



Sexual experience can affect use of public information in mate choice

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The mate choices of sexually experienced, female Japanese quail, *Coturnix japonica*, are influenced by information acquired by observation of potential partners engaging in social interactions. Female quail show an increased preference both for males that they have seen mate with another female and for the less aggressive of a pair of males that they have watched interact aggressively. We examined effects of females' prior sexual experience on their use of such public information when choosing a partner. We found that virgin female quail, like female quail with sexual experience, increased their preference for a male after seeing him mate with another female. Whereas sexually experienced females preferred the less aggressive member of a pair of males that they had seen engage in an agonistic encounter, virgin female quail preferred the more aggressive member of such a pair. We interpret the results as indicating that sexual experience plays little role in the development of mate-choice copying by female quail, whereas experience of punishing aspects of interactions with conspecific males reverses naive female quails' positive response to relatively aggressive members of the opposite sex.

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A growing body of evidence suggests that the public information (Valone 1989) a female acquires while observing potential mates engage in social interactions can influence her choice of sex partner. For example, in many species of Poecilidae (guppies: *Poecilia reticulata*; Dugatkin 1996, and sailfin mollies: *Poecilia latipinna*; Witte & Ryan 1998) females offered a choice between a male they have seen mate with another female and a male they have not seen so engaged, prefer to affiliate with the male seen mating.

Observation of aggressive interactions between males, can also influence females' mate choices. For example, female Siamese fighting fish, *Beta splendens* (Doutrelant & McGregor 2000), great tits, *Parus major* (Otter et al. 1999), and black-capped chickadees, *Parus atricapillus* (Mennill et al. 2002) that have watched a pair of males interact aggressively subsequently prefer the winner to the loser.

Female Japanese quail, *Coturnix japonica*, the subjects in the experiments described here, like female Poecilidae, prefer to affiliate with males they have seen mating with

other females (Galef & White 1998; White & Galef 1999b, 2000a, b; Ophir & Galef 2003a). In quail, such affiliative preference has been shown to predict both a female's choice of partner for copulation (White & Galef 1999a) and the probability that a female will lay fertilized eggs after copulating with a male (Persaud & Galef, in press). Unlike females of other species examined to date, female Japanese quail prefer to affiliate with the less aggressive of two males that they have watched engage in an aggressive interaction (Ophir & Galef 2003b).

A variety of hypotheses have been proposed to explain females' use of public information when choosing among males (for review, see Valone & Templeton 2002). For example, female mate-choice copying has been suggested to either decrease the cost or increase the accuracy of mate assessment (Gibson & Höglund 1992; Pruett-Jones 1992; Nordell & Valone 1998). In the former case, some cost of sampling males is assumed, as is mitigation of that cost by copying the choices of other females (Magnhagen 1991; Real 1991). In the latter case, determining male quality is presumed to be difficult or error prone, so females that have difficulty in determining the relative quality of males might gain from copying the mate choices of others, especially those with greater ability to discriminate among males (Gibson & Höglund 1992; Dugatkin & Godin 1993; but see, Bikhchandani et al. 1992).

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Female quails' preference for the less aggressive of a pair of males may reflect females' avoidance of male harassment (Persaud & Galef 2003) together with a tendency for males that are more aggressive towards conspecific males to also be more aggressive towards conspecific females (Ophir & Galef 2003b). During courtship, male quail chase females, peck at females' heads, pull them around by their head feathers, and repeatedly jump onto their backs (see Persaud & Galef 2003 for detailed description). The relative aggressiveness of a male quail when engaged in aggressive interactions with other males is highly correlated with his frequency of engaging in potentially harmful acts while courting and mating with females (Ophir & Galef 2003b).

There is a rich theoretical literature, as well as considerable empirical evidence, that animals both should and do make use of public information when choosing mates and making other biologically significant decisions (see Valone & Templeton 2002, for review). However, essentially nothing is known of factors that might affect the development of use of public information in decision making. Dugatkin & Godin (1993) found that younger female guppies, *Poecilia reticulata*, are more likely to copy the mate choices of older conspecifics than vice versa. They interpreted their finding as reflecting an information asymmetry resulting from the greater experience of older than younger animals (Boyd & Richerson 1985). However, their experiment provided no insight into the nature of the experiences that might have resulted in such an information asymmetry. We undertook the present pair of experiments to examine the importance of females' prior sexual experience in mediating use of public information when choosing a mate.

