



# Female Japanese quail aggregate to avoid sexual harassment by conspecific males: a possible cause of conspecific cueing

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In a series of three experiments, we examined the hypothesis that female Japanese quail, *Coturnix japonica*, are motivated to form aggregations to reduce the probability of harassment by conspecific males. When in the presence of a conspecific male, female quail both sought others of their sex and remained near them. However, if no males were present, females were indifferent to or tended to avoid one another. We interpret these data as consistent with the hypothesis that one function of aggregations of female quail is to avoid harassment by conspecific males. Skew in male mating success would be a probable consequence of such aggregations of females.

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The frequently observed skewed mating success of male birds on leks (Wiley 1991) is often interpreted as resulting, at least in part, from nonindependence of the mate choices made by females (e.g. Bradbury & Gibson 1983; Clutton-Brock et al. 1989; Hoglund et al. 1990, 1995; Gibson et al. 1991). Two general types of nonindependent female mate choice can result in females tending to choose the same partners: (1) 'mate choice copying', defined as an increased probability of mating with a male resulting from a female observing a male's mating history or some part of it (Dugatkin 1996), or (2) 'conspecific cueing', an increased tendency on the part of females to mate with the same male as a consequence of their correlated movement or settlement patterns (Pruett-Jones 1992).

Definition of terms to describe social influences on mate choice is ongoing (e.g. Westneat et al. 2000). However, there is general acceptance of a distinction between correlated female mate choices resulting from females observing and then copying the mate choices of others and various 'pseudocopying' processes (Brooks 1998), of which conspecific cueing is but one example. In conspecific cueing, mate choices of females are positively correlated because females are attracted to one another, particular males, or particular locales (Brooks 1998). Thus, in conspecific cueing, as in other pseudocopying processes, females are not actually influenced by one another's mate choices, although their behaviour can produce skew in male mating success that gives the appearance of mate choice copying by females.

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Results of experimental studies with guppies, *Poecilia reticulata*, and Japanese quail, *Coturnix japonica*, are consistent with the hypothesis that, at least under laboratory conditions, females of some species spontaneously copy the mate choices of those they observe mating (Dugatkin 1992; Dugatkin & Godin 1992; Galef & White 1998; White & Galef 1999a, b). Most relevant to the experiments described below, in which Japanese quail served as subjects, a series of experiments have demonstrated that female Japanese quail that have seen a male mate with another female are likely to affiliate and mate with him (Galef & White 1998; White & Galef 1999a, b, 2000a, b). Unlike mate choice copying, pseudocopying processes have not received systematic study under controlled conditions.

Below, we consider the possibility that female Japanese quail aggregate to avoid sexual harassment by conspecific males (Clutton-Brock & McComb 1993). Harassment-induced aggregations of females could give particular males access to groups of females and lead to skew in male mating success.

## EXPERIMENT 1

If female Japanese quail aggregate to avoid harassment by conspecific males, then females should be more likely to remain near one another when a male is present than when no male is in view.

### Methods

#### Subjects

Eleven sexually mature male and 23 sexually mature female Japanese quail, obtained from Speck's Poultry

Farm (Vineland, Ontario, Canada) when 48 days of age, served as subjects. After transport to the laboratory, each bird resided in a commercial quail-breeding cage (Berry Hill, St Thomas, Ontario), measuring  $51.2 \times 25.5 \times 22.6$  cm, housed in a single temperature- and humidity-controlled colony room illuminated on a 16:8 h light:dark cycle. Birds remained undisturbed with ad libitum access to Mazuri Pheasant starter (PMI Feeds, St Louis, Missouri, U.S.A.) and water for 3 weeks until both males and females were sexually mature.

Sexual maturity in females was indicated by their laying one egg daily either every day or every other day. To determine whether males were in breeding condition, for 5 min/day, starting when each male was approximately 70 days of age, we placed him with a series of sexually mature females in alternating end chambers of the apparatus we subsequently used for experiments (see Fig. 1). We paired each male with a different female each day until he either successfully copulated with two females in succession or 1 week passed without his mounting a female. All 23 female subjects participated in tests of male sexual maturity before they served as subjects in experiment 1. We discarded the few males that failed to show an interest in females, and left the remaining males undisturbed for 4–7 days after they had reached criterion for sexual maturation before using them as subjects in experiment 1.

