

MATE ASSESSMENT AND NON-INDEPENDENT MATE CHOICE BY FEMALE  
JAPANESE QUAIL

By  
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MATE ASSESSMENT AND NON-INDEPENDENT MATE CHOICE BY FEMALE  
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# Abstract

The body of this thesis is comprised primarily of two published papers (Chapters 2 and 3) and a third paper (Chapter 5) accepted for publication. All three investigate the influence of social information on mate choice in female Japanese quail, *Coturnix japonica*.

In Chapter 1, I review the theoretical and empirical literature on mate choice and eavesdropping that are relevant to the main topics with which this thesis is concerned. I demonstrate, in Chapter 2, that female Japanese quail use information garnered from video images of males interacting with other females when subsequently choosing between the live males that appeared in the videos. The results of this experiment provide evidence of the utility of a technique to investigate social influences on the behavior of Japanese quail, and possibly, other avian species as well.

In Chapter 3, I show that females use social information acquired by observing inter-male aggression to select mates, and provide evidence that the threat of injury posed by aggressive males influences females to select less aggressive males as mates. In Chapter 4, I provide a control for the possibility that females were not actually choosing to stay near less aggressive males in the experiments described in Chapter 3, but were preferring locations where those males had been seen engaged in agonistic interaction. Finally, in Chapter 5, I examine the role of sexual experience in determining whether when selecting a mate female quail copy the mate choices of other females or attend to the relative aggressiveness displayed by males engaged in intra-sexual competition when selecting a mate. I report that prior sexual experience is necessary for females to avoid the more aggressive of two males but not for expression of mate-choice copying. Taken together, the results of Chapters 3, 4 and 5 are consistent with the hypothesis that the relative costs and benefits of associating with dominant and submissive males may determine which type of male females will prefer as a partner. The view that females should invariably prefer dominant males because such males are likely to be a source of superior genes or can provide females with greater resources considers only the benefits and not the potential costs to females of consorting with relatively aggressive males.

In Chapter 6 I summarize the major findings of the thesis, and then briefly describe a failed experiment to determine whether the technique developed in Chapter 2 could be used to examine effects of female observation of inter-male aggression on subsequent mate choice in the absence of audience effects, and discuss the conflicting selection pressures that Japanese quail of either sex may face.



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# Preface

The body of this thesis is comprised of four Chapters. Chapter 2, 3 and 5 have been published or accepted for publication in *Animal Behaviour*. Chapter 4 is an unpublished study that clarifies interpretation of data presented in Chapter 3. Each chapter was a collaborative effort coauthored by B. G. Galef, Jr. I was involved extensively in all aspects of each paper, formulating questions, designing and conducting experiments, analyzing data, and preparing manuscripts for publication.



# Chapter 1

## Introduction

### 1.1 Introduction

Ever since the publication of Darwin's classic "The Descent of Man and Selection in Relation to Sex" (1871), female mate choice and male-male competition have been subjects of interest to evolutionary biologists. However, it is only during the last few years that attention has begun to focus on interaction between these two aspects of sexual selection, on how females use information obtained from observation of inter-male aggression to modify their subsequent mate choices.

The body of this thesis consists of three papers, two published and a third accepted for publication in a refereed journal. The first paper (Chapter 2) investigates the response of Japanese quail (*Coturnix japonica*), the subject species in all three papers, to video images. This paper provides the first report of an animal identifying individual conspecifics on a video display and one of very few reports of an animal transferring information from a two-dimensional video image to the object that video image represents. The method developed in the paper provides a technique for controlling for effects of interaction between observer and observed in studies of mate-choice copying and provides evidence that previously demonstrated mate-choice copying by female Japanese quail is a result of 'eavesdropping'.

In the second paper (Chapter 3), I show that female Japanese quail use information obtained by observing males fight to choose the less aggressive of two males that they have seen engage in agonistic interactions. I then provide an explanation for this unexpected preference for less aggressive males in terms of the costs and benefits to females of consorting with dominant and submissive males.

My finding that females prefer less aggressive males, or perhaps more accurately, avoid more aggressive males, is unusual. Previous research on female mate choice following observation of interacting males has focused on investigations of benefits accruing to females choosing to mate with dominant males, and has largely ignored any costs that females might incur as a consequence of choosing dominant males as partners.

Chapter 4 describes the results of an unpublished study that provides a potentially important control for the experiment reported in Chapter 3. This control, although not particularly

informative in itself, both replicates the main finding described in Chapter 3, and sharpens interpretation of the data reported there, serving as a control for preference for particular sites rather than particular males as a cause of the findings reported in Chapter 3.

Chapter 5 consists of a manuscript in press that describes experiments exploring the role of sexual experience in determining how female quail use information acquired from observing inter-male interaction when choosing a mate. Perhaps surprisingly, sexually naïve females, unlike the sexually experienced females that served as subjects in Chapter 3, prefer the more aggressive of two males that they observe engaged in agonistic interaction.

Finally, in Chapter 6, I summarize the results of Chapters 2 to 5 and describe briefly the results of an inconclusive study undertaken to integrate the material described in the preceding chapters.

In the remainder of the present chapter, I first very briefly review basic sexual selection theory and then discuss in greater detail non-independent mate choice. I explore possible costs and benefits to females of consorting with dominant males and consider why females should or should not prefer to mate with dominant individuals. I then consider the literature on eavesdropping, a phenomenon that is closely related to non-independent mate choice in general and mate-choice copying in particular, though the literatures of the two fields have developed essentially independently. Finally, I discuss what is known of the natural history, mating system and aggressive behavior of Japanese quail (*Coturnix japonica*), the subject species in this thesis.

## 1.2 Sexual Selection

Bateman (1948) demonstrated that reproductive success of male *Drosophila* is directly related to the number of mates that a male secures. Consequently, males often compete with one another, either directly or indirectly, to gain access to females (Trivers, 1972). Females often do not increase their fitness by engaging in multiple matings, at least not to the extent that males do, and are more likely to maximize their reproductive success by selecting high quality mates as fathers of their offspring or by investing directly in young.

In a few species, reproductive roles of males and females are reversed, and males invest more in production of offspring than females. In species with such “sex-role reversed” mating systems, for example, pipefish, *Syngnathus sp.*, (Berglund & Rosenqvist, 1990, 1993) and jacanas, *Jacana jacana*, (Emlen, Wrege, & Webster, 1998), males are choosier than females, and females compete for access to males. For simplicity, and because it is the more frequent arrangement, I shall discuss females as the choosy sex and males as competitors. Furthermore, I shall limit discussion to female mate selection, although males also have important decisions to make when choosing a female to court.

Males may offer *direct* benefits to females: territorial resources, protection from harassment by other males, investment in young that reduces the energetic costs to females of reproduction, etc. Alternatively, females may gain *indirect* benefits from males (e.g. good genes or parental investment) that affect the survival not of the female herself, but of her offspring. Thus, females should be expected to assess the net potential payoff a male offers.

## 1.3 Mate Assessment

Females have evolved a variety of strategies to identify high quality potential mates. For example, females may select males based on phenotypic characteristics that are predictors of mate quality (Zahavi, 1975; Hamilton & Zuk, 1982; Cronin, 1991). Alternatively females may use information acquired by observing conspecifics interact to select a male to fertilize their eggs (Pruett-Jones, 1992; McGregor & Peake, 2000; Westneat, Walters, McCarthy, Hatch, & Hein, 2000).

### 1.3.1 Independent Assessment

#### Good-gene models

Much theory and some empirical data suggest that females have been selected to prefer males with “good” genes coding for favorable traits (Fisher, 1915; Williams, 1966; Zahavi, 1975; Hamilton & Zuk, 1982; Kodric-Brown & Brown, 1984; Andersson, 1986). Other “indicator models”, of which good-gene models are a subset, propose that an elaborate trait may evolve to advertise characteristics other than good genes, such as an ability to provide for offspring (Grafen, 1990; Heywood, 1989; Hoelzer, 1989; Price, Schluter, & Heckman, 1993).

For selection of this kind to work to females’ benefit, the characteristics that females use to discriminate among males must be honest signals of male quality. One theory suggests that because of the high cost of developing and maintaining elaborate characteristics and the increased vulnerability to predation such traits often produce, elaborate characteristics are difficult to fake, so females should use such traits when selecting a mate (Zahavi, 1975; Grafen, 1990). For example, Petrie (1994) found that peacocks, *Pavo cristatus*, with more elaborate tails that are, presumably, expensive to grow and maintain, and expose their possessors to increased predation pressure, produce offspring that grow faster and are more likely to survive than offspring of males with less elaborated tails.

Berglund, Bisazza, and Pilastro (1996) have extended the good-gene model arguing that elaborate ornaments can serve a dual purpose signaling both genetic quality to females and competitive ability to males. On such a model, dominance testing, as well as increased predation risks and greater metabolic costs, maintain the honesty of traits that females use to assess males.

#### Dominance rank as an indicator of quality

**Selection of dominant males.** It has been proposed that success in male-male competition reflects a lifetime of relative success in food collection, disease resistance, and injury avoidance (Borgia, 1979). If so, females seeking high-quality males should attend to males’ relative dominance as well as to traits indicative of high status, such as large body size or badges indicative of status (Cox & LeBoeuf, 1977; Andersson, 1994; Berglund et al., 1996). In fact, many female mammals (e.g. pronghorn, *Antilocapra americana*: Byers, Moodie, & Hall, 1994; bank voles, *Clethrionomys glareolus*: Horne & Ylönen, 1996; Syrian hamsters, *Mesocricetus auratus*: Brown, Humm, & Fischer, 1988), birds (e.g. Cock-of-the-Rock, *Rupicola rupicola*:

Trail, 1985; domestic fowl, *Gallus gallus domesticus*: Graves, Hable, & Jenkins, 1985), fish (e.g. *Gambusia holbrooki*; Bisazza & Marin, 1991) and insects (e.g. *Physiphora demandata*; Alcock & Pyle, 1979) prefer males that are dominant in male-male competition. Even in sex-role reversed species such as pipefish, *S. typhle*, males prefer dominant females whose competitive displays are more reliable indicators of their quality than is their ornamentation (Berglund & Rosenqvist, 2001).

In some species, (e.g. jungle fowl, *Gallus gallus spadiceus*: Thornhill, 1988; boat-tailed grackles, *Quiscalus major*: Poston, 1997; robins *Erithacus rubecula*: Tobias & Seddon, 2002; sailfin mollies, *Poecilia latipina*: Farr & Travis, 1986; *Padogobius martensi*: Bisazza, Marconato, & Marin, 1989a; *Gambusia holbrooki*: Bisazza, Marconato, & Marin, 1989b; *Scatophaga stercoraria*: Borgia, 1981; *Linyphia litigiosa*: Watson, 1990) females actually incite male-male contests, possibly to facilitate identification of dominant males. For example, female elephant seals, *Mirounga angustirostris*, vocalize loudly when a male attempts to copulate. This behavior attracts other males, resulting in intense aggressive contests between males and permitting dominant males to drive off subordinate, possibly inferior, mating partners (Cox & LeBoeuf, 1977).

