



'Culture' in quail: social influences on mate choices of female *Coturnix japonica*

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We have shown previously that after a focal female Japanese quail, *Coturnix japonica*, sees a conspecific male mating, the focal female's tendency to affiliate and to mate with that male is significantly increased. Here we describe two experiments demonstrating that a focal female quail that has seen a conspecific male mating subsequently shows an enhanced tendency to affiliate not only with that particular male, but also with other males that share his characteristics. The results have important implications for our understanding of the role of social learning in the evolution of male characteristics.

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Biologists have long been interested in understanding the causes of female preference for particular males and the effects of such female choice on evolution of male characteristics (Darwin 1871; Wallace 1891; Cronin 1991). Until recently, the general view has been that natural selection produces females with stable, inherent preferences for males expressing particular epigamic characteristics (Kirkpatrick & Ryan 1991). However, during the last two decades considerable evidence has indicated that females' mate choices are modifiable by social experience (ten Cate & Bateson 1988; Freeberg 1998; Owens et al. 1999). For example, Bradbury & Gibson (1983) and Bradbury et al. (1985) found that the highly skewed mating success of lekking male sage grouse, *Centrocercus urophasianus*, could not be explained plausibly on the assumption that female grouse choose males independently and suggested that mate choice copying might be responsible for the great variance in mating frequencies observed among male grouse.

Mathematical models of effects of gene–culture interactions guiding mate choices of females on male reproductive success have shown that mate choice copying can increase variance in male mating success (Wade & Pruett-Jones 1990). However, models of effects of gene–culture interaction on the spread of epigamic male traits have also shown that, if social learning is to play a role in the evolution of male characteristics, then females must display an increased probability of mating with not only a particular male seen mating, but also other males that

share his distinctive characteristics (Boyd & Richerson 1985; Brooks 1998; Gibson & Hoglund 1992; Kirkpatrick & Dugatkin 1994; Laland 1994; Servedio & Kirkpatrick 1996). If, for example, a female observes another mating with the larger of two males, the former female must display an enhanced preference for large males in general, not just for the particular large male she has observed mating, if her socially induced change in preference is to have effects on the evolution of mate choice at the population level (Brooks 1998).

We have previously shown that after a focal female Japanese quail, *Coturnix japonica*, sees a male quail mate, the focal female's tendency to affiliate and to mate with that male is significantly enhanced (Galef & White 1998; White & Galef 1999a, b). This socially induced change in female preference is not a result either of changes in the appearance or behaviour of recently mated males (Goldschmidt et al. 1993) or of a tendency of females to move into areas where they have recently seen other females (Keister 1979). Rather, changes in female mate choice appear to reflect true copying of the mate choice on one female by another (White & Galef 1999a). Our findings, as well as similar results from studies of social influences on the mate choices of female guppies, *Poecilia reticulata* (e.g. Dugatkin 1992, 1996; Dugatkin & Godin 1992) suggest that females in many species do, in fact, copy the mate choice of others. Mate choice copying would permit a female to avoid any costs associated with independently assessing male quality while still selecting a mate of the same quality as that of the female whose mate choice she copied (Pruett-Jones 1992). A tendency to prefer males seen mating with others should enhance particularly the fitness of females with a less than average ability to identify desirable males (Losey et al. 1986;

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Wade & Pruett-Jones 1990; Gibson & Hoglund 1992; Pruett-Jones 1992; Dugatkin & Godin 1993; Servadio & Kirkpatrick 1996). Trait copying by females seems to be potentially advantageous whenever: (1) females that choose males independently select males that enhance their mates' fitness more than would the average male in the population; and (2) distinguishing characteristics of superior males are honest indicators of their value as mates.

Previous studies with guppies and quail have not demonstrated that a female's socially enhanced preference for a male generalizes from the particular male that she sees mating to other males that share his distinctive characteristics. Such a demonstration is necessary if mate choice copying were to affect not only variance in male mating success, but also the evolution of male characteristics (Brooks 1998). Here we show, for the first time, that a female that has observed a visually distinctive male mate will subsequently prefer not only the particular male that she saw mating, but also other males that share his distinctive characteristics. This demonstration substantially increases the probability that theoretical models of potential effects of social learning on the evolution of male traits are applicable to avian species.

