2 was an observation period during which 'focal' females had the opportunity to observe one of the two males that she had seen during the pre-test mate and the other not mate. Phase 3 was a post-test that we used again to determine a focal female's preference between the same two males she had seen during the pre-test. Experiments differed only in manipulations carried out during phase 2.

Pre-test

To begin an experiment, we placed a sexually proven male quail in each of the end chambers 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 15 cm, allowing the focal female to move into the larger enclosure.

We began taking data as soon as the focal female took her first step after we had raised the cage holding her. During the next 10 min, we recorded the time that she spent on each side of the midline of the enclosure.

We considered the male held on the side of the enclosure where the female spent the majority of the pre-test to be her 'preferred' male and the other male to be her 'non-preferred' male.

Observation

To begin the observation phase, we returned the focal female to the holding cage, then placed a second female (the model female) into the end compartment that contained the focal female's non-preferred male. We then left the four birds undisturbed for 10 min so that the focal female could observe the non-preferred male mate with the model female and the preferred male remaining celibate.

During the observation phase, we also determined whether the non-preferred male mated successfully with the model female.

Post-test

At the end of the observation phase, we removed the model female from the apparatus, again restrained the focal female in the holding cage and, finally, repeated the procedure we had used during the pre-test (i.e. after 30 s of confinement, we released the focal female from the holding cage and, once she had started to move, recorded the time she spent on each side of the midline of the enclosure).

Inter-observer reliability

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

Testing schedule

To ensure that we did not repeatedly use the same males and females, before beginning each experiment, we randomly assigned two females to each of the 28 combinations of males that we could create using our eight sexually active male subjects. 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.

Practical constraints made it impossible to maintain the hundreds of sexually active quail that would have been needed so as to never use any subject twice in the four experiments. We did, however, ensure that within any experiment: (1) no two focal females ever chose between the same pair of males; (2) no female ever saw any male twice; (3) no female ever served twice as the model female for the same focal female; and (4) on those days late in an experiment when scheduling required that a female participate in an experiment twice on the same day, she never served twice as either a focal female or a model female, and she always served as a focal female before she served as a model female. Thus, each trial involved a focal female choosing between two males that she had never seen before and watching a model female that she had never seen before interacting with one of those males. We conducted five trials per day and allowed no subject to participate in more than two trials on the same day.

EXPERIMENT 1: EFFECTS OF OBSERVATION ON CHOICE

We undertook experiment 1 to determine whether a female Japanese quail would increase the amount of time that she spent near her non-preferred male after seeing him mate. From the mate-choice copying hypothesis, we expected focal females that had seen their respective non-preferred males mate with a model female during the observation phase to spend more time near that male during the post-test phase than she had during the pre-test phase. We also expected that focal females that had not seen their respective non-preferred males mate during the observation phase would show no increase in the time they spent near the non-preferred male in the post-test as compared with the pre-test phase.

Methods

Subjects

We randomly assigned the 28 quartets of quail to experimental and control groups ($N=14$ quartets each). We discarded data from three quartets when non-preferred males failed to mount the

model female placed with them during the observation phase. All other non-preferred males vigorously courted and copulated with any females to whom they were given access. We also lost the data from an additional quartet due to equipment failure.

Procedure

At the end of the pre-test, we placed a model female in the end chamber of the enclosure containing the non-preferred male of each focal female that we had randomly assigned to the experimental condition. We treated each focal female that we had 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.

Results and Discussion

Pre-test

During the pre-test, focal females assigned to the experimental group spent an average \pm SE of 7.79 ± 0.40 min on the side of the cage containing their preferred males, and females assigned to the control group spent an average of 7.90 ± 0.45 min near their preferred male.

Post-test

Focal females assigned to the experimental group (i.e. those that had had an opportunity to see their respective non-preferred males mate during the observation phase) spent significantly more time with their non-preferred male during the post-test than they had during the pre-test (Wilcoxon signed-ranks test: $T=4$, $P<0.005$; Fig. 2). On the other hand, focal females assigned to the control condition (i.e. those that did not have an opportunity to see their non-preferred males mate with a model female during the observation phase) did not show a change between pre-test and post-test in the time that they spent on the side of the enclosure containing their non-preferred males ($T=23$, NS; Fig. 2).