**Selection against dominant males.** Dominance status is often not indicative of the willingness of males to provide resources for females or their young (Qvarnström & Forsgren, 1998). Consequently, depending on the quality of a choosing female (Bakker, Künzler, & Mazzi, 1999), the degree of parental investment she requires from a mate (Qvarnström, Pärt, & Sheldon, 2000) and, possibly, the relative parental investment that dominant and subordinate males are willing to provide, male contributions to rearing offspring may be more important in determining mate choice than male aggressive ability. For example, in sand gobies, *Pomatoschistus minutus*, females prefer males that provide good paternal care rather than winners of male-male competitions, who often provide poorer paternal care than losers in aggressive interactions (Forsgren, 1997).

Furthermore, if dominant males are more promiscuous than subordinates, dominance could be a poor predictor of a male's providing resources because the resources that he commands may have to be shared among a number of females and their young. Consequently, in species where dominant males have greater numbers of mates than their subordinates, females choosing mates should attend to cues such as territory quality and number of females already settled on that territory as well as male status (Orians, 1969).

In a variety of species, ranging from wax moths, *Achroia grisella*, (Cremer & Greenfield, 1998) to macaque monkeys, *Macaca fuscata*, (Soltis et al., 1997), male dominance is not an attractive attribute to females (see Qvarnström & Forsgren, 1998 and references therein). Indeed, in many avian species examined to date as well as some mammals there appears to be a trade-off between male success in male-male contests and male willingness to invest in a female or her offspring (Ketterson, Nolan, Wolf, & Ziegenfus, 1992; Clark, Desousa, Vonk, & Galef, 1997).

### Potential costs of mating with dominant males

Qvarnström and Forsgren (1998) have identified three important direct costs that females may incur as a result of affiliating with dominant males: disease transmission, fertilization failure resulting from male sperm depletion, and physical injury. Such potential costs of mating with dominant males may explain why females of some species prefer subordinate to dominant males as partners.

**Disease transmission.** Choosing females may attend to the dominance status of a male to reduce their exposure to disease. Freeland (1981) has argued that in mice, *Mus domesticus*, the outcome of male-male competitions reflect a male's disease state, in that infection handicaps males and prevents them from winning fights and becoming dominant. If so, female mice might avoid infection or disease by preferentially mating with dominant individuals (e.g. Mossman & Drickamer, 1996). On the other hand, the elevated levels of androgen associated with increased male dominance in many species (Rose, Holaday, & Bernstein, 1971; Mendoza, Coe, Lowe, & Levine, 1979; Creel, Creel, Mills, & Monfort, 1997; Machida, Yonezawa, & Noumura, 1981; Schuurman, 1980) can suppress the immune system (Folstad & Karter, 1992; Wedekind & Folstad, 1994), so dominant males may actually be more susceptible to disease and parasite infection than their subordinates. Furthermore, when dominant males gain access to females more frequently than their subordinates, dominant individuals will have greater numbers of sex partners and will therefore, be more likely than subordinates to be infected with sexually transmitted diseases. Consequently, although there is no *a priori* general expectation as to the direction of the relationship between male dominance status and male health (Qvarnström & Forsgren, 1998), in each species, dominance status might allow females to assess the health of potential mates.

**Fertilization failure caused by sperm depletion.** Sperm is often discussed as if it were an inexhaustible resource. However, transitory sperm depletion can result from high frequencies of ejaculation (e.g. humans, *Homo sapiens sapiens*: Freund, 1963; lemon tetra, *Hyphessobrycon pulchripinnis*: Nakatsuru & Kramer, 1982; fruit flies: Pitnick & Markow, 1994). In mating systems where dominant males monopolize matings, as in harems, females with dominant male partners may be less likely to be fertilized than females mating with subordinates (Qvarnström & Forsgren, 1998). If so, females might choose to mate with lower ranking males simply to increase their chances of fertilization. Choice of subordinates as a result of sperm depletion of dominants might be expected to occur only when costs to females of mating are high, variance in male quality is low, and offspring fitness is not greatly affected by the status of sires.

**Risk of injury or death.** Males can injure or even kill females during courtship and mating (Linklater, Cameron, Minot, & Stafford, 1999; Clutton-Brock, Hiraiwa-Hasegawa, & Robertson, 1989; Le Boeuf & Mesnick, 1990), particularly when males are larger than females (Qvarnström & Forsgren, 1998). Sometimes females can reduce risk of injury by choosing a dominant male as a mate because dominants can exclude rival males, thus decreasing the

probability that a female will be injured during male-male contests and reducing the frequency of harassment of a female by males other than her mate (Qvarnström & Forsgren, 1998). Conversely, if males that are dominant exhibit higher levels of aggressive behavior toward females as well as toward males, females may incur more damage affiliating with dominants than with subordinates and may prefer to mate with the latter. For example, cockroach females, *Nauphoeta cinerea*, reduce damage from male manipulation and aggression by using chemical cues to select less dominant males as mates (Moore, Gowaty, Wallin, & Moore, 2001).

### 1.3.2 Non-independent Assessment

Although many models of sexual selection have treated females as making mate choices independently (e.g. Fisher, 1930, 1958; Lande, 1981; Kirkpatrick, 1982; Zahavi, 1975; Hamilton & Zuk, 1982), non-independent mate choice, i.e. assessment of potential mates indirectly using socially acquired information, may be common. Pruett-Jones (1992) provided a formal definition of non-independent mate choice that has been both adopted and adapted by others (e.g. Dugatkin, 1996). Pruett-Jones (1992) first defined the *absolute probability* that a female selects a male as a mate as her probability of choosing him in the absence of any social influence, and the *conditional probability* that she will select him as the probability of her doing so given knowledge of other females' choices. When absolute and conditional probabilities of choice are equal, mate choice is *independent*, and when conditional and absolute probabilities are not equal, *non-independent* mate choice has occurred.

#### Why choose non-independently?

Females that select mates on the basis of observations of interactions between potential mates with others can reduce the time and energy they expend in searching for an appropriate partner (Boyd & Richerson, 1985; Sullivan, 1994; Real, 1991), their exposure to predation while searching (Travers & Sih, 1991; Magnhagen, 1991) and can avoid aggressive responses of rejected males (Manson, 1994). Such females may also reduce the metabolic demands of developing and maintaining neural circuitry to make direct comparisons between males (Stamp Dawkins & Guilford, 1996), though they incur whatever costs are involved in developing and maintaining the physiological substrate for mate-choice copying.

When a female matches her mate choice to that of other females she will select males of the same quality as the mates of females that she has copied and will do so without incurring whatever costs are involved in independent mate assessment. Indeed, Bikhchandani, Hirshleifer, and Welch (1992) have provided formal models that lead to the possibly counter-intuitive suggestion that, in general, individuals who observe two or more others make the same choice and then copy that choice will do better than those who choose for themselves. Females should therefore sometimes ignore their own preferences and select previously chosen males as mates. The simplifying assumptions of the model (e.g. that individuals value outcomes equally, that all have an equal ability to appraise, etc.), may limit its usefulness in real situations.

Relatively inexperienced females might be expected to copy mate choices of more experienced individuals when mate assessment is difficult (Gibson & Höglund, 1992; Støhr, 1998).

Furthermore, when there is marked asymmetry in male quality, individual assessment and attending to mate choices of others should produce the same result, and using information obtained by observing others may avoid many of the costs involved in individual assessment of potential mates.

In sum, non-independent mate choice should be beneficial to females if significant costs are associated with mate assessment, if females vary in ability to assess males, and if mate assessment is difficult (Gibson & Höglund, 1992; Brooks, 1996). Such arguments should, however, be restricted to species in which males do not make substantial investment in either their mate or her offspring, because in species where males make appreciable parental investment, there may be substantial costs to mating with a male that has mated with another.

### Types of Non-Independent Mate Choice

**Mate-Choice Copying.** One female is said to have copied the mate choice of another when the probability of her choosing a particular male increases after observing him mate with another female (Pruett-Jones, 1992; Dugatkin, 1996). As Dugatkin (1996, p. 87) has emphasized, in mate-choice copying “information about a male’s mating history (or some part of it) must be obtained by the female via observation [of the behavior of another female]” for true mate-choice copying to occur.

Pruett-Jones (1992), Westneat et al. (2000) and Bradbury and Gibson (1983) have each described behavioral mechanisms other than ‘true’ mate-choice copying that, at least in principle, could produce non-independent mate choice and that might appear to an observer to be instances of mate-choice copying, though they were not. The goal of all three authors has been to distinguish true mate-choice copying from other behavioral processes that may lead to non-independent mate choice, but do not involve actual copying of the observed choices of others.

**Conspecific Cueing.** When females of a species are attracted to one another and move about in groups, the presence of one female on a territory predicts that other females will also be present there. A male may, therefore have opportunity to mate with several females whenever he has opportunity to mate with one. In such cases, skew in male mating success results, not from females copying one another’s mate choices, but from the tendency of females to aggregate. Such *conspecific cueing* may be fairly common because clustering offers several potential benefits to females, reducing risk of predation (Hamilton, 1971), increasing foraging efficiency (Ward & Zahavi, 1973), and reducing sexual harassment by males (Clutton-Brock & Parker, 1995; Pilastro, Benetton, & Bisazza, 2003; Persaud & Galef, 2003), and may only indirectly increase the probability that several females will tend to mate with the same male.

Clutton-Brock et al.’s (1989) study of mating success in fallow deer, *Dama dama*, provides an example of how conspecific cueing can be distinguished from mate-choice copying. Female fallow deer tend to join males that already have large harems. This preference could reflect either a tendency of females to copy the mate choices of other females or a tendency of females to prefer to join larger herds. Clutton-Brock and McComb (1993) allowed females in estrus to choose between enclosures containing (1) males alone, (2) males with varying numbers of

females or (3) females alone.

Female deer preferred males with harems to lone males, but showed no preference when choosing between herds of approximately equal size with and without male members. Furthermore, females that saw a male actually mate showed no tendency to join his harem. Thus, the data indicate that female fallow deer join large groups of other females and do not copy their mate choices.

**Does conspecific cueing differ from mate choice copying?** Jennions and Petrie (1997) have argued that the distinction between mate-choice copying and conspecific cueing results from a confusion of proximate and ultimate explanations of behavior. They suggest that mate-choice copying and conspecific cueing have the same ultimate effect of increasing variance in male reproductive success. However, although mate choice-copying and conspecific cueing both increase reproductive skew, mate-choice copying can have other important evolutionary consequences that conspecific cueing cannot. In particular, females that mate-choice copy can learn the characteristics of males that they see mate and modify their subsequent mate choices accordingly. Females moving about in groups that mate with the same male need not learn anything about the characteristics of the males with whom they mate. Consequently, mate-choice copying can produce idiosyncratic “traditions” of preference for particular kinds of males, whereas conspecific cueing can not. For example, White and Galef (2000b) showed that female Japanese quail that observed other females mating with a distinctively marked male subsequently showed increased preferences not only for the particular male they had seen mating, but for all males with similar characteristics. Thus, the distinction between conspecific cueing and mate-choice copying may be relevant to those interested in functions of behavior as well as its proximal causes.

**Other Types of Non-independent Mate Choice.** Non-independent mate choice can be a result of processes other than either mate-choice copying or conspecific cueing. For example, recently mated males might look or behave differently from unmated males, and congruence in female mate choice could result from female preference for males that had recently mated (Bradbury & Gibson, 1983).

Westneat et al. (2000) have provided a taxonomy of forms of non-independent mate choice that, like conspecific cueing, might be confused with mate-choice copying by an observer of populations in which some males enjoy far greater mating success than others.