EXPERIMENT 1: MATE-CHOICE COPYING

On the hypothesis that relatively naïve females mate-choice copy to take advantage of other females' greater experience in assessing males, sexually naïve females should be more likely than more experienced females to mate-choice copy.

Methods

Subjects

Forty-five female and 40 male Japanese quail acquired when 52 days old from Speck's Poultry Farm (Vineland, Ontario, Canada) served as subjects. After we transported subjects to our laboratory (Hamilton, Ontario), we placed them in racks containing individual, commercial quail cages (Berry Hill, St Thomas, Ontario), each measuring $55 \times 55 \times 110$ cm, that we maintained in a single temperature- and humidity-controlled colony room illuminated on a 16:8 h light:dark cycle, with light onset at 0700 hours. All subjects had ad libitum access to water and Mazuri Pheasant Breeder (PMI Feeds, St Louis, Missouri, U.S.A.).

While in their cages each quail could see and hear many others, and female subjects could make physical contact with their immediate neighbours that were always other

females. However, no physical contact between female and male subjects was possible. Males in their home cages could also make physical contact with their immediate male neighbours, so we never assigned immediate neighbouring males to the same group of four (see Procedure).

Experiments began only after subjects had achieved sexual maturity. We considered females to be sexually mature once they started to lay one egg every other day (approximately 65 days after hatching). We tested males for sexual maturity once they started to call regularly at about 70 days of age. To perform such a test, we placed a male in one end chamber of the apparatus (Fig. 1) with a succession of sexually mature females for 10 min/day for 5–7 consecutive days. We observed the behaviour of pairs on closed-circuit television, and after a male had mounted and made cloacal contact with females on 3 successive days, we considered him sexually mature.

Apparatus

We performed experiments in an apparatus constructed of painted plywood, transparent Plexiglas and wire mesh (Fig. 1) that rested on an aluminium tray lined with absorbent paper pads (Tray liners, Lilo Products, Hamilton, Ontario). The apparatus was divided into four sections: a 'central area', measuring $61 \times 61 \times 30$ cm, two 'end chambers', each measuring $61 \times 30 \times 30$ cm, and an 'ancillary cage', measuring $44 \times 30 \times 30$ cm. Wire-mesh partitions separated both the central area from each end chamber and the ancillary cage from the central area.

An opening, measuring 26×26 cm, in the centre of the roof of the central area, allowed a transparent Plexiglas 'holding cage', measuring $25 \times 25 \times 40$ cm, to be raised and lowered using a pulley system. A vertical line drawn at

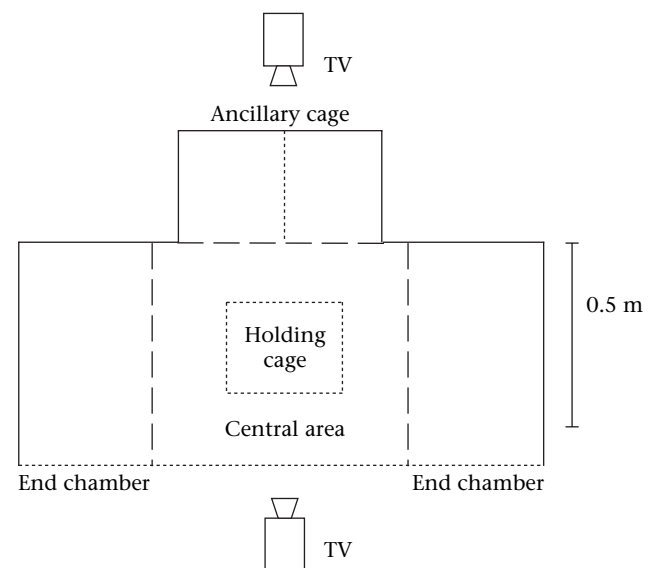


Figure 1. Overhead schematic of the apparatus. Solid lines = opaque walls; dotted lines = transparent Plexiglas; dashed lines = wire mesh. The camera viewing the ancillary cage was mounted directly above its midpoint, facing down, and the camera viewing the central area was located at its midpoint and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

the midpoint of the transparent Plexiglas front wall of the central area enabled experimenters to determine the end chamber of the apparatus to which a subject was closer. Because we did not use the ancillary cage in experiment 1, we placed an opaque barrier between it and the central area.