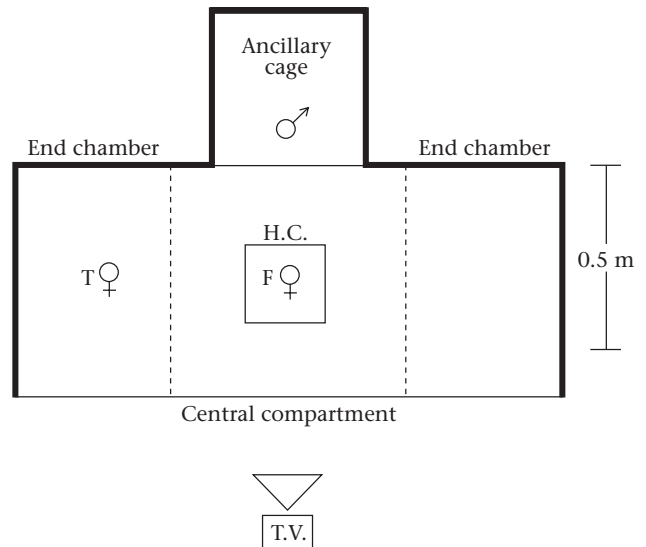
Each female quail served as both a 'focal' and a 'target' subject in experiment 1. A female always served as a focal subject before serving as a target subject, and no pair of females served together more than once. The 11 male quail each served once as a 'stimulus' subject.

### Apparatus

The experiment took place in an enclosure constructed of transparent Plexiglas, painted plywood and half-inch (1.27-cm) wire mesh (Fig. 1) that rested on aluminium trays covered with absorbent paper pads (Tray liners, Lilo Products, Hamilton, Ontario). The enclosure, described in detail in White & Galef (2000a), consisted of a central compartment, two end chambers separated from the central compartment by screen partitions, and an ancillary cage separated from the central compartment by both clear and opaque Plexiglas barriers. The opaque barrier between the ancillary cage and central compartment could be removed to permit an occupant of the central compartment to see into the ancillary cage.

A rope and pulley permitted a holding cage constructed of transparent Plexiglas, measuring  $25 \times 25 \times 50$  cm and centred on the midpoint of the central compartment, to be raised through an opening cut in the lid of the central compartment, while the experimenter was in an adjacent room. Raising the holding cage freed a subject restrained in it, permitting her to move freely about the central compartment.

Closed-circuit television and a video recorder permitted real-time observation of subjects in the apparatus and recording of test sessions for later scoring.



**Figure 1.** Illustration of the apparatus configured for the male-present condition of experiment 1 with a focal female in the holding cage, a male in the ancillary cage, and a target female in one end compartment. Dashed lines indicate screen partitions, heavy lines indicate opaque walls and light lines indicate transparent walls. H.C.=holding cage; F=focal; T=target; T.V.=closed-circuit television.

### Procedure

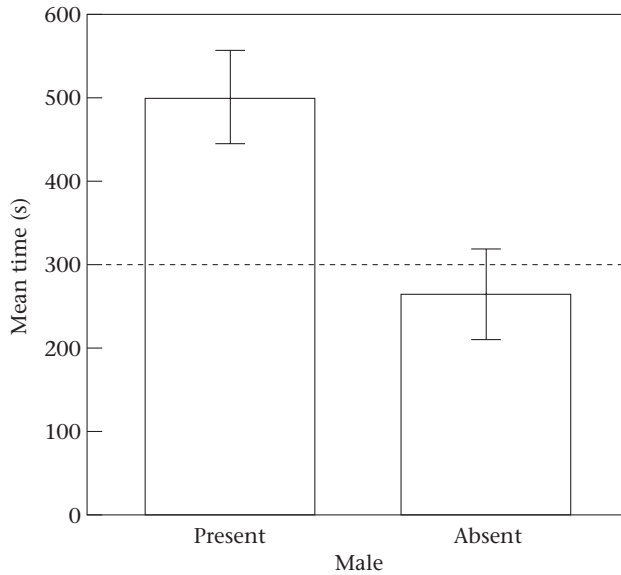
To begin, the experimenter placed a 'focal' female quail in the holding cage, a 'target' female quail in a randomly selected end chamber of the apparatus and either a sexually mature male (male-present condition,  $N=11$ ) or nothing (male-absent condition,  $N=12$ ) in the ancillary cage. The experimenter then removed the opaque barrier separating the ancillary cage from the central compartment, left the room containing the apparatus, and raised the holding cage to free the focal female.