**Non-learned mechanisms of non-independent choice.** Westneat et al. (2000) discuss three non-learned mechanisms that could account for skew in males' mating success: (1) stimulus enhancement/reduction, (2) contagion/inhibition, and (3) stimulus response.

Spence (1937) introduced the term *stimulus enhancement*, to explain the observation that, in studies of social facilitation of the acquisition of operant responses, subjects were more likely to make contact with a manipulandum after observing a conspecific do so. In Westneat et al.'s (2000) taxonomy of non-independent mate choice, stimulus enhancement refers, in analogous fashion, to situations where the presence of females near a male or a male's displays



while courting or mating make him more noticeable than his competitors, thus increasing his probability of attracting members of the opposite sex. The process is in some ways similar to mate-choice copying. However, in the case of stimulus enhancement, females are not copying the choices of others but simply attending to males that become more conspicuous as the result of interaction with other females. For example, White and Galef (1999b) found that female Japanese quail increase their preference for males that they have seen standing next to another female.

Second, postcopulatory display or other male behavior following copulation may increase female receptivity which Westneat et al. (2000) term *contagion*. Finally, the term *stimulus response* is used by Westneat et al. (2000) to describe situations in which females prefer males seen near salient non-social stimuli. For example, female fathead minnows, *Pimephales promelas*, (Unger & Sargent, 1988), river bullheads, *Cottus gobio*; (Marconato & Bisazza, 1986) and fantail darters, *Etheostoma flabellare*; (Knapp & Sargent, 1989) all prefer to mate with males that have eggs in their nests deposited there by other females. Jamieson (1995) argues that such female preference can be explained as an evolved response to egg predation in cases where the probability of survival of an individual egg increases with increasing numbers of eggs in a nest, and may only incidentally result in social influence on mate choice.

**Learned mechanisms of non-independent choice.** Westneat et al. (2000) also discuss three types of non-independent mate choice, that depend on learning: *association to a location*, *association to a male*, and *association to a trait*. If, as is the case in *association to a location*, females prefer to mate in locations where they have seen other females mate, and males tend to remain in the same location, then a female that observes another female mate is likely to mate with the male that she observed mating. Gibson, Bradbury, and Vehrencamp (1991) have suggested that females in lekking species may simply prefer to copulate at sites where the rate of male displays is highest. For example, Gibson et al. (1991) found that the success of male sage grouse, *Centrocercus urophasianus*, in their first season on a territory varied with the mating history of the territory rather than the mating history of the male.

In cases of *association to a male*, a female forms an association between the mating behavior of another female and her male consort. Using such a definition, mate-choice copying is an association to a male when such learning results in females showing enhanced acceptance of a male. In principle, association to a male can result in either enhanced acceptance or rejection of males seen consorting with other females. Nakatsuru and Kramer (1982), in fact, report that female lemon tetras are more likely to reject males they have observed spawning with another female, presumably to avoid sperm-depleted males. If the experiments described in the body of this thesis had involved females learning to avoid males observed interacting aggressively with other females, rather than with males, they would have provided evidence of non-independent mate choice based on association to a male.

Last, *association to a trait* occurs when a female associates another female's mate choice not with a particular male, but with a characteristic of that male, and subsequently exhibits a change in her receptivity to all males sharing the characteristic to which she formed an association. For example, White and Galef (2000b) found that female quail that had observed other females mate with a male with either a red or blue spot on his breast, subsequently

showed an enhanced preference for all males with the same color spot on their breasts.

**Confusion resulting from unneeded categorization.** Although the distinctions Westneat et al. (2000) make can, as indicated, be applied in some cases, and it is useful to have a discussion of the full range of factors that can result in non-independent mate selection, the proposed categories are difficult to apply to most data sets. Furthermore, at least in the hands of Westneat et al. (2000), the proposed categories lead to some rather unlikely explanations of non-independent mate choices. For example, in discussing association to trait, Westneat et al. (2000) describe inbreeding avoidance by female Japanese quail (Bateson, 1982) as resulting from females' preferences for males unlike the males that their mothers chose as mates. However, young female quail in Bateson's (1982) study never saw their father, so it is hard to see how they could associate anything with his characteristics.

Also, it is important to keep in mind that the various forms of non-independent mate choice are not mutually exclusive. For example, females can both mate-choice copy and tend to move about in groups. Indeed, Galef and White (1998), in a study of the behavioral processes supporting non-independent mate choices of female Japanese quail, found evidence of both conspecific cueing and mate-choice copying by their subjects. Analyses of behavioral processes can determine necessary and sufficient conditions for non-independence in mate choice without an elaborate vocabulary, and attempts to categorize other types of social learning (see Galef, 1988; Whiten & Ham, 1992) have not proven particularly useful.

### Studies of Non-independent Mate-Choice in the Field

The frequently observed, highly skewed mating success of males on leks (Wiley, 1991) has led several investigators to surmise that the exceptional reproductive success of some males results from a tendency of females to copy one another's mate choices. In a pioneering study of lekking white-bearded manakins, *Manacus manacus trinitatis*, Lill (1974) noted that matings were clumped in time and suggested that females visited leks to observe other females selecting mates and returned at a later time to copy these choices. More recently, in a study of the mating behavior of lekking sage grouse, Gibson et al. (1991) failed to find any physical characteristics that differentiated successful males from their unsuccessful fellows, but discovered that as mating frequency increased, females' mate choices converged. They interpreted that result as suggesting mate-choice copying.

Höglund, Alatalo, and Lundberg (1990) and Höglund, Alatalo, Gibson, and Lundberg (1995) observed that female black grouse, *Tetrao tetrix*, enter leks, observe other females mating, and return later to mate. They too suggested that female black grouse may be copying the choices of others, and attempted to test this hypothesis. Höglund et al. (1995) found that females preferred male territories where males were given the opportunity to court taxidermic models of female black grouse. The data strongly suggest that female mate choices are not independent, but provide relatively little insight into the causes of this non-independence.

### Studies of Non-Independent Mate-Choice in the Laboratory

Dugatkin (1992) was the first to demonstrate true mate-choice copying by showing that ‘focal’ female guppies, *Poecilia reticulata*, that watched the less preferred of two males court a ‘model’ female, consistently increased their subsequent preference for the less preferred male (Dugatkin, 1992). Dugatkin and Godin (1992) demonstrated further that: (1) seeing the less preferred of a pair of males matched for size and coloration court can reverse a female’s initial preference, (2) copying can reverse an inherent preference for males with more orange coloration (Dugatkin, 1996, 1998) and (3) the longer a focal female watches the less attractive member of a pair of males court a model female, the greater the handicap in inherent attractiveness that can be overcome (Dugatkin & Godin, 1998; Godin & Dugatkin, 1996).

Furthermore, and as theory predicts, small (presumably younger) female guppies are more likely to copy the mate preferences of larger (presumably older) females than the reverse (Dugatkin & Godin, 1993). Contrary to theory, (1) increasing the apparent predation risk to females, and consequently the cost of independent assessment, did not affect their probability of copying (Briggs, Godin, & Dugatkin, 1996) and (2) well-fed females are more likely to copy the mate choices of others than are food-deprived females (Dugatkin & Godin, 1998).

Unfortunately, there has been no independent replication of Dugatkin et al.’s basic finding of mate-choice copying in guppies, although there have been published failures to find the effect (Lafleur, Lozano, & Sclafini, 1997; Brooks, 1996, 1999). The fact that different researchers have used guppies taken from different populations provides a possible explanation for the divergent outcome of their very similar experiments, though why copying should occur in some populations and not others is unclear.

Similar contradictions have arisen in studies of mate-choice copying by Japanese medaka, *Oryzias latipes*. Grant and Green (1996) found that females preferred males seen near a spawning female to males seen near non-spawning females. Howard, Martens, Innis, Drnevich, and Hale (1998), to the contrary, found no evidence of copying in the species.

Mate-choice copying has been reliably established in two other species: sailfin mollies and Japanese quail. Both female (Schlupp, Marler, & Ryan, 1994; Schlupp & Ryan, 1996) and male mollies mate-choice copy (Schlupp & Ryan, 1997) and, in females, observing mate-choices of other females has long lasting effects (Witte & Noltemeier, 2002; Witte & Massmann, 2003). Witte and collaborators have provided evidence that the body length of male sailfin mollies influences copying behavior (Witte & Ryan, 1998), that females not only copy acceptance but also rejection of males (Witte & Ueding, 2003), and that mate-choice copying can serve as a mechanism for traditions of mate preferences in females (Witte & Noltemeier, 2002).

Perhaps most relevant to the work in the body of this thesis is a series of experiments conducted by Galef and White (1998, 2000) and White and Galef (1999a, 1999b, 1999c, 2000a, 2000b) with Japanese quail. White and Galef demonstrated numerous times that female quail increase their preference for previously non-preferred males seen courting, mating or affiliating with another female (Galef & White, 1998; White & Galef, 1999b). This increased preference is not a result of changes in males’ appearance or behavior as a result of mating or of attraction of females to locations where females saw two conspecifics. A female has to observe a male and target female interact for there to be a change in her preference for a male; simply watching a

non-preferred male court an invisible partner does not change a female's subsequent attraction to the courting male (Galef & White, 1998; White & Galef, 1999b). Such effects on females of seeing a non-preferred male court and mate persist for several days (White & Galef, 2000b). The basic effect has been replicated in another laboratory (Akins, Levens, & Bakondy, 2002).

### 1.3.3 Eavesdropping

Historically, study of eavesdropping and of mate-choice copying have proceeded independently of one another, and there is essentially no cross-citation in the literatures of the two areas. This is somewhat surprising in that both areas of investigation face similar problems of definition of phenomena, and true mate-choice copying may be one of the most biologically important forms of eavesdropping.

McGregor considers several ways an individual can assess potential mates or rivals by intercepting signals intended for other receivers (McGregor, 1993; McGregor & Peake, 2000). He considers communication as taking place within a network of potential signalers and receivers where such interception of signals is probable. This approach arises from McGregor's reconsideration of previous views of communication as involving signals that pass from a sender to a receiver and ignore the possibility that the signals will be "overheard" by other members of a communication network. McGregor's particular concern is with the subset of signals (adaptations selected to enhance communication or transmission of information) that arise directly from the interaction between two individuals and are only one source of information on relative features (such as fighting ability) of interacting individuals. In McGregor's terminology, *bystanders* attend not only to aspects of signals that result from interactions among individuals, but also to other aspects of the signal or signaler that are not a feature of the interaction per se. *Eavesdroppers*, to the contrary, make use only of information arising directly from the fact that an interaction is taking place. For example, an eavesdropping male songbird would learn about the relative rank of potential opponents by attending only to the temporal relationship of their songs, which is, clearly, a characteristic of their interaction (e.g. Mennill, Ratcliffe, & Boag, 2002). A bystanding male songbird would attend not only to the temporal relationship of potential opponents' songs, but also to attributes of the songs themselves (their pitch and content) and the physical condition of those engaged in song display (e.g. Freeman, 1987).

Furthermore, in McGregor's terminology, both eavesdropping and bystanding must be free of *audience effects*. The distinction between interactants aware and unaware of an audience is important because the behavior of interacting individuals may change depending on whether they are aware of the presence of third parties (Dewsbury, 1992; Evans & Marler, 1984; Marler, Dufty, & Pickert, 1986), and such changes in behavior could in turn affect an observer's subsequent behavior.