EXPERIMENT 1

In experiment 1 we created two distinctly coloured populations of male Japanese quail, allowed 'focal' females to see a male of one colour mate and then offered each focal female a choice between two new males, one the same colour as the male that she had seen mate, the other a different colour.

Methods

Subjects

Sixty-two Japanese quail, transported to our laboratory from Speck's Poultry Farm (Vineland, Ontario, Canada) when 42 days old, served as subjects. We housed each subject in an individual stainless-steel cage measuring 45.7×61.0 cm and 40.6 cm high, and maintained them until they became sexually mature with ad libitum access to Mazuri Pheasant Starter 5637 (PMI Feeds, St Louis, Missouri) on a 16:8 h light:dark cycle. Each bird also received a handful of autoclaved hay twice a week for environmental enrichment.

We considered females to be in breeding condition as soon as they began to lay at least one egg every other day. To determine when males were ready to breed, we placed each male with a female in the apparatus that we subsequently used for experiments (Fig. 1). Thus we habituated males and females to breeding in the apparatus at the same time that we determined males' readiness to breed.

When each male was 75 days old, we paired him with a different female each day until he either mounted two females in succession or 2 weeks passed without his showing interest in females. In the latter case, we did not use the male in the experiment.

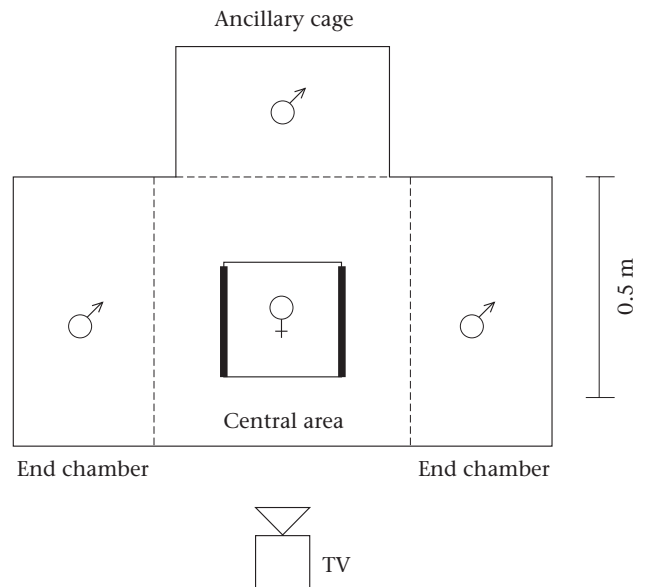


Figure 1. Overhead schematic of the apparatus as configured for an observation period with a sample male alone in the ancillary cage, target males in the end chambers and a focal female in the holding cage. Dashed lines indicate screen partitions, and heavy black lines, the opaque walls of the holding cage.

Apparatus

We conducted the experiment in an enclosure constructed of Plexiglas, painted plywood, and $\frac{1}{2}$ -inch (1.27-cm) wire mesh (Fig. 1) that rested on aluminium trays covered with absorbant paper pads (Tray liners, Lilo Products, Hamilton, Ontario, Canada). Three mesh partitions divided the enclosure into a 'central area', measuring 61×61 cm and 30 cm high, two end chambers, each measuring $30 \times 30 \times 30$ cm, and an ancillary cage, measuring 44×30 cm and 30 cm high (Fig. 1). A hole measuring 26 cm^2 cut in the centre of the Plexiglas roof of the central area allowed us to raise or lower a 25-cm^2 Plexiglas 'holding cage' using a rope and pulley system operated from an adjacent room. This holding cage had two transparent walls and two opaque walls and was oriented so that a subject held within it could see into the ancillary cage, but could not see into the two end chambers of the apparatus (Fig. 1).

We drew a vertical line at the midpoint of the Plexiglas wall that formed the front of the central area so that we could easily determine to which end of the central area a subject was closer. A colour CCTV video camera (Panasonic WV-CP412) connected to a VHS videocassette recorder (Panasonic AG-1240) and colour video monitor (Panasonic CT 1331Y) faced the front wall of the enclosure and enabled us to observe in real time and to record for later analysis the behaviour of subjects in the enclosure.

Treatment groups

We created two groups of males ($N=9/\text{group}$) to whose breast feathers we applied either blue or red food colouring (Club House Foods, London, Ontario, Canada) to create a roughly circular patch 3.5–4.0 cm in diameter.