The change between pre-test and post-test in time spent by focal females assigned to the experimental group with their respective non-preferred males was significantly greater than was the change between pre-test and post-test in the time

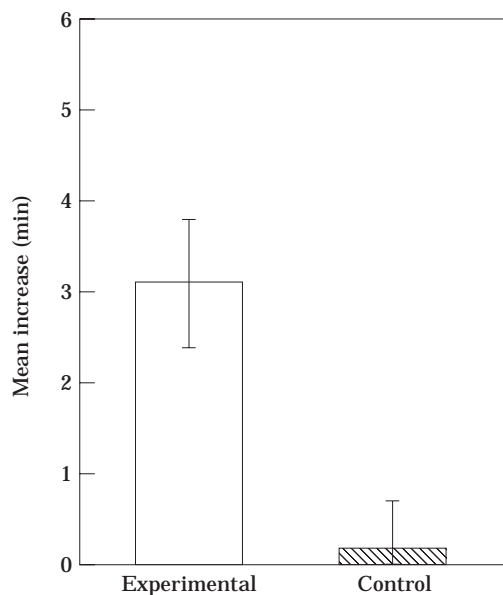


Figure 2. Mean (\pm SE) increase from pre-test to post-test that focal females assigned to control (▨) and experiment (□) conditions in experiment 1 spent on the side of the apparatus containing their respective non-preferred males.

spent with non-preferred males by focal females assigned to the control group (Mann-Whitney U -test: $U=24$, $N_1=13$, $N_2=11$, $P<0.01$; Fig. 2).

Also consistent with the hypothesis that focal females increased their tendency to affiliate with males after they had seen those males mate was the observation that eight of 11 experimental focal females spent more than half of the 10-min post-test phase on the side of the cage containing the male that they had not preferred during the pre-test, but none of the 13 control focal females showed a comparable change in preference between pre-test and post-test (Fisher's exact test: $P<0.0002$).

The results are consistent with the hypothesis that female quail tend to increase the time that they spend near males that they have seen mating. The results are also consistent with the hypotheses that: (1) watching a male quail mate causes a change in the internal state of an observing conspecific female that reverses the criteria that she uses to choose a male with which to affiliate; or (2) males change their behaviour after mating and become more attractive to females. We tested both these hypotheses in the following experiments.

EXPERIMENT 2: DOES WATCHING MATING CHANGE FEMALES' CRITERIA FOR CHOOSING MALES?

In experiment 2, we again examined the effect of observing a male mate on an observing female's subsequent tendency to spend time near that male. Unlike in experiment 1, we controlled for the possibility that watching a pair mate somehow reversed a female's criteria for selecting a male with whom to affiliate.

Methods

Subjects and procedure

We randomly assigned 28 quartets of quail to two conditions (14 quartets per condition) that differed with respect to whether focal females had watched their preferred or non-preferred male copulate with a model female during the observation phase. The procedure was identical to that of experiment 1, except in the following two respects. Focal females assigned to the preferred-male condition observed the model female in their quartet mate with their preferred male. Focal females assigned to the non-preferred-male condition observed the model female in their quartet mate with the male that they had not preferred during the pre-test.

Results and Discussion

Pre-test

During the pre-test, focal females assigned to the preferred-male condition spent an average of 7.43 ± 0.31 min on the side of the enclosure containing their preferred male, and focal females assigned to the non-preferred-male condition spent an average of 7.60 ± 0.49 min on the side of the enclosure where their respective non-preferred males were held.