McGregor and colleagues have used their definitions to severely restrict use of the term eavesdropping. For example, McGregor and Peake (2000) argue that Freeman's (1987) finding that male red-winged blackbirds, *Agelaius phoeniceus*, intrude less frequently into territories of focal males seen vigorously attacking stuffed male blackbirds placed in their territory than into territories of males less vigorous in territory defense is not an instance of eavesdropping. Because one of the participants in the aggressive display was a model, "there was no signaling

interaction because the mounted specimen could not interact with the focal male.” (McGregor & Peake, 2000, p. 75).

Assessment by intruding red-winged blackbirds must, therefore, have been based on characteristics of the physical attacks by territorial males on models, which McGregor and Peake argue do not arise from an interaction. Furthermore, in Peake and McGregor’s view, experiments showing that an individual observing interactions between conspecifics through one-way glass, to prevent audience effects (e.g. Doutrelant & McGregor, 2000; Earley & Dugatkin, 2002) fail to provide evidence of eavesdropping because assessment may have been based on observation of physical attributes of interactants and not on observation of the interaction itself (Peake & McGregor, in press; also see Dugatkin, 2001).

Despite efforts of McGregor and colleagues to define eavesdropping narrowly, there is little agreement in the literature as to when the term should be used (Dugatkin, 2001; McGregor & Peake, 2000; Peake & McGregor, in press). Some employ eavesdropping to refer to the behavior of individuals observing interactions between predator and prey (Balcombe & Fenton, 1988; Morris, Mason, Wall, & Belwood, 1994; Sakaluk & Belwood, 1984) or to describe an individual learning about availability of food by listening to others interact (Madsen, Wahlberg, & Møhl, 2002). Still others have used eavesdropping to refer to interactions among plants (Dicke & Bruin, 2001; Kobayashi & Yamamura, 2003; Dicke, Agrawal, & Bruin, in press).

Although it may be theoretically valuable to distinguish behavioral changes resulting from observing interactions from changes in behavior resulting from observing signals or cues produced by those engaged in an interaction, it is all but impossible to do so experimentally without using artificial stimuli. Observers of more natural interaction will acquire information about both the interaction and the individuals participating in it. Consequently, it may be more useful to those with an interest in social learning generally to broaden the definition of eavesdropping to include all cases where information is acquired by a bystander observing interactions among conspecifics. For example, Mennill et al. (2002) have proposed that eavesdropping on interactions is a way for individuals to compare potential partners or rivals on the basis of their relative performance. Johnstone (2001) has defined eavesdropping as a tactic by which an individual extracts information from either an interaction between others or the outcome of such an interaction.

Peake and McGregor (in press), who are concerned with distinguishing between different sources of available information, would no doubt take issue with such relatively broad definitions of eavesdropping, but such definitions permit empirical investigations to proceed without endless argument as to whether a given instance is eavesdropping, bystanding, or observing. Consequently, I will consider as eavesdroppers all who exhibit changes in behavior towards a conspecific as a result of observing him or her interacting with conspecifics.

### **Examples of Eavesdropping**

Examples of eavesdropping have been discussed in two general domains; eavesdropping to gain information about the fighting ability of potential opponents and eavesdropping to gain information about the quality of potential mates.

**Assessment of Potential Competitors.** How males that eavesdrop to assess the competitive ability of other males use the information they acquire by eavesdropping varies from species to species. For example, Naguib and Todt (1997) and Naguib, Fichtel, and Todt (1999) found that male nightingales, *Luscinia megarhynchos*, respond more intensely to the more aggressive of two simulated males they have heard interact. Earley and Dugatkin (2002) showed that male green swordtails, *Xiphophorus helleri*, that eavesdrop on other males fighting, are less likely to approach the winner than the loser of an aggressive interaction.

Johnstone (2001) has developed a model indicating that selection should favor eavesdropping on agonistic interactions whenever the cost of losing an escalated contest exceeds the value of the contested resource. His modeling reveals that a mixed equilibrium of ‘Hawks’, (individuals that escalate displays to fights), ‘Doves’ (individuals that display, but defect before fighting) and ‘Eavesdroppers’ (individuals that switch between Hawk and Dove tactics depending on whether their opponent played Hawk or Dove in a fight that the Eavesdropper has witnessed) will be evolutionarily stable (Maynard Smith, 1982).

One prediction of Johnstone’s model, namely that when costs associated with fighting are relatively high eavesdropping should be common, is consistent with empirical findings (e.g. Earley & Dugatkin, 2002; Freeman, 1987; Oliveira, McGregor, & Latruffe, 1998; McGregor, Otter, & Peake, 2000). A second prediction, that eavesdropping increases the frequency of aggression because eavesdroppers can more strategically engage in or defect from escalated fights, is also supported by data (e.g. Earley & Dugatkin, 2002; Freeman, 1987; Oliveira et al., 1998; McGregor et al., 2000), but merits some modification on a species by species basis as different species may make use of information they acquire by eavesdropping in different ways (Johnstone, 2001). For example, in species where eavesdropping males escalate fights with winners rather than losers (e.g. Naguib & Todt, 1997; Naguib et al., 1999), eavesdropping may produce a reduction in frequency of fighting but an increase in fighting intensity as the payoff for winning relative to the cost of losing is high.

**Assessment of Potential Mates.** In mate-choice copying, a female observes an interaction between members of a mating pair and this observation affects the observing female’s subsequent choice of a partner (e.g. Dugatkin, 1992; Schlupp et al., 1994; Grant & Green, 1996; Galef & White, 1998). Similarly, a female’s observation of agonistic interactions between two males can influence her subsequent decisions as to which of the males she chooses as a mate (e.g. Otter et al., 1999; Doutrelant & McGregor, 2000; Mennill et al., 2002). For example, Female great tits, *Parus major* (Otter et al., 1999), and black-capped chickadees, *Parus atricapillus* (Mennill et al., 2002) that have eavesdropped on a pair of males interacting aggressively subsequently prefer the winner to the loser.

Males can also use information obtained by eavesdropping on the interactions of females and their partners to choose a target for seduction. For example, Tobias and Seddon (2002) investigated the influence of female robins’, *Erithacus rubecula*, ‘seep’ calls on neighboring males. Females produce these seep calls and their mates respond by provisioning the calling female with food. Tobias and Seddon (2002) found that male neighbors of a pair more often approached territories from which ‘seep’ calls emanated at a high rate than at a low rate and in response to calls emanating from the fringe of a neighboring male’s territory rather

than from its center. Tobias and Seddon (2002) suggest that neighboring males eavesdrop on neighboring females' calls because such calls provide clues as to the location and fertility status of their female neighbors and may facilitate acquisition of extra-pair matings.

**Eavesdropping by both Males and Females.** In some species, both males and females have been shown to use information acquired by eavesdropping on aggressive interactions between males. For example, male Siamese fighting fish, *Betta splendens*, eavesdropping on an agonistic interaction between a pair of conspecific males are less likely to approach the winner of the interaction and display more often to the loser (Oliveira et al., 1998). Female eavesdroppers on the same interaction subsequently prefer to affiliate with the winner (Doutrelant & McGregor, 2000). Consequently, male *Bettas* that win a male-male competition receive not only whatever direct benefits are associated with winning a fight, but also gain indirect benefits resulting from reduced future competition with other males and an increased probability that females will choose them.

## 1.4 Japanese Quail

The experiments to follow use as subjects Japanese quail, a species that have been used in numerous previous investigations of sexual behavior. The final section of this introduction reviews what is known of the natural history and laboratory behavior of *Coturnix japonica*.

Japanese quail (*Coturnix japonica*), Phasianidae in the order Galliformes, are terrestrial, birds indigenous to Japan, China, Korea, and Indochina, where they inhabit agricultural fields and grasslands (Taka-Tsukasa, 1935; Wetherbee, 1961), although they have also been found on riversides and in alpine meadows (Nichols, 1991). Wild populations still exist in the Far East (Wetherbee, 1961) and in areas of Hawaii where they were introduced in 1921 (Schwartz & Schwartz, 1949).

### 1.4.1 Japanese and European Quail

Much of what is known about wild Japanese quail is reported in older literature that treated Japanese quail as a subspecies of the European or common quail (*Coturnix coturnix*) (Wetmore, 1952). However, discovery of hybrid inviability has provided strong evidence that Japanese and European quail are, in fact, separate species (American Ornithologist's Union, 1983; Arrington, Abplanalp, & Wilson, 1962; Howard & Moore, 1991). This failure to distinguish Japanese from European quail is almost surely responsible for some of the contradictions in the literature concerning the behavior of Japanese quail in nature (Crawford, 1990).

### 1.4.2 Distinguishing the Sexes

Adult females are slightly larger than adult males, and the dimorphic breast plumage of males and females aids in distinguishing them. Chests of males are burned-yellow to orange in color, while those of females are primarily cream colored with black or dark brown speckles. However, both sexes exhibit many heritable phenotypic variants (Cheng & Kimura, 1990).

Males produce loud “ko-turr-neex” calls in the absence of females (Potash, 1973; Wetherbee, 1961). These calls may assist in individual recognition or act as contact calls when members of a pair are out of sight of one another (Guyomarc’h, Aupiais, & Guyomarc’h, 1998; Potash, 1973). Females produce a much quieter, cricket-like “weet-weet” call and a “peu-peu” call that they frequently produce in response to male calls (Wetherbee, 1961; Campbell, 1952).

Laboratory studies indicate that both male and female *C. japonica* can discriminate the sex of conspecifics visually (Domjan & Hall, 1986). The sexually dimorphic plumage of the head and neck, the most salient stimulus for release of sexual behavior (Domjan & Nash, 1988; Domjan, Greene, & North, 1989), is also likely to play a major role in such sexual identification. Members of both sexes are also able to recognize individuals of the opposite sex visually (Riters & Balthazart, 1998; White & Galef, 2000b).

### 1.4.3 Reproduction

There are few studies of mating behavior in free-living *Coturnix* (Campbell, 1952; Kawahara, 1967; Nichols, 1991; Schwartz & Schwartz, 1949), and most of those were conducted before *C. coturnix* (European quail) and *C. japonica* (Japanese quail) had been distinguished as separate species (Crawford, 1990). Some confusion about the natural behavior of Japanese quail has resulted, and most of what is known with certainty about the reproductive behaviors of Japanese quail comes from more recent studies of captive animals. Although research on captive populations is surely helpful, caution must be exercised when extrapolating observations of behavior of captive animals to that of their free-living fellows (Wolff, 2003).

In the laboratory, male and female quail both reach sexual maturity rapidly: males as early as 28 days after hatching and females at between 31 and 42 days of age (Cooper, 1987; Wetherbee, 1961). Members of both sexes can be kept reproductively active by exposing them to illumination for 12 to 16 hr per day depending on prior photoperiod history (Mills, Crawford, Domjan, & Faure, 1997), although there may be some adverse effects of such treatment as birds age (Eroschenko, Wilson, & Siopes, 1977). High temperatures and auditory stimulation from conspecifics also aid in maintaining reproductive activity (Mills et al., 1997).

Females kept under standard laboratory conditions rarely engage in parental behavior (Hess, Petrovich, & Goodwin, 1976; Nichols, 1991), and parental behavior has never been observed in males in the laboratory (Nichols, 1991).