Two colour closed-circuit television video cameras (Panasonic WV-CP230), one facing the transparent front wall of the apparatus and the other mounted directly above the ancillary cage, both connected to VHS video-cassette recorders (Panasonic AG-1240), permitted experimenters to both record and observe behaviour of subjects without disturbing them.

Procedure

The experiment consisted of three 10-min phases: (1) a pretest, during which focal females chose between two unfamiliar target males, each confined in one of the end chambers of the apparatus, (2) an observation phase, during which each focal female was confined in the holding cage and saw the male that she spent less time nearer during the pretest (her nonpreferred male) court and mate with a model female, and (3) a post-test, during which each focal female chose between the same two target males she had encountered during the pretest.

To begin, we randomly assigned females to either virgin ($N = 18$) or experienced ($N = 18$) conditions, or to serve as 'model' females ($N = 9$). For 10 min/day for 8 or more days, we placed each female assigned to the experienced condition in the central area of the apparatus (Fig. 1) with a sexually experienced male. We treated females assigned to the virgin condition and the experienced condition similarly, except that we placed no male in the central area of the apparatus when females assigned to the virgin condition were there. We used the nine model females both to test males for sexual maturity and as 'models' during the observation phase of the experiment described below.

In the experiment proper, each focal female subject first chose between two males (pretest phase), then watched her less-preferred male mate with another female (observation phase), and finally (post-test) chose for a second time between the same pair of males she had chosen between during the pretest (Galef & White 1998). Before testing subjects, we assigned each female subject in virgin and experienced conditions to a group of four quail, each composed of a 'focal female' (the subject), a 'model female', and two 'target' males. To construct groups, we first assigned males to the 780 unique pairs that can be constructed using 40 male subjects. We then randomly selected 36 of these 780 pairs to serve as target pairs and randomly assigned a model female and a focal female to each target pair. Target males were used no more than once per day.

Pretest. To begin a pretest, we placed a target male in each end chamber of the apparatus, and a focal female in the holding cage (Fig. 1). We then raised the holding cage, allowing the focal female to move freely about the central area. After a focal female took her first step, we recorded the time she spent nearer to each male. We considered the

male to which the focal female was nearer for more than half of the 10-min pretest to be her 'preferred male' and the other male her 'nonpreferred male'.

Observation phase. At the end of the pretest, we returned each focal female to the holding cage and placed a model female in the end chamber that contained the focal female's nonpreferred male. We then left the nonpreferred male and model female undisturbed for 10 min to court and mate, while the focal female observed them. At the end of the observation phase, we removed the model female from the apparatus.

Post-test. To start a post-test, we raised the holding cage restraining the focal female, thus permitting her to move freely about the central area of the apparatus for 10 min. As in the pretest, we recorded the time that each focal female spent closer to each target male.

Data analysis

As in previous studies of mate-choice copying by female Japanese quail (e.g. Galef & White 1998; White & Galef 1999b; Ophir & Galef 2003a), we determined effects of the observation phase on each female's preference for her nonpreferred male, by subtracting the time that she spent closer to him during the pretest from the time she spent closer to him during the post-test. We used two-sample Student's t tests to compare the change in time spent nearer to nonpreferred males by focal females assigned to virgin and experienced conditions and one-sample t tests to examine each group's divergence from chance.

Results and Discussion

Interobserver reliability

To determine the interobserver reliability of the dependent variable, change from pre- to post-test in time spent with the nonpreferred male, we randomly selected videotapes of 14 focal females' behaviour during pre- and post-tests and had two observers independently score those videotapes. There was substantial agreement between observers as to the change in time spent with the nonpreferred males from pretest to post-test (Pearson's correlation: $r_{12} = 0.94$, $P < 0.0001$).