Males with red and blue chest patches are referred to below, respectively, as 'red' and 'blue' males.

Two days after we dyed the males we assigned both males and females to groups of either four or five and groups to experimental and control conditions. Each group was composed of a 'focal' female that, after she observed a 'sample' red or blue male either alone (control condition) or interacting with a 'model' female (experimental condition), chose between one red and one blue 'target' male.

To assign subjects to groups, we first listed all 81 possible combinations of one red male and one blue male. We then randomly selected 36 of these pairs to serve as target males in the experiment. Next, we randomly assigned a focal female and sample male to each of 18 groups comprising the control condition, and a focal female, model female and sample male to each of the 18 groups comprising the experimental condition.

We used each female as a focal female only once, and two males served together as a target pair only once. Females always served as focal females before they served as model females.

Procedure

The experiment consisted of two 10-min phases: (1) an observation phase, during which focal females assigned to the experimental condition saw a red or blue sample male in the auxiliary cage court and mate with a model female, and focal females assigned to the control conditions saw a red or blue sample male alone in the auxiliary cage; and (2) a choice phase, during which the focal female could affiliate with red and blue target males each confined in one of the end chambers of the apparatus.

Observation phase. To begin the experiment, we confined a focal female in the holding cage in the centre of the apparatus with the two opaque walls of the holding cage oriented so that the female could not view the end chambers, in one of which we placed a red and in the other a blue target male (positions of red and blue target males were counterbalanced across focal females). Next, we placed either a red or blue target male in the ancillary cage, and in the case of focal females assigned to the experimental group, but not of focal females assigned to the control group, we then placed a model female in the ancillary cage. We then left the subjects undisturbed for 10 min.

Choice phase. To begin the choice phase of the experiment, we placed an opaque partition between the ancillary cage and the central area of the apparatus, removed subjects from the ancillary cage, left the room containing the apparatus, and 1 min later, raised the holding cage to permit the focal subject to move freely about the central area.

During the next 10 min we recorded the time the focal female spent closer to each of the two end chambers of the apparatus, one containing a red and one a blue target male. Such tests of affiliative preferences of female quail

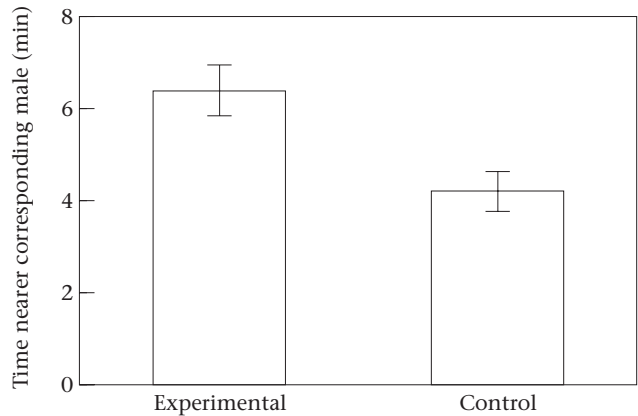


Figure 2. Mean \pm SE number of min during the 10-min choice phase that focal female quail assigned to experimental and control conditions spent nearer the target male that was the same colour as the sample male that they had seen during the observation phase.

have proven strong predictors of their actual mate choices (White & Galef 1999b).

We recorded each female's behaviour on videotape, and when two observers independently scored the time that each of 10 focal females spent nearer each end chamber, interobserver reliability was better than 0.99 (Pearson's product-moment correlation).

Results and Discussion

Observation phase

All sample males assigned to the experimental condition courted and mated with the model female placed with them in the ancillary cage.

Choice phase

Focal females assigned to the experimental condition spent significantly longer nearer the end chamber holding a target male of the same colour as their respective sample males than did focal females assigned to the control condition (Student's t test: t_{34} , $P < 0.01$; Fig. 2).

EXPERIMENT 2

The results of experiment 1 show that female quail develop an enhanced attraction to any male displaying a conspicuous, artificial phenotypic characteristic after seeing one male with that trait court and mate another female. In experiment 2, we determined whether generalized attraction to a class of males sharing a trait after seeing one of the members of that class mate would be found if the trait that the males shared was a rather subtle, naturally occurring one.