Observation of a feral Hawaiian population of *C. japonica* suggests that males are territorial, and that pair-bonded couples mate and nest within a male’s territory (Schwartz & Schwartz, 1949). Kawahara (1967) further reports that male and female members of a mated pair stay in close proximity before and during egg laying, and Mills et al. (1997) have suggested that this affiliative behavior could be a form of mate guarding, which in turn suggests the possibility of extra pair copulations, as is common in other Galliforms, (e.g. European quail: Rodríguez-Teijeiro, Puigcerver, Gallego, Cordero, & Parkin, 2003). However, Kovach (1974) cites Dement’ev et. al. (1967) and describes *C. japonica* as polygamous, consistent with the observation that, under laboratory conditions, males are eager to mate promiscuously (Kovach, 1974).

On the other hand, Orcutt and Orcutt (1976) report that captive male “common quail”



courted only their own female, and demonstrated a strong pair bond with her, and Guyomarc'h (1974 cited in Mills et al., 1997) found that members of a pair recognize the calls of their mates. Such observations suggest a socially monogamous mating system.

In a Master's thesis investigating behavioral differences between feral and domestic Japanese quail maintained in large (14.6 m<sup>2</sup>) semi-natural enclosures, Nichols (1991) concluded that *C. japonica* pairs are socially monogamous, but noted occasional opportunistic forced extra-pair matings and mate switching. Adkins-Regan (1995) suggests that the sexually dimorphic proctodeal gland in quail suggests a polygamous mating system. Mills et al. (1997) speculate that Japanese quail exhibit serial monogamy with opportunistic extra-pair matings, as has been suggested for European quail (Saint-Jalme, 1993; Rodríguez-Teijeiro et al., 2003).

Male courtship is typically either brief or absent altogether. When courtship does occur, it consists of: (1) heightened postures, (2) chasing and circling of females, (3) strutting and (4) tidbitting (Adkins & Adler, 1972; Nichols, 1991; Ramenofsky, 1984; Schleidt, Yakalis, Donnelly, & McGarry, 1984; Wilson & Bermant, 1972). Before mating, males also sometimes produce low "brr-up" calls that have been interpreted as an invitation to copulate (Naumann, 1905), and occasionally ruffle their feathers or adopt a wing-out posture otherwise associated with invitations to allopreen (Adkins & Adler, 1972; Nichols, 1991; Ramenofsky, 1984; Schleidt et al., 1984; Wilson & Bermant, 1972).

Copulation appears to be both aggressive and coercive. Males peck and grab at a female's head, neck and body, drag her about by her neck feathers, repeatedly jump onto her back with one or both sharply clawed feet, and hold her neck feathers in their beak as they attempt to make cloacal contact (Adkins-Regan, 1999; Adkins & Adler, 1972; Ramenofsky, 1984; Schleidt et al., 1984; Wilson & Bermant, 1972).

#### 1.4.4 Aggressive Behavior

Male *C. japonica* react aggressively to the presence of both unfamiliar males (Selinger & Bermant, 1967) and their own mirror images (personal observation). They are so aggressive that they are still used for 'cock' fighting in some parts of Asia (Mills et al., 1997). The highly aggressive nature of males' interactions is consistent with the hypothesis that they are polygamous and territorial (Sachs, 1966). However, both the frequency and intensity of aggressive behavior in male quail is influenced by nutritional, environmental, and hormonal factors (Edens, Bursian, & Holladay, 1983; Kuo, 1960a, 1960b, 1960c, 1960d; Sachs, 1966). Level of aggressiveness is, however, heritable in Japanese quail (Boag & Alway, 1981), and therefore, is still open to selection both natural and artificial.

Agonistic encounters between males involve threat displays, violent pecks and grabs directed at the head and neck and especially at the eyes of opponents (Edens et al., 1983; Kuo, 1960a, 1960b, 1960c, 1960d; Sachs, 1966). Submissive individuals adopt a crouched posture, concealing their head and neck by lowering them (Edens et al., 1983).

Males construct dominance hierarchies (Boag & Alway, 1981; Otis, 1972), dominants acquire preferred mating sites and food sources (Edens et al., 1983), and, as a result, are generally believed to enjoy greater access to mates (Andersson, 1994).

#### 1.4.5 Domestication

Japanese quail were first domesticated for egg and meat production in Japan 1000 or more years ago (Mills et al., 1997), and sometime later, were selected for singing ability by members of the Japanese imperial court (Howes, 1964). Today, quail continue to be raised as sources of both meat and eggs, as well as for use as subjects in laboratory studies.

Japanese quail are well suited to life in the laboratory. They provide a low-cost alternative to more commonly used laboratory species such as rats and mice (Mills et al., 1997). Because of the readiness of quail to breed year round and the absence of any cyclicity in their sexual behavior when maintained under certain photoperiodic conditions, they have been extensively used as subjects in investigations of both stimulus control (e.g. Domjan, 1992; Gutierrez & Domjan, 1997; Hilliard, Nguyen, & Domjan, 1997; Köksal & Domjan, 1998) and neuroendocrine control of sexual behavior (e.g. Adkins, Boop, Koutnik, Morris, & Pniewski, 1980; Balthazart, Baillien, Chailier, Cornil, & Ball, 2003; Domjan, 1987; Schumacher & Balthazart, 1986; Wada, 1982; Watson & Adkins-Regan, 1989), as well as in studies of mate choice (e.g. Bateson, 1978, 1982, 1983; Galef & White, 1998; White & Galef, 1999a, 1999b, 1999c, 2000a, 2000b).

Japanese quail were chosen as subjects for the studies described in Chapters 2 to 5 both because of their suitability as subjects in studies of sexual behavior and because of the very aggressive nature of males' courtship and mating. Because of the general aggressiveness of male Japanese quail toward conspecific females, although females may benefit either directly or indirectly from consorting with dominant, highly aggressive males, females may also incur significant risk of injury when interacting with them. Consequently, interesting questions arise as to how female Japanese quail balance the potential costs and benefits of choosing dominant or subordinate males as partners.

## Chapter 2

# Females copy the choices of conspecifics on video

Never miss a chance to have sex or appear on television.

*Gore Vidal*

### 2.1 Preface

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### 2.2 Abstract

A female Japanese quail, *Coturnix japonica*, will increase her tendency to affiliate and mate with a conspecific male after seeing him court and mate with another female. In the present study, we found that female quail increased the time they spent near a live target male after seeing that same male court and mate with another female in a 5-min video displayed on an active-matrix TFT monitor. However, female quail that were shown 5-min video sequences of either a target male standing alone or a randomly selected male courting and mating did not subsequently increase the time they spent near a live target male. These findings provide the first demonstration of which we are aware of birds transferring individual identification from a video sequence to a real animal.

## 2.3 Introduction

Replacing live stimulus animals with video recordings can facilitate research by increasing control of stimuli while reducing: (1) variability inherent in direct interactions between living individuals, (2) disruption of normal behaviour caused by handling and (3) the number of subjects needed for experiments. Video sequences have been used to study a range of topics and species, including social facilitation (domestic fowl, *Gallus gallus domesticus*: Keeling & Hurnik, 1993), social learning (Burmese junglefowl, *G. g. spadecius*: McQuoid & Galef, 1993), theory of mind (chimpanzees, *Pan troglodytes*: Premack & Woodruff, 1978), motion perception (domestic fowl: Lea & Dittrich, 1999), audience effects (domestic fowl: Evans & Marler, 1991), predator recognition (domestic fowl: Evans, Macedonia, & Marler, 1993), foraging behaviour (anuran sp.: Roster, Clark, & Gillingham, 1995), aggressive interactions (anoles, *Anolis grahami*: Macedonia & Stamps, 1994; jacky dragons, *Amphibolurus muricatus*: Ord, Peters, Evans, & Taylor, 2002), song learning (zebra finches, *Taeniopygia guttata*: Adret, 1997; northern cardinals, *Cardinalis cardinalis*: Yamaguchi, 1999), and, most relevant to the present studies, mate choice (jumping spiders, *Maevia inclemens*: Clark & Uetz, 1990, 1992; wolf spiders, *Schizocosa ocreata*: Uetz & Smith, 1999; Uetz & Roberts, 2002; three-spined sticklebacks, *Gasterosteus aculeatus*: McKinnon, 1995; guppies, *Poecilia reticulata*: Kodric-Brown & Nicoletto, 1997; Nicoletto & Kodric-Brown, 1999; green swordtails, *Xiphophorus helleri*: Rosenthal, Evens, & Miller, 1996; Rosenthal & Evans, 1998; Amazon mollies, *P. formosa*: Landmann, Parzefall, & Schlupp, 1999; fiddler crabs, *Uca pugilator*: Pope, 2000).

As might be anticipated in work involving such a wide variety of species and issues, as well as equipment of varying degrees of sophistication, some studies have not found exposure to video sequences as effective as exposure to living animals in evoking behaviour (species identification in chickens and pigeons, *Columba livia*: Ryan & Lea, 1994; social recognition in domestic fowl: D'Eath & Dawkins, 1996; individual and species recognition in domestic fowl: Patterson-Kane, Nicol, Foster, & Temple, 1997; and tutoring in African grey parrots, *Psittacus erithacus*: Pepperberg, 1994; Pepperberg, Naughton, & Banta, 1998). Such relative failures have been reported in the literature particularly often when birds have been used as subjects, perhaps as a consequence of properties of both avian visual systems and video playback.

D'Eath (1998) described five features of video playback that might be responsible for failure of subjects to respond to such stimuli in the same way that they respond to live conspecifics: (1) failure to match spectral characteristics (Fleishman, McClintock, D'Eath, Brainards, & Endler, 1998; Cuthill et al., 2000) and (2) depth cues (Zeil, 2000), (3) presence of flicker, and (4) reduced acuity (Fleishman & Endler, 2000) and (5) absence of interaction (Ord et al., 2002). The first four of these five potential causes of relative lack of efficacy of video playbacks in eliciting normal behaviour can be ameliorated by improving video equipment itself.

Relative to cathode ray tube (CRT) monitors, used in almost all previous studies of responses to video sequences, active matrix, thin-film transistor (hereafter TFT) video monitors that have recently become available for use in research, enhance contrast and brightness and increase the likelihood of producing percepts of lifelike, continuous motion. Consequently, video sequences presented on TFT monitors might be expected to be more effective than

those presented on CRT monitors in eliciting natural behaviours, especially in birds whose visual acuity, colour perception and high maximum critical flicker-fusion frequencies may make them particularly susceptible to the inadequacies of CRT displays. Consistent with such a view, Ikebuchi and Okanoya (1999) found that male zebra finches, *Taeniopygia guttata castanotis*, and Bengalese finches, *Lonchura striata domestica*, directed song towards live conspecific females or towards video sequences showing conspecific females when they were presented on TFT video monitors, but not when they were presented on CRT video monitors.

We undertook the experiments described here to determine whether female Japanese quail, *Coturnix japonica*, would copy the mate choices of female conspecifics seen courting and mating on a TFT video monitor. Female quail show an increased probability of affiliating and mating with males they have seen court and mate with other females (reviewed in Galef & White, 2000), a strategy hypothesized to reduce costs associated with mate choice and increase the accuracy of assessment of potential mates (Gibson & Höglund, 1992).

‘Focal’ female Japanese quail increase the time that they spend near a previously non-preferred ‘target’ male after seeing him court and mate with another female (Galef & White, 1998; White & Galef, 1999b). If female quail perceive moving TFT video images of conspecific males as they perceive live individuals, then they should show a similar increase in time spent affiliating with nonpreferred males whether they see them court and mate with other females live or on a TFT video monitor.