Pretest and observation phase

During the pretest, focal females assigned to virgin and experienced conditions spent a mean \pm SE of 7.2 ± 0.4 and 8.0 ± 0.3 min, respectively, closer to their preferred than nonpreferred target males ($t_{34} = 1.60$, $P = 0.12$). During the observation phase, all nonpreferred target males courted and achieved cloacal contact with their model females.

Post-test

Sexually experienced and virgin females did not differ in the effect that observation of males interacting with model females had on their subsequent mate choices (Student's t test: $t_{34} = 0.44$, $P = 0.66$; Fig. 2). Females

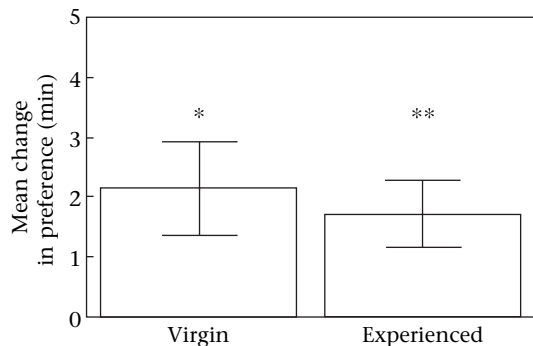


Figure 2. Mean (\pm SE) change in time (min) between pretest and post-test that virgin and experienced focal females in experiment 1 spent nearer to the target male that they had not preferred during the pretest. * $P < 0.02$; ** $P < 0.01$.

assigned to both conditions in the present experiment, like other females with extensive previous sexual experience observed in our laboratory (e.g. Galef & White 1998), showed a significant increase between pre- and post-test in the time that they spent with their respective nonpreferred target males (one-sample t tests: virgin females: $t_{17} = 2.66$, $P < 0.02$; experienced females: $t_{17} = 2.78$, $P < 0.01$; Fig. 2).

EXPERIMENT 2: OBSERVING MALE AGGRESSIVE INTERACTIONS

Ophir & Galef (2003b) have found that female Japanese quail with information about the relative aggressiveness of a pair of males tend to avoid the more aggressive of the two. If female quail need to learn that males will behave aggressively towards them, then virgin females would be expected to differ from sexually experienced females in their response to males that they have seen behave aggressively.

Methods

Subjects

Thirty-nine male and 32 female, sexually mature, Japanese quail acquired from Speck's Poultry Farm served as subjects. We maintained subjects as described in the Methods of experiment 1.

Apparatus

We used the same apparatus that we used in experiment 1 (Fig. 1), but modified it in two ways. First, we removed the opaque partition separating the central area and ancillary cage to allow females placed in the holding cage in the central area to observe males in the ancillary cage. Second, we divided the ancillary cage into two compartments of equal size with both a fixed, transparent Plexiglas partition and a removable opaque partition.

Procedure

We randomly assigned females to virgin ($N = 18$) or experienced ($N = 14$) conditions. We placed each sexually mature female assigned to the experienced condition in the central area of the apparatus together with a series of sexually experienced males for 10 min/day for 5 days. As in experiment 1, we placed females assigned to the virgin condition alone in the central area of the apparatus so that females assigned to virgin and experienced conditions differed primarily in sexual experience.

We assigned subjects to trios, each composed of a focal female and two target males. To construct trios we first assigned males to the unique pairs we could construct from the 39 male subjects, then assigned a female to each of 32 of these pairs.

Fight phase

To begin the fight phase of the experiment, we placed a focal female in the holding cage and one target male on each side of the barriers bisecting the ancillary cage. We then lifted the opaque partition, leaving the males separated by the transparent partition. For the next 10 min, we used the closed-circuit television camera suspended directly above the midpoint of the ancillary cage and a videocassette recorder to make a permanent record of the behaviour of target males.

Two independent observers reviewed videotapes of each pair of target males and determined the number of times that each pecked the transparent Plexiglas partition separating them. We considered the target male in each pair that pecked the transparent partition more frequently during the fight phase to be the 'winner', and the male that pecked the partition less frequently to be the 'loser'.