Single locus mutations in Japanese quail occasionally result in individuals having one or more white feathers that contrast with their normal, dark plumage (Cheng & Kimura 1990). It is a simple matter to create pseudo-mutant quail that, like their truly mutant fellows, have a few unmelanated feathers, and to use such pseudo-mutants to examine the effects of observing one

pseudomutant mating on females' tendency to affiliate with other pseudomutant males.

Methods

Subjects

Twenty male and 31 female sexually mature Japanese quail served as subjects (Fig. 1).

Apparatus

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

Procedure

Sample and target males. We created 10 'pseudomutant' male quail by gluing (Instant Crazy Glue, Elmer's Products, Brampton, Ontario, Canada) three 1-cm long white feathers taken from an albino quail on to the crowns of 11 normal males. We also glued three, dark, 1-cm long feathers taken from normal quail to the crowns of another 10 'control' males. To ensure that the results of our experiment did not reflect a sampling error in assignment of males to pseudomutant and control conditions, midway through the experiment we changed the feathers we had attached to males' crowns, so that each control male became a pseudomutant and each pseudomutant male became a control.

Observation phase. As in experiment 1, we left each focal female undisturbed in the holding cage for 10 min. Ten focal females observed a pseudomutant male mating with a sexually active female from our colony, and 10 others saw a pseudomutant male alone in the ancillary cage. Eleven additional focal females saw an empty ancillary cage containing neither a pseudomutant male nor a female.

Choice phase. The 10-min choice phase of the present experiment was identical to that of experiment 1 except that each focal female chose between pseudomutant and control target males confined in the end chambers of the apparatus.

Results

Observation phase

As in experiment 1, all sample males courted and mated with a model female when given access to one.

Choice phase

During the 10-min affiliation test, there was a significant effect of treatment of focal females during the observation phase on their affiliative behaviour during the choice phase ($F_{2,28}=7.43$, $P<0.003$; Fig. 3). During the choice phase of the experiment, focal females that had observed a pseudomutant sample male mating in the ancillary cage during the 10-min observation phase spent significantly more time than females that had seen either an empty ancillary cage or a pseudomutant male alone in

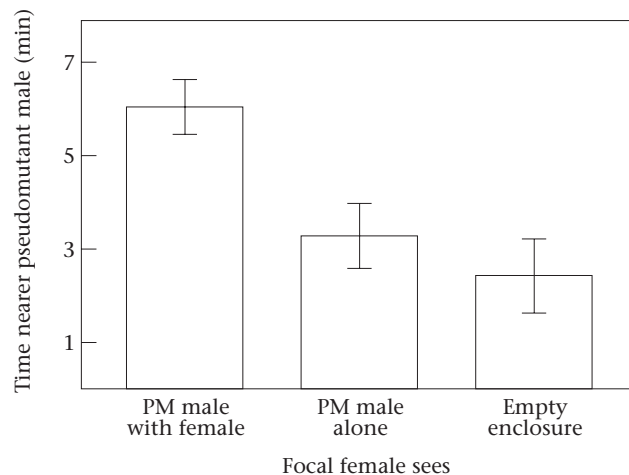


Figure 3. Mean \pm SE number of min of 10 spent nearer a pseudomutant (PM) than a control target male by focal females that had previously observed either: (1) a pseudomutant sample male with female, (2) a pseudomutant sample male alone, or (3) an empty enclosure.

the ancillary cage nearer the pseudomutant than the control target male (Tukey-Kramer multiple comparisons test: both $P_s<0.05$).

GENERAL DISCUSSION

Previous research has repeatedly demonstrated that a female Japanese quail will display an enhanced preference for an individual male that she had seen mating. Theoretical models have shown that generalized, socially induced preferences of females for male characteristics can affect the evolution of male traits (Boyd & Richerson 1985; Kirkpatrick & Dugatkin 1994; Laland 1994). However, as Brooks (1998) has made clear, there are important differences between the copying of individual decisions and cultural inheritance (Galef 1992) of mate preferences. 'Cultural' inheritance of mate preference does not require that females copy the particular mate choices of other females. Rather a cultural contribution to mate choice requires that females make the same type of choices that they have seen other females make (Brooks 1998). The present results provide the first empirical evidence of social enhancement of preference for the traits of successful males rather than for the particular males bearing those traits. These demonstrations of trait preference thus provide an important link in the nexus of deduction and empirical evidence indicating that 'cultural' factors may play a role in evolution of vertebrate mate preferences.

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