We conducted the same basic experiment twice to confirm the results of our investigation of female Japanese quails’ use in mate selection of information acquired from video sequences. In experiment 1, a live nonpreferred male was always on the same side of the experimental apparatus where we had shown a female a video clip of that male courting and mating with another female. Although this procedure avoided any disruption of behaviour that might have been caused by moving live males, it also produced an obvious confound between where females had previously seen movement on a video monitor and where a nonpreferred male was to be found. In experiment 2, we moved the live nonpreferred male to the opposite side of the apparatus from where a video clip of him courting and mating had been displayed. We thus controlled for alternative explanations of any bias induced in mate preferences of female subjects in experiment 1 while repeating our basic observation.

## 2.4 Experiment 1

We examined effects on affiliative preferences of focal female Japanese quail of seeing digital video sequences presented on a TFT monitor that showed a previously nonpreferred target male quail courting and mating with a model female.

### 2.4.1 Methods

#### Subjects

Subjects were 30 male and 30 female 52-day-old Japanese quail acquired from a local commercial breeder (Speck's Poultry Farm, Vineland, Ontario, Canada). After we transported subjects to our laboratory, we placed them in individual, commercial quail cages (55 x 55 x 110 cm; Berry Hill, St Thomas, Ontario).

Throughout the experiment, the cages resided in a temperature- and humidity-controlled colony room illuminated for 16 h/day. We maintained all subjects on ad libitum Mazuri Pheasant Starter 5637 (PMI Feeds, St Louis, Missouri, U.S.A.) and tap water. For environmental enrichment, twice each week, we provided each bird with a handful of autoclaved hay. All procedures were approved by the McMaster University Animal Research Ethics Board (Animal Utilization Proposal No. 99-05-26).

To allow birds to come into breeding condition, we waited 40 days before starting the experiment. We considered a female ready to breed when she started to lay an egg at least once every other day. To determine whether a male was in breeding condition, as soon as he began to call regularly, we paired him for 5 min daily with a series of sexually mature females. We considered a male to be sexually mature when he mounted and made cloacal contact with females on 2 successive days. One male subject failed to reach criterion for sexual maturity after 10 days of pairing with females, and we did not use him in the experiment. We randomly assigned sexually mature subjects to 23 trios, each consisting of one 'focal' female and two 'target' males. Seven females served only as 'model' subjects.

#### Apparatus

**Filming.** We recorded each male subject in a 10-gallon (37.9-litre) glass aquarium (41 x 21 x 27 cm), both while he courted and mated with a female and while he stood alone. We made video recordings of males using a CCD digital camcorder (Panasonic Digital Palmcorder, PV-DV910) with EIA Standard (525 lines with 60 fields) NTSC colour signal and optical resolution in the CCD of 680 000 pixels. Such digital video images have greater intensity bandwidth and reproduce spatial detail substantially better than the VHS analogue equipment used in most similar experiments in the past (Ord et al., 2002).

During filming, we disabled the auto-focus, set the zoom lens to its widest angle, and placed the camera 52 cm from the centre of the front wall of the aquarium that held the male and elevated it 14 cm above the surface on which the aquarium rested. The result was both to fill the total viewing area of the camera with an image of the aquarium wall and to provide life-size images of target male quail for presentation to focal females.

To visually isolate the aquarium from its surroundings while filming, we covered the aquarium floor with white absorbent liners (Tray Liners, Lilo Products, Hamilton, Ontario) and lined three of its walls with white Bristol board. We positioned lights to minimize reflection and glare from the walls of the aquarium (Fig. 2.1).

We edited video sequences to 5.17 min using Apple iMovie 2.0.3 software. Each video clip opened with 5 s showing a black background with white text that identified the male subject.

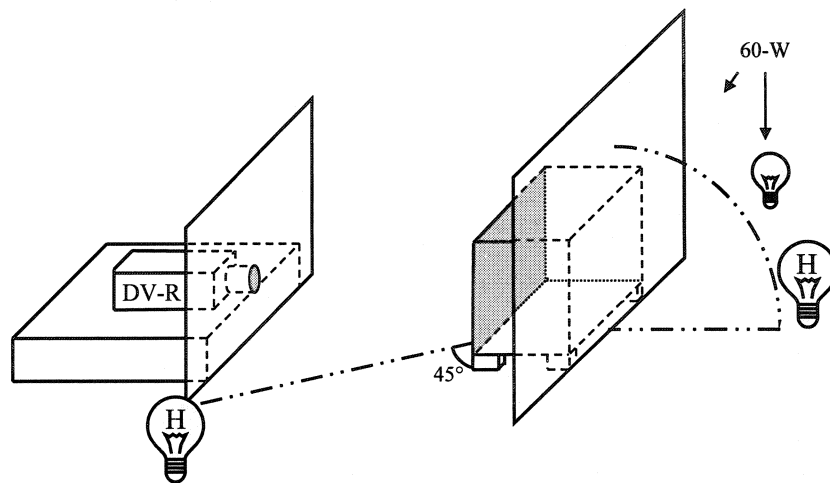


Figure 2.1: Illustration of the apparatus used to produce video clips of male quail either mating or standing alone. The positions of 60-W incandescent lamps and 150-W halogen floodlights (H) were arranged to avoid glare and reflections, and the distance from camera to aquarium was selected to give life-size images of quail during the observation phase of experiments. Shading indicates transparent surfaces. DV-R=Digital video recorder.

Thus each stimulus lasted a total of 5.25 min. (Portions of the video clips can be found at [http://www.science.mcmaster.ca/Psychology/ophir/ago\\_research\\_video.html](http://www.science.mcmaster.ca/Psychology/ophir/ago_research_video.html) >.) When we presented video sequences to subjects, we muted the sound so that females were exposed solely to the visual information presented on the TFT monitor.

**Testing.** We tested subjects in an apparatus consisting of three aquaria (Fig. 2.2): two 'end tanks' (41 x 21 x 27 cm) and a 'central tank' (61 x 32 x 41 cm) all with floors covered with absorbent paper liners. White Bristol board covers on two walls of the central tank restricted the view from within it, and a CCTV video camera (Panasonic WV-CP230) mounted above the central tank and connected to both a video monitor and video-cassette recorder (Panasonic PV9664) permitted observation and recording of behaviour. Each end tank was lined on three sides with white Bristol board and had its transparent wall located 56 cm from the nearer end wall of the central tank.

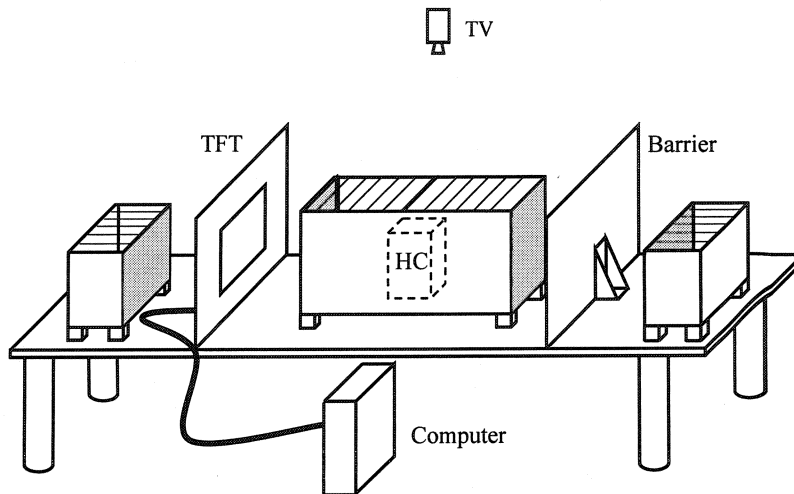


Figure 2.2: Illustration of the apparatus configured for presentation of video sequences during the observation phase of experiments 1 and 2. Shading indicates transparent surfaces. TFT=Active matrix, thinfilm transistor video monitor; HC=holding cage.

A holding cage, constructed of transparent Plexiglas (18 x 18 x 30.5 cm) with a removable opaque shell constructed of white Bristol board, could be placed at the midpoint of the central tank.

Using a firewire cable, we transferred each video stimulus in DV format from the camcorder to an Apple G4, 733-MHz computer. We used iMovie 2.0.3 to display these video clips in DV format without compression on a 15-in active-matrix, TFT monitor (VG-151, ViewSonic, Walnut, California, U.S.A.) with RGB display set at 16.7 million colours. The monitor's resolution was 1024 x 786 pixels and the viewable area was 30.5 x cm.

To reduce extraneous visual stimuli, we placed in front of the monitor a white Bristol board shield (71 x 56 cm) into which we cut a 30.5 x 23 cm window. Whenever the monitor was used as a stimulus, we placed both it and a Bristol-board barrier (71 x 56 cm) 25.5 cm from each of the end tanks (Fig. 2.2).



## 2.4.2 Testing

### Design

Each test trial consisted of three phases, a 10-min pretest, a 5.25-min observation phase, and a 10-min post-test. During the pretest, we determined a ‘focal’ female’s preference between a pair of males. During the observation phase, each focal female viewed: (1) a video clip of the male that she did not prefer during the pretest standing alone, (2) a video clip of the nonpreferred male mating with another female, or (3) her nonpreferred male mating live with another female. We counterbalanced across focal females the order in which they participated in the three test conditions, and no focal female ever encountered any male in more than one test condition. Because we were concerned with effects of viewing video sequences of males’ mating on females’ subsequent affiliative behaviour, we did not assign focal females to view live males standing alone during the observation phase. In previous studies in our laboratory we have repeatedly found that females that see a live, nonpreferred male mating during the observation phase show an increase from pretest to post-test in the time that they spend with their nonpreferred male. To the contrary, females who see a nonpreferred male standing alone during the observation phase show no change from pretest to post-test in the time they spend near him (Galef & White, 1998; White & Galef, 1999b, 2000a).

### Pretest

To begin a test trial, we placed a focal female in the holding cage in the central tank with the opaque shell in place, and then placed a target male in each end tank. Next, we removed the holding cage and opaque shell and waited until the focal female took her first step. For the next 10 min, we recorded the time that the focal female spent closer to each of the two end tanks, each containing a target male, and defined the target male that a female spent less time closer to as her ‘nonpreferred male’.

### Observation Phase

To begin the observation phase, we returned the focal female to the holding cage with its opaque shell in place. We then placed the Bristol-board barrier between the end tank housing a focal female’s preferred male and the central tank. When a focal female was assigned to either the ‘video-mating’ or ‘video-alone’ conditions (see below), we placed the TFT monitor between the central tank and the end tank containing a focal female’s nonpreferred male. We then removed the opaque shell from the holding cage and allowed the focal female to observe a 5.25-min video clip of her nonpreferred male either courting and mating (video-mating condition) or standing alone (video-alone condition). When a focal female was assigned to the ‘live-mating’ condition, we placed a model female in the end tank with the focal females nonpreferred male, and allowed the focal female to observe him court and mate for 5.25 min.

### Posttest

We conducted the post-test exactly as we had conducted the pretest, allowing a focal female to choose for 10 min between the same two target males that she had chosen between during the pretest. We left both males in the same positions that they had occupied during the pretest.