Schlinger et al. (1987) have reported that the relative number of pecks that two males direct towards a conspecific on the far side of a glass partition separating them predicts which male will win a subsequent unrestrained fight. Ethical problems associated with staged aggressive interactions led us to use Schlinger's indirect measure of male aggression rather than repeatedly staging unrestrained fights between males.

Choice phase

Upon completion of the fight phase, we placed each target male in the end chamber of the apparatus closer to the side of the ancillary cage he had just occupied. We then lifted the holding cage and waited until the released focal female took her first step. We allowed the focal female to move freely about the central area for the next 10 min while we recorded her behaviour using the video camera located in front of the transparent front wall of the central area (Fig. 1). As in experiment 1, we considered a female to prefer the target male that she spent more than half of the 10-min choice phase nearer. We excluded data from five trios when the focal female member of that trio failed to take a first step within 3 min of our raising the holding cage.

Results and Discussion

Interobserver reliability

Independent observers reviewing a random selection of 10 videotapes of fight phases and 10 randomly selected videotapes of choice phases agreed on both the number of pecks delivered by each target male during the fight phase (Pearson's correlation: $r_{18} = 0.94$, $P < 0.0001$) and the time focal females spent nearer to each target male during the choice phase ($r_8 = 0.99$, $P < 0.0001$).

Fight phase

Winners assigned to virgin and experienced conditions did not differ in the frequency with which they pecked at the Plexiglas partition separating them from losers (Mean \pm SE: virgin condition 541.9 ± 70.2 times; experienced condition 588.4 ± 99.7 times; $t_{25} = 0.39$, $P = 0.70$). Losers assigned to virgin and experienced conditions also did not differ in the frequency with which they pecked at the partition separating them from winners (virgin condition: 293.1 ± 39.4 times and experienced condition: 239.3 ± 71.9 times; $t_{25} = 0.71$, $P = 0.49$). There was also no significant difference between pairs of males assigned to virgin and experienced conditions in the mean total number of pecks they delivered to the Plexiglas partition ($t_{25} = 0.05$, $P = 0.96$).

Choice phase

We found a significant effect of group assignment on focal females' preferences for winning and losing males ($t_{25} = -4.15$, $P < 0.001$; Fig. 3). During the choice phase, focal females assigned to the experienced condition spent significantly more time nearer losers than winners (one-sample t test: $t_{10} = -3.33$, $P < 0.01$; Fig. 3). On the other hand, focal females assigned to the virgin condition preferred winners to losers ($t_{15} = 2.35$, $P < 0.05$; Fig. 3).

GENERAL DISCUSSION

In the present paper, we examined whether female quails' prior sexual experience influences their use of public information during mate choice. In experiment 1, we

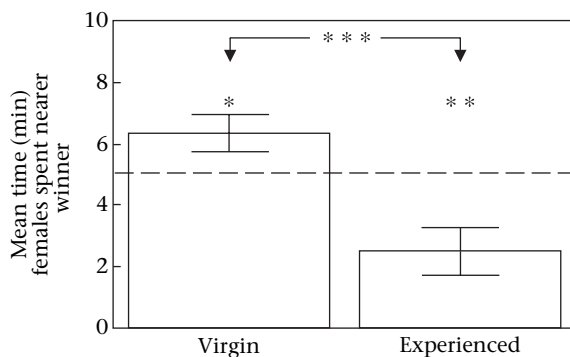


Figure 3. Mean time (\pm SE) during the choice phase that virgin and sexually experienced focal females in experiment 2 spent closer to the male that won during the fight phase. Dashed line = chance. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

examined whether females' sexual experience influenced their use of information acquired by observing males interacting with females, and in experiment 2, whether females' sexual experience influenced their use of information acquired by observing males interact with other males.