Post-test

The results were largely consistent with the hypothesis that female Japanese quail prefer to associate with males that they have seen mate with other females. Focal females assigned to the non-preferred-male condition spent significantly more time during the post-test than during the pre-test on the side of the enclosure containing the non-preferred male (Wilcoxon signed-ranks test: $T=5$,

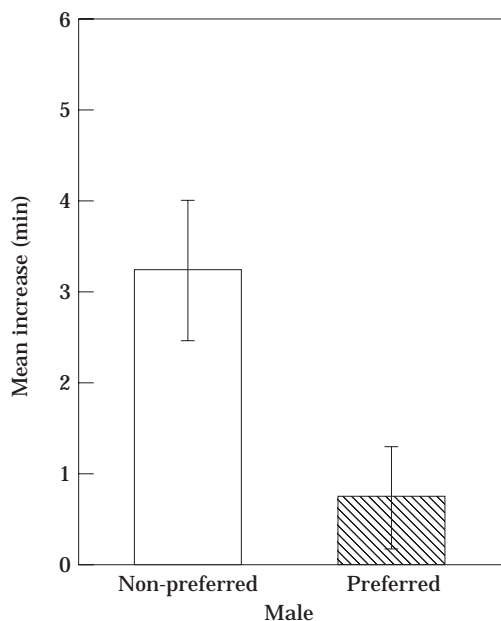


Figure 3. Mean (\pm SE) increase from pre-test to post-test that focal females assigned to preferred-male (▨) and non-preferred-male (□) conditions in experiment 2 spent on the side of the apparatus containing their respective non-preferred males.

$P < 0.005$; Fig. 3). On the other hand, focal females assigned to the preferred-male condition did not show a significant change in the time they spent near their respective preferred males between pre-test and post-test as a result of observing their preferred male mate during the observation phase ($T = 68$, NS; Fig. 3). The failure of focal females assigned to the preferred-male condition to change their mate choices after observing mating would not be predicted from the hypothesis that observing mating causes female quail to change criteria for selecting a mate.

There was a significantly greater increase in the time spent with a male seen mating when that male was the non-preferred male rather than the preferred male in the pre-test ($U = 44$, $N_1 = 14$, $N_2 = 14$, $P < 0.01$; Fig. 3). This result could reflect a greater effect of seeing mating by a non-preferred than by a preferred male on the tendency of females to affiliate with that male. We suspect, however, that this result instead reflected an upper bound on the possible increase in the amount of time that focal females assigned to the preferred-male condition could spend with their preferred male during the

post-test. Focal females assigned to the preferred-male condition had spent an average of almost 75% of the pre-test closer to their preferred male. There was not much room for increase during the post-test.

EXPERIMENT 3: CHOOSING MALES OR CHOOSING LOCATIONS?

In experiments 1 and 2, female quail increased the time that they spent near non-preferred males that they saw mating. This result could have been obtained, not because of an increase in female preference for affiliating with non-preferred males observed copulating, but because of an increase in female preference for locations where they saw mating take place.

In the present experiment, we (a) conducted the usual pre-test, (b) then permitted focal females to observe their respective non-preferred males mate with a model female and (c) reversed the location of preferred and non-preferred males before (d) conducting the usual post-test.

Methods

Subjects

Fourteen quartets, each consisting of two males, a model female and a focal female, served as subjects.

Procedure

The procedure was identical to that used with subjects assigned to the non-preferred-male condition of experiment 2 and the experimental condition of experiment 1, except that at the end of the observation phase, and before starting the post-test, we reversed the position in the apparatus of preferred and non-preferred males.

Results and Discussion

Pre-test

During the pre-test, focal females spent an average of 7.25 ± 0.39 min on the side of the enclosure where their respective preferred males were being held.

Post-test

Focal females increased the time that they spent on the side of the enclosure to which the

non-preferred male they had observed mating had been moved ($\bar{X} \pm SE = 4.36 \pm 1.08$ min; $T=7$, $P<0.005$). The results are consistent with the view that females remain near males they have seen mating, not near locations where they have seen males mate.

EXPERIMENT 4: CHANGES IN FEMALE PERCEPTION OR MALE BEHAVIOUR?

Although the results of experiment 3 indicate that female quail increase their tendency to affiliate with non-preferred males after seeing them mate, it is not clear whether this increased attractiveness of non-preferred males is a result of females seeing them mate or of some change in males' behaviour or appearance that occurs as a consequence of having mated.

Methods

Subjects

We used 28 quartets of quail, each composed of two males, one model female and one focal female.

Procedure

The procedure was identical to the one we used with subjects assigned to the experimental condition in experiment 1 and to the non-preferred-male condition in experiment 2, except for the treatment of focal females during the observation phase. In the present experiment, we modified the holding cage in which we placed focal females during the observation phase by making two of its walls opaque.