### Data Analysis

We calculated the difference between pretest and posttest in the time that each focal female spent with her nonpreferred male when in each of the three test conditions. We used a one-way, repeated measures analysis of variance (ANOVA) and planned-comparison, Bonferroni-adjusted, paired  $t$  tests to analyse the data.

### 2.4.3 Results

Data from eight of the 23 focal females were not used. Five focal females did not approach both males during one or more pretests, one focal female laid an egg during a pretest and two focal females were severely disturbed during observation periods by loud noises associated with construction under way in the building.

#### Interobserver reliability

A naïve observer, unaware of the condition in which a subject was being run, scored a random sample of 15 videotapes of focal subjects' behaviour during pretests and post-tests. Her scoring was highly correlated with that of one of the authors (A.G.O.; Fisher's Exact Test :  $r_{13} = 0.92$ ,  $p < 0.0001$ ).

#### Pretest

During pretests focal females in the video-mating, video-alone, and live-mating conditions, spent a mean ( $\pm$  SE) of, respectively,  $6.4 \pm 0.3$ ,  $7.0 \pm 0.4$  and  $7.0 \pm 0.4$  min closer to their preferred than non-preferred target males (repeated measures, one-way ANOVA,  $F_{2,14} = 1.29$ , *NS*).

#### Observation phase

During the observation phase all males assigned to the live-mating condition courted and successfully copulated with their model females.

#### Post-test

There was a significant effect of the type of stimulus to which we exposed focal females during the observation phase on their change in response from pretest to posttest towards nonpreferred target males (repeated-measures ANOVA:  $F_{2,14} = 8.23$ ,  $p < 0.01$ ; Fig. 2.3).

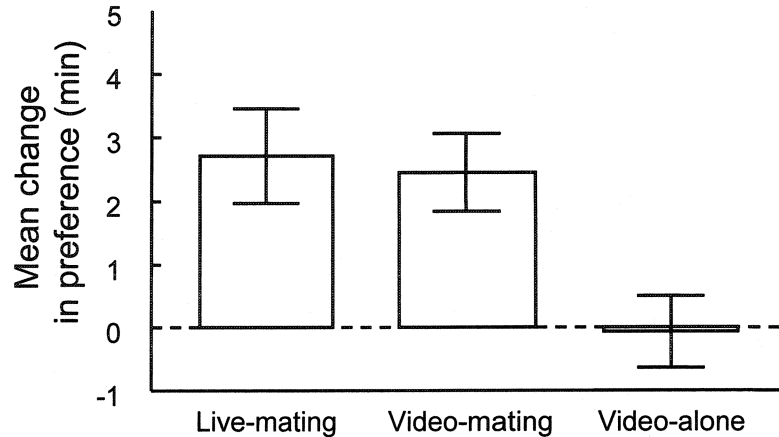


Figure 2.3: Mean  $\pm$  SE change in time (min) between pretest and post-test that focal female subjects assigned to video-mating, video-alone and live-mating conditions spent nearer to the target subject they had not preferred during the pretest (experiment 1).

After females had observed a video clip of a nonpreferred target male courting and mating on a TFT monitor, they showed a significantly greater increase in time spent closer to that target male than when they observed a video clip of a nonpreferred target male standing alone (Bonferroni corrected paired  $t$  test:  $t_{14} = 3.16$ ,  $p < .01$ ) Furthermore, seeing a video clip of a nonpreferred target male court and mate had the same effect on the change between pretest and post-test in the time that the female spent closer to a nonpreferred target males as did seeing a live male court and mate ( $t_{14} = 0.56$ ,  $NS$ ).

#### 2.4.4 Discussion

The results of experiment 1 are consistent with the hypothesis that focal females, when assigned to the video-mating condition, recognized target males that they had observed courting and mating on a TFT monitor, just as they recognized target males seen mating live when in the live-mating condition. In both cases, focal females increased the time that they spent near nonpreferred target males significantly more than when they saw such males in the video-alone

condition. There are, however, alternative interpretations of the results of experiment 1. For example, during the post-test, focal females may have spent increased time at the end of the central tank closer to where, during the observation phase, they had seen any male courting and mating, two quail doing nothing at all, or any motion.

## 2.5 Experiment 2

The hypothesis that focal females in the video-mating condition of experiment 1 experienced increased attraction to the nonpreferred male that they saw court and mate on video leads to two predictions. First, exchanging the locations of preferred and nonpreferred target males between the observation phase and post-test should have no effect on the behaviour of focal females during the post-test. Focal females should continue to show an increased preference between pretest and post-test for nonpreferred target males seen courting and mating in video clips. Second, seeing video clips of an unfamiliar male courting and mating during the observation phase should have no effect on focal females' response to their respective nonpreferred target males during the post-test.

In experiment 2, during the observation phase, we allowed focal females, when assigned to the 'switch condition' to see a video clip of their nonpreferred target male courting and mating during the observation phase, then reversed the locations of the two target males before starting the post-test. During the observation phase, focal females when assigned to the 'third-male condition' observed a video clip of an unfamiliar male courting and mating. We then conducted the normal post-test, allowing focal females to choose for 10 min between the same two target males that they had chosen between during the pretest.

### 2.5.1 Methods

#### Subjects and Apparatus

The same 30 male, 15 focal female and 7 model female subjects in experiment 1 also served in experiment 2. We assigned focal females and target males to trios in experiment 2 so that no female was in a trio with either male that she had seen in experiment 1. We used the same apparatus for testing and the same video stimuli as in experiment 1 (Fig. 2.2).

#### Procedure

The procedure was the same as that used in experiment 1, except that we assigned each of the 15 focal females to both switch and third-male conditions. When a focal female was in the switch condition, at the end of the observation phase, we placed the opaque shell around the holding cage, reversed the locations of her two target males, and, to reduce any effects of handling on behaviour, waited 3 min before starting the post-test. When in the third-male condition, each focal female saw a video of an unfamiliar male, rather than of her nonpreferred target male, courting and copulating during the observation phase. We counterbalanced across focal females the order in which they participated in the two conditions, and no focal female ever encountered any male in more than one test condition.

### 2.5.2 Results

Data from three focal females were excluded when they failed to approach both males during a pretest.

#### Pretest

Focal females when assigned to switch and third-male conditions spent, respectively, an average of  $6.6 \pm 0.3$  and  $6.7 \pm 0.3$  min closer to their preferred than to their non-preferred males (Student's paired  $t$  test:  $t_{11} = -0.74$  *NS*)

#### Post-test

When assigned to the switch condition, focal females showed a significant increase between pretest and post-test in the time that they spent closer to their respective non-preferred males ( $t_{11} = 3.14$   $p < 0.01$ ; Fig. 2.4). To the contrary, when assigned to the third-male condition, focal females did not show any increase between pretest and post-test in the time they spent closer to their non-preferred male ( $t_{11} = 0.93$  *NS*; Fig. 2.4), and when in the switch condition focal females showed a significantly greater increase in the time they spent nearer their respective nonpreferred males than when in the third-male condition (paired  $t$  test;  $t_{11} = 3.02$   $p < 0.02$ ).

### 2.5.3 Discussion

The results of experiment 2 are consistent with the hypothesis that, during the post-test, focal females in experiment 1 did not remain nearer the end of the central tank closer to where they saw courting and mating during the observation phase. Rather, during the post-test, focal females increased the time that they spent near the end of the central tank closer to a nonpreferred male that they saw court and mate during the observation phase.

## 2.6 General Discussion

A female Japanese quail that sees a conspecific male court and mate with another female subsequently shows an enhanced tendency to affiliate with the male she saw courting and mating (Galef & White, 1998; White & Galef, 2000a). The results of the present experiments indicate that a female quail who views a video clip of a conspecific male courting and mating on a TFT monitor subsequently shows a similar increase in her tendency to affiliate with the nonpreferred male that she saw courting and mating on video. This increased attraction is specific to the male seen mating and is not a result of a general tendency on the part of females to approach areas where they have seen conspecifics either standing alone or engaged in reproductive behaviours.

Lea and Dittrich (2000, p. 156) suggested that, in birds 'There are as yet no experiments successfully testing transfer of learned discriminations between moving video images and real

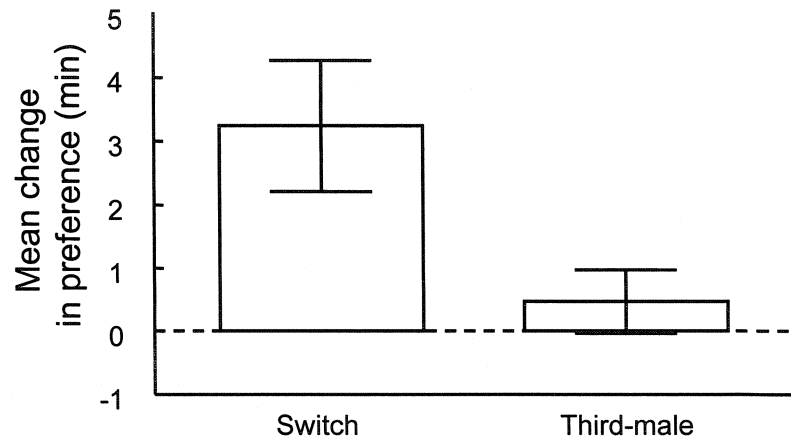


Figure 2.4: Mean  $\pm$  SE change in time (min) between pretest and post-test that focal female subjects assigned to switch and third-male conditions spent nearer to the target subject they had not preferred during the pretest (experiment 2).

objects, and there are some well documented failures'. As far as we know, the present studies provide the first such demonstration. Although McQuoid and Galef (1993) showed that Burmese junglefowl transferred CRT images of distinctively coloured food dishes from video to their real counterparts, such a transfer is considerably less difficult than that demonstrated here from video sequences of an individual male to the male himself.

Our success, despite the failure of others to provide similar demonstrations in birds, may be attributable to our use of TFT rather than CRT video displays (but see Yamaguchi, 1999, our using quail as subjects (Cuthill et al., 2000; Fleishman & Endler, 2000) or our use of mate choice as a dependent variable (Hunt, Cuthill, Bennett, Church, & Partridge, 2001). In a pilot study, male Japanese quail were attracted to a TFT monitor showing a video of a moving female, but not to a CRT monitor displaying the same video images (A. G. Ophir, J. Tangen & B. G. Galef, Jr, unpublished data; see also Ikebuchi & Okanoya, 1999). It seems reasonable to hypothesize that birds may perceive video sequences presented on a TFT monitor as more lifelike than the same sequences presented on a CRT monitor.

## 2.7 Acknowledgments

This research was supported by a Natural Sciences and Engineering Research Council of Canada operating and equipment grants to B.G.G., Jr. We thank Jason Tangen and Nav Mangat for technical assistance and Chris Evans for his extensive and most useful comments on an earlier draft of the manuscript.

## Chapter 3

# Females prefer less aggressive males

For the woman, the man is a means: the end is always the child.

*Friedrich Nietzsche*

### 3.1 Preface

This chapter is reprinted from *Animal Behaviour*, Vol 66, Ophir, A. G. & Galef, B. G. Jr., Female Japanese quail that 'eavesdrop' on fighting males prefer losers to winners, Pages 399 - 407, Copyright 2003, with permission from Elsevier. The paper was first submitted to *Animal Behaviour* on July 9, 2002. It was initially accepted October 10, 2002 and its final acceptance was November 15, 2002 (MS. number A9398).