The results of experiment 1 indicate that sexual experience per se does not affect the reliance of female Japanese quail choosing a mate on public information acquired by observing the mate choices of other females. These results raise a question as to whether, in Dugatkin & Godin's (1993) study of effects of size on use of public information by guppies, the differences observed were actually the result of differences in the 'information' available to large and small females. All guppies in the Dugatkin & Godin study were sexually experienced, so differences in their behaviour might have reflected differences in age rather than in specific experiences, although, of course, use of public information may well develop differently in different species.

In experiment 2, we found a dramatic effect of sexual experience on responses of females to males observed engaging in aggressive interactions. Sexually inexperienced female quail preferred to affiliate with the more aggressive member of a pair of males they had seen fighting, whereas sexually experienced females making similar choices preferred less aggressive males. Persaud & Galef (2003) found that females adjust their likelihood of affiliating with a male depending on his aggressiveness during courtship and mating. Ophir & Galef (2003b) found that males that are more aggressive when interacting with other males more frequently engage in potentially damaging behaviours when courting and mating with females. The results of experiment 2 suggest that it is experience with courting and mating males that causes sexually naïve females to reverse their initial preference for more aggressive males.

It has been proposed that mate-choice copying may be most beneficial to females choosing between males when either assessment of males is difficult or there is asymmetry in the information that individuals possess (Gibson et al. 1991; Dugatkin & Godin 1992, 1993; Nordell & Valone 1998). For example, Dugatkin (1996; Dugatkin & Godin 1993) and coworkers have provided evidence that mate-choice copying in guppies is more frequent when the males that a female is choosing between are similar in size than when they differ in size and when smaller females observe larger females mating rather than when the reverse is true.

There is reason to believe that discrimination of high-quality males is difficult for female Japanese quail, because females show little or no consistency in affiliative preference when given a choice between the same pairs of male quail of similar age (unpublished observation). Thus, the dependence of female quail on public information when making mate choice decisions is, in this respect, consistent with theory. However, the present finding that both virgin and sexually experienced female quail were significantly influenced in their mate choices by observing the mate choices of others suggests that, in Japanese quail, the impact of public information on mate-choice copying may not be particularly experience dependent.

The effects of sexual experience on responses of female quail to information acquired by observing aggressive interactions between conspecific males reported in experiment 2 suggest that public information and individual learning interact in complex fashion, allowing experienced female quail to minimize potential costs of mating. By observing the relative aggressiveness of interacting males, females can judge both males' relative condition (Otter et al. 1999; Doutrelant & McGregor 2000) and the likelihood that males will engage in potentially injurious behaviours while courting and mating (Ophir & Galef 2003b). Mate choices of female quail that have experienced the punishing physical consequences of courtship and mating appear to be guided less by indications of male quality than by the need to avoid injury while mating.

The results of experiment 2 thus suggest that female quail have to experience the consequences of interacting with males to be able to use to use information acquired by observing males interact to select an appropriate mate. This is, so far as we know, the first demonstration of a role of individual experience in the development of an ability to use public information.

Female quail must balance the benefits resulting from acquiring genes associated with dominance (Boag & Alway 1981) against the costs of associating with highly aggressive males. Consequently, male quail may face a trade-off between the benefits of intrasexual dominance (Otis 1972) and reproductive costs resulting from the reduced attractiveness of aggressive males to sexually experienced females.

There is, of course, always a question as to how relevant results obtained from experiments with captive animals are to the behaviour of free-living animals. Free-living female Japanese quail may rarely see males interact aggressively. They may be able to avoid the punishment that results from interaction with aggressive males in laboratory situations, and therefore, may not need to attend to the relative aggressiveness of potential partners when selecting a mate. However, Nichols (1991, page 41), who observed both feral and domestic Japanese quail maintained in 14.6-m² enclosures, reported that, before pair formation, 'feral males were significantly more aggressive to females than were domestic males and it appears this aggression plays a significant role, not only in pair formation but its maintenance'. There is no indication that small enclosure size (Adkins-Regan 1995) or domestication were responsible for the high levels of aggression of males towards females that we observed. At the least, the present results suggest that, in species where males sexually harass or coerce females, field workers need to consider the possibility that females use information acquired by observing male-male competitions to choose partners, and that sexually inexperienced and experienced females may use such information differently.

Acknowledgments

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