The experimenter, watching on closed-circuit television, waited until the focal female had taken her first step, and for the next 10 min, determined how long she spent closer to the end chamber containing the target female than to the empty end chamber. We considered a focal female that spent more than 5 min of the 10-min test session closer to the end chamber containing the target female to have 'preferred' the target female.

### Results and Discussion

Focal females assigned to the male-present condition spent significantly more time closer to the end chamber containing the target female than did focal females assigned to the male-absent condition (Student's  $t$  test:  $t_{21}=2.97$ ,  $P<0.01$ ; Fig. 2). Nine of 11 focal females assigned to the male-present condition preferred the target female to the empty compartment, whereas only 4 of 12 focal females assigned to the male-absent condition did so (chi-square test:  $\chi^2_1=5.56$ ,  $P<0.02$ ).

Females assigned to the male-absent condition did not spend more time closer to the end chamber containing the target female than would be expected on the null



**Figure 2.** Mean ( $\pm$ SE) number of seconds that focal females assigned to male-present and male-absent conditions in experiment 1 spent nearer the end chamber containing the target female during a 10-min test. The dashed line indicates behaviour expected on the hypothesis that focal females would be indifferent to the presence of a target female in one end chamber.

hypothesis that focal females were indifferent to the presence of the target female (one-sample  $t$  test:  $t_{11} = -0.63$ , NS).

The results of experiment 1 were consistent with the hypothesis that female quail affiliate to reduce the probability of male harassment. Females assigned to the male-present condition were significantly more likely to remain near target females than were females assigned to the male-absent condition.

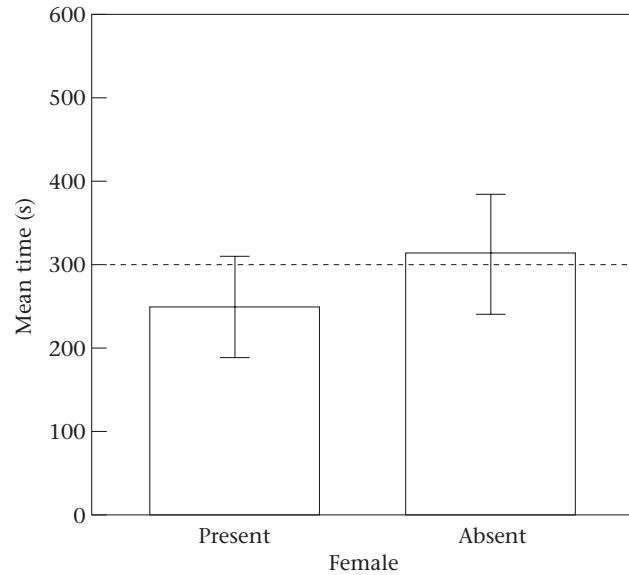
## EXPERIMENT 2

Of course, the results of experiment 1 could reflect an affiliative response of females not to the presence of males in particular, but to the presence of any conspecific. In experiment 2, we repeated experiment 1, except that for subjects assigned to the experimental group, we placed a female rather than a male quail in the ancillary cage. If female quail aggregate to avoid harassment by male quail, then female quail would be expected to aggregate in the presence of male, but not female, conspecifics.

## Methods

### Subjects

Twenty-four sexually mature female quail that 7 days previously had served as subjects in experiment 1, served as subjects in experiment 2. Subjects were randomly assigned either to trios consisting of a focal female, target female and 'stimulus' female (female-present condition), or to pairs consisting of a focal female and target female (female-absent condition). No subject served as a target or



**Figure 3.** Mean ( $\pm$ SE) number of seconds that focal females assigned to female-present and female-absent conditions in experiment 2 spent nearer the end chamber containing the target female during a 10-min test. The dashed line indicates behaviour expected on the hypothesis that focal females would be indifferent to the presence of a target female in one end chamber.

stimulus female before she served as a focal female, and each female served as a focal female only once.