We placed randomly assigned 14 quartets each to a control and to an experimental ('blind') condition. We placed control focal females in the holding cage with its opaque walls facing the front and back of the enclosure and its transparent walls facing the ends of the enclosure holding preferred and non-preferred males. Thus, control focal females could observe non-preferred males mate with model females during the observation phase.

We placed experimental focal females in the holding cage with its opaque walls facing the end enclosures holding preferred and non-preferred

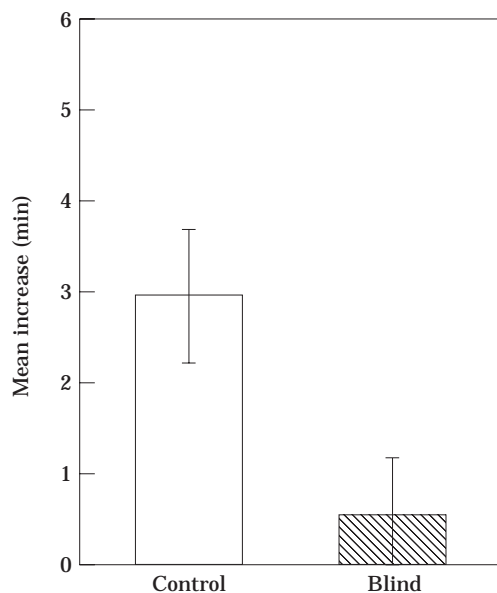


Figure 4. Mean (\pm SE) increase from pre-test to post-test that focal females assigned to control (\square) and blind (\boxtimes) conditions in experiment 4 spent on the side of the apparatus containing their respective non-preferred males.

males, so that these females could not see the other birds in the test enclosure during the observation phase, although they could hear them.

Results and Discussion

Pre-test

During the pre-test, control focal females spent 7.08 ± 0.44 min closer to whichever male they preferred, and subjects assigned to the blind condition spent 6.95 ± 0.31 min there.

Post-test

Control focal females showed a significantly greater increase in the time that they spent near their non-preferred male than did focal females that we had assigned to the blind condition ($U=47$, $N_1, N_2=14$, $P<0.01$; Fig. 4). Indeed, only control focal females showed a significant increase between pre-test and post-test in the time they spent on the side of the enclosure containing their non-preferred male (control group: $T=5$, $P<0.005$; blind group: $T=38$, NS; Fig. 4).

The data are consistent with the hypothesis that females are attracted to males that they see

mating, not to males that have undergone some change in behaviour or appearance as a result of their having mated.

GENERAL DISCUSSION

Taken together, the results of the four experiments described here provide evidence that the attractiveness of a previously non-preferred male Japanese quail to a reproductively active female of his species is markedly increased after she sees him mating. Our results are similar to those reported by Dugatkin in guppies (see Introduction). They are also consistent with suggestions, based on field observations, that the skewed mating success of male birds on leks may be a consequence of mate-choice copying (Hoglund et al. 1990, 1995; Gibson et al. 1991).

Of course, the present results are not sufficient to conclude that mate-choice copying plays a role in mate selection by female Japanese quail. Choice of a male with which to affiliate need not correlate with choice of a male with which to copulate, though, as discussed in the introduction observations of Japanese quail in semi-natural conditions (Nichols 1991) suggest that affiliation of females with males does play a role in mate selection in Japanese quail. Furthermore, changes in affiliative behaviour observed in the laboratory need not provide insight into the behaviour of free-living animals.

Even in the laboratory, however, much remains to be learned about what a female quail sees that causes her to increase her tendency to affiliate with a previously unattractive male. Is it necessary that a female sees a relatively unattractive male actually mate, or is observation of him courting or close to a female sufficient to increase her probability of affiliating and/or mating with him? Determination of the relationship between a female quail's tendencies to affiliate and to mate with males is also needed. We anticipate that further examination, under controlled conditions, of the social stimuli promoting both affiliation and willingness to mate in female quail will lead to testable hypotheses concerning the role of social influence in mate selection by free-living birds.

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