### Apparatus

The apparatus was that used in experiment 1.

### Procedure

The procedure was identical to that of experiment 1, with one exception. In the present experiment, we placed a stimulus female, rather than a stimulus male in the ancillary cage during the 10 min that the focal female chose between an end chamber containing the target female and the empty end chamber.

## Results and Discussion

Focal females assigned to the female-present condition did not differ from those assigned to the female-absent condition in the amount of time they spent closer to the end chamber containing the target female (Student's  $t$  test:  $t_{22} = 0.695$ , NS; Fig. 3). In both female-present and female-absent conditions, 6 of 12 focal females preferred the end chamber containing the target female to the empty end chamber (chi-square test:  $\chi_1^2 = 0.00$ , NS). In neither condition did focal females spend significantly more than 300 s closer to the end chamber containing the target female. The results are those that would be expected on the null hypothesis that focal females, when in the presence of a stimulus female, are indifferent to target females (one-sample  $t$  tests: both  $t_s < 0.21$ , NS; Fig. 3). Clearly, the tendency of focal females in experiment 1 to affiliate with target females was the result of the

presence of a male conspecific in the apparatus, not a general response to the presence of others.

### EXPERIMENT 3

The results of experiments 1 and 2 indicate that the presence of a male Japanese quail causes conspecific females to increase the time they spend near other females. Such enhanced affiliation could result from either a reflex-like response bias or a motivated preference for other females when a male is present. Irwin (1958) proposed that the critical experiment for differentiating between a motivated preference and a response bias in a choice situation requires examining subjects' behaviour in the absence of the stimulus towards which the behaviour is oriented. If a subject learns to approach or avoid a location where a stimulus was present, even when that stimulus is no longer there, then it can be inferred that the subject actually preferred the stimulus. If, to the contrary, the presence of the stimulus is necessary to orient the subject's behaviour, then the response is, in Irwin's terms, a simple response bias, not a motivated preference.

In experiment 3, we allowed a focal female to learn where a target female could be found, removed the target female from that location, and then introduced either a male quail (male-present condition) or nothing (male-absent condition) in place of the target female. If female quail are motivated to seek out other females in the presence of a male, then focal females assigned to the male-present condition should spend more time close to where they had previously seen a target female than females in the male-absent condition.

### Methods

#### Subjects

Twenty-eight sexually mature, female Japanese quail served as focal and target subjects and 13 male quail served as stimulus animals. Each female participated in the experiment as a focal subject before participating as a target subject, and no pair of female subjects participated together in the experiment more than once.

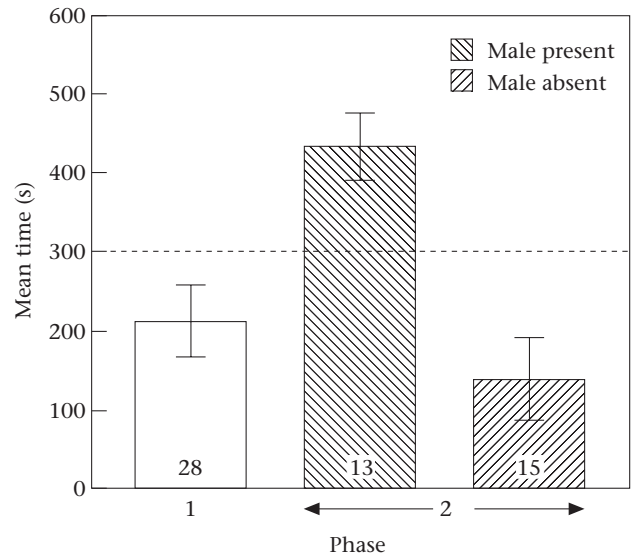
#### Apparatus

The apparatus was that used in experiments 1 and 2, except that the opaque partition separating the ancillary cage from the central compartment of the apparatus was left in place, and the ancillary cage was not used.

#### Procedure

The experiment consisted of two 10-min phases. To begin the first phase, we placed a focal female in the holding cage and a target female in one of the end chambers of the apparatus. We then raised the holding cage and gave the focal female 10 min in which to choose between the two end chambers of the apparatus.

To begin phase two, we returned the focal female to the holding cage, removed the target female from the apparatus, and either introduced (male-present condition,



**Figure 4.** Mean ( $\pm$ SE) number of seconds that focal females spent nearer the end chamber containing the target female during a 10-min test in phase 1 of experiment 3 and in male-present and male-absent conditions in phase 2 of experiment 3. The dashed line indicates behaviour expected on the hypothesis that focal females would be indifferent to the presence of a target female in one end chamber. Numbers within histograms =  $N$ /condition.

$N=13$ ) or did not introduce (male-absent condition,  $N=15$ ) a male into each of the two end chambers of the apparatus.

During both phases 1 and 2, an observer watching on closed-circuit television determined the time that focal subjects spent closer to each end chamber of the apparatus and calculated the number of focal females that preferred the end chamber that had contained a target female during phase 1.

### Results

#### Phase 1

During phase 1, focal females did not tend to remain nearer the end chamber of the apparatus containing the target female. In fact, the data for phase 1 from all 28 focal females showed a marginal tendency to avoid the side of the enclosure where a target female was present (one-sample  $t$  test:  $t_{27} < -1.98$ ,  $P < 0.06$ ; Fig. 4). In analysing the data from phase 1, we combined data for focal females that would be assigned to male-present and male-absent conditions during phase 2 because, until the start of phase 2, we treated focal females assigned to both conditions identically.

#### Phase 2

During phase 2, the 13 focal females assigned to the male-present condition spent significantly more time closer to the end chamber that had contained a target female during phase 1 than did the 15 females assigned to the male-absent condition (Student's  $t$  test:  $t_{26} = 4.36$ ,  $P < 0.0002$ ; Fig. 4). Females assigned to the male-absent condition tended to avoid the end chamber that had

contained the target female during phase 1 ( $t_{14}=3.10$ ,  $P<0.02$ ). Eleven of 13 focal females assigned to the male-present condition preferred the end chamber that had contained the target female, whereas only 3 of 15 females assigned to the male-absent condition did so (chi-square test:  $\chi^2_1=11.63$ ,  $P<0.001$ ).

## Discussion

As in experiments 1 and 2, females in experiment 3 failed to associate with others of their sex in the absence of males (phase 1, phase 2 of the male-absent condition). However, when males were present (phase 2 of the male-present condition), focal females returned to the area where they had previously seen a female. The data are consistent with the hypothesis that, in Irwin's (1958) terms, affiliation in female Japanese quail results from a motivated preference for conspecific females when in the presence of males.

## GENERAL DISCUSSION

Results of the present experiments indicate that female Japanese quail are generally uninterested in remaining near other females, but are motivated to join other females when a sexually active male is present. Field data from other studies suggest that males sometimes cause females significant harm during sexual encounters (e.g. fallow deer, *Dama dama*: Clutton-Brock & McComb 1993; horses, *Equus caballus*: Linklater et al. 1999), and Smuts & Smuts (1993) proposed that, under some circumstances, females form coalitions to protect each other from such male harassment. The sexual encounters of male and female Japanese quail, like those of horses and fallow deer, seem violent to a human observer. A male quail chases a female, seizes the feathers at the back of her head in his beak, and often drags her by the head feathers prior to pinning her down and mounting to achieve cloacal contact.

Males will mate repeatedly with a single female, and several inseminations are necessary to fertilize all eggs in a single clutch (Adkins-Regan 1995). However, once a female has secured the sperm she requires from a male, she incurs unrewarded risks by further sexual contact with him. If a male is more likely to repeatedly mount a female he has previously inseminated when she is alone than when she is part of a group, females could reduce their risk of damage from unnecessary sexual encounters by forming groups in the presence of a sexually active male. This interpretation leads to a prediction that we are currently testing. When a male is present, females with stored sperm should be less likely than females without active sperm stores to remain near other females.

Taken together, results of the present experiments and previous research suggest that both mate choice copying (Galef & White 1998; White & Galef 1999a, b, 2000a, b) and female quails' motivation to aggregate when a male is present can skew male reproductive success. Both mate choice copying and conspecific cueing are factors that may influence male access to female Japanese quail.

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