### 3.2 Abstract

In a series of four experiments, we examined the relationship between male dominance and female preference in Japanese quail, *Coturnix japonica*. Female quail that had watched an aggressive interaction between a pair of males preferred the loser of an encounter to its winner. This superficially perverse female preference for losers may be explained by the strong correlation between the success of a male in aggressive interactions with other males and the frequency with which he engages in courtship behaviours that appear potentially injurious to females. By choosing to affiliate with less dominant male quail, female quail may lose direct and indirect benefits that would accrue from pairing with dominant males. However, they also avoid the cost of interacting with potentially harmful, more aggressive males.



### 3.3 Introduction

In a series of papers, McGregor and his coworkers explored effects on a nonparticipant ‘eavesdropper’ of monitoring interactions between others of its species (reviewed in McGregor & Peake, 2000). Eavesdroppers can use information extracted from observed interactions to evaluate both potential opponents in future aggressive encounters (e.g. Naguib & Todt, 1997) or, more relevant to the present studies, to select a future mate. For example, female Siamese fighting fish, *Betta splendens*, eavesdropping on an aggressive interaction between a pair of conspecific males subsequently spent more time near the winner than the loser of the interaction that they observed (Doutrelant & McGregor, 2000). After eavesdropping on a similar interaction, male Siamese fighting fish took longer to display to the winner than to the loser (Oliveira et al., 1998).

As suggested by the preceding examples, studies of eavesdropping have focused on the consequences of observing aggressive interactions between males, although eavesdropping on other sorts of interaction might also affect the subsequent behaviour of eavesdroppers (McGregor & Peake, 2000). In particular, results of studies of aftereffects of eavesdropping on sexual encounters between male and female Japanese quail, *Coturnix japonica*, indicate that female quail prefer a male that they have watched court another female, whereas males avoid a female that they see with another male (Galef & White, 1998; White & Galef, 2000a). In the studies described below, we extended previous work on the effects of eavesdropping on subsequent sexual interactions in Japanese quail to examine the effects on preferences of female quail of observing conspecific males win or lose an aggressive interaction.

Otis (1972) suggested that male Japanese quail live in dominance hierarchies (Boag & Alway, 1981) that give dominant individuals priority of access to resources. Consequently, females might be expected to prefer to affiliate and mate with winners of aggressive interactions to increase access both to resources and to the potentially superior genetic material of dominant individuals (Qvarnström & Forsgren, 1998).

### 3.4 Experiment 1: Do Female Quail Prefer Male “Winners”?

We undertook experiment 1 to determine the effects on affiliative preferences of female Japanese quail of observing an aggressive encounter between two conspecific males. In Japanese quail, affiliative preference is an excellent predictor of choice of a partner for copulation (White & Galef, 1999a).

To provide evidence that any effects on females’ preferences resulted from observing males interact rather than from changes in appearance of males after winning or losing an aggressive encounter, we also examined females choosing between winners and losers of fights that had taken place out of sight of choosing females.

### 3.4.1 Methods

#### Subjects

Subjects were 37 female and 34 male Japanese quail, acquired from Speck's Poultry Farm (Vineland, Ontario, Canada) when 52 days of age. After transporting subjects to our laboratory (Hamilton, Ontario), we placed them in individual cages (55 x 55 x 110 cm), housed 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.) for the duration of their stay in the laboratory. All procedures were approved by the McMaster University Animal Research Ethics Board (Animal Utilization Proposal No. 99-05-26).

Experiments began only after subjects had achieved sexual maturity. We considered females to be sexually mature when they began to lay at least one egg every other day. To determine whether a male was mature, when he started to call regularly (at about 70 days of age), we placed him together with a succession of sexually mature females, for 5 min/day for 7 consecutive days, in alternating end chambers of the apparatus (Fig. 5.1). We observed the behaviour of pairs on closed-circuit television, and when a male mounted and made cloacal contact with females on 2 successive days, we considered him to be sexually mature.

#### Apparatus

We performed the experiment in an apparatus constructed of painted plywood, Plexiglas and wire mesh (Fig. 5.1; White & Galef, 2000b). In brief, the apparatus consisted of a main enclosure and an ancillary cage. The main enclosure was divided into three segments (two end chambers and a central area) by two wire-mesh partitions. A holding cage, with two transparent Plexiglas and two opaque walls, placed in the middle of the central area, could be raised through the roof of the central area to release a restrained subject.

The ancillary cage was divided into two compartments of equal size by both a permanent transparent Plexiglas partition and a removable opaque partition. A wiremesh barrier separated the ancillary cage from the main enclosure.

### 3.4.2 Procedure

#### Group assignment

We assigned subjects to trios each composed of a 'focal' female and two 'target' males. To construct trios, we first assigned males to 37 unique pairs and then randomly assigned a focal female to each pair. We then assigned 19 trios to 'eavesdrop' (E) and 18 trios to 'not-eavesdrop' (Not-E) conditions.

#### 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 barrier dividing the ancillary cage. We then lifted the

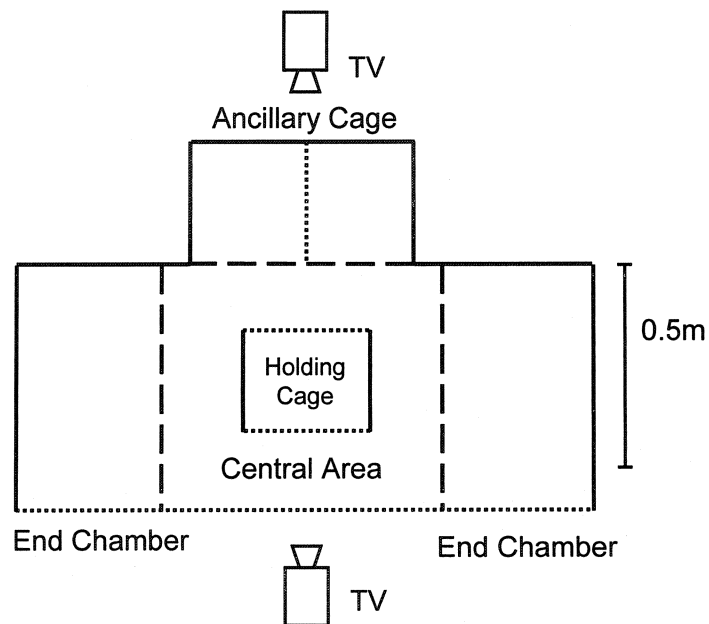


Figure 3.1: Overhead schematic of the apparatus used in all experiments. Solid lines: Opaque walls; dotted lines: transparent Plexiglas; dashed lines: wire mesh. The camera viewing the ancillary cage was mounted directly above its midpoint, facing down, and the camera viewing the central area was located at its midpoint and oriented horizontally.

opaque partition separating the males, leaving the transparent Plexiglas partition in place. For the next 10 min, we used a closedcircuit television camera suspended directly above the midpoint of the ancillary cage and a video-cassette recorder to make a permanent record of the behaviour of the two target males. Two independent observers subsequently scored these videotapes to determine the number of times that each target male pecked the transparent Plexiglas partition during the 10-min fight phase.

Throughout the fight phase, focal females assigned to the E condition had one transparent wall of the holding cage facing the ancillary cage. Focal females assigned to the Not-E condition had an opaque wall of the holding cage facing the ancillary cage blocking their view of the ancillary cage and the target males it contained.

We considered the target male in each trio that pecked the transparent partition more frequently during the fight phase the ‘winner’ of the fight and the male that pecked it less frequently the ‘loser’ of that fight. Schlinger, Palter, and Callard (1987) staged direct aggressive encounters between eight pairs of males and found in all eight cases that the male that had previously pecked more at a Plexiglas barrier separating him from a conspecific target won the aggressive encounter. Because of ethical problems associated with staging aggressive interactions, we used Schlinger et al.’s indirect measure of male aggression.

### Choice phase

As soon as the fight phase ended, we placed each target male in the end chamber of the main enclosure that was closer to the side of the ancillary cage he had occupied during the fight phase. We then lifted the holding cage, waited until the released focal female took her first step, and allowed the focal female to move freely about the central area for 10 min, recording her behaviour using a video camera in front of the central area (Fig. 5.1). We considered a female to ‘prefer’ whichever target male she spent nearer to for more than half of the 10-min choice phase. We excluded data from four trios in which focal females either failed to take a first step within 3 min of our lifting of the holding cage or failed to enter both sides of the central area during the 10-min choice phase.

## 3.4.3 Results and Discussion

### Interobserver reliability

There was considerable agreement between independent observers’ scoring a random selection of videotapes for both number of pecks delivered by each target male during the fight phase (Pearsons correlation:  $r_{22} = 0.98$ ,  $P < 0.001$ ) and amount of time focal females spent nearer to each target male during the choice phase ( $r_8 = 0.99$ ,  $P < 0.001$ ).

### Fight Phase

Winning and losing target males assigned to E and Not-E conditions pecked the Plexiglas partition separating them for a mean  $\pm$  SE of  $597.0 \pm 88.5$  times (winners assigned to the E-condition),  $224.9 \pm 36.1$  times (losers assigned to the E condition),  $378.4 \pm 71.7$  times

(winners assigned to the Not-E condition), and  $184.2 \pm 48.5$  times (losers assigned to the Not-E condition). Winners assigned to both E and Not-E conditions thus pecked the Plexiglas partition more than twice as often as did the losers with whom they interacted. There was, however, no statistically reliable difference in number of pecks delivered by winners (two-sample Student's  $t$  test:  $t_{31} = 1.94$ ,  $P = 0.07$ ) or losers (two-sample Student's  $t$  test:  $t_{31} = 0.70$ ,  $P > 0.50$ ) assigned to E and Not-E conditions, or by both members of pairs assigned to E and Not-E conditions ( $t_{31} = 1.62$ ,  $P = 0.11$ ).

### Choice phase

We found a significant effect of group assignment on focal females' preferences for males that won and lost during the fight phase (two-sample  $t$  test:  $t_{31} = 3.57$ ,  $P < 0.01$ ; Fig. 3.2). During the choice phase, focal females assigned to the E condition spent more time nearer losers than winners (one-sample  $t$  test:  $t_{14} = 3.01$ ,  $P < 0.01$ ; Fig. 3.2). In contrast, focal females assigned to the Not-E condition showed a marginal tendency to remain closer to winners than to losers (one-sample  $t$  test:  $t_{17} = 1.91$ ,  $P = 0.07$ ), and might best be considered indifferent between winners and losers (see Results of experiments 2 and 3).

Of course, the finding that females that have eavesdropped on a pair of fighting males subsequently prefer to affiliate with the loser of the fight that they observed may have nothing to do with information that females acquired about the relative fighting ability of males they observed engaged in an aggressive interaction. For example, losers (which spent less time pecking at their opponents during the fight phase than did winners) may have spent more time than winners interacting with observing females, and may have become preferred as a consequence.

To determine whether differences in males' interactions with females during the fight phase might explain female preferences during the choice phase, an observer, unaware of group assignment of males, determined the time that each male spent with his beak pointed within the 45 degrees of arc centred on the holding cage. We found no difference in the time that winners ( $X \pm SE = 279.8 \pm 31.9$  s) and losers ( $328.7 \pm 34.8$  s) assigned to the E-condition or winners ( $190.7 \pm 30.1$  s) and losers ( $204.7 \pm 25.2$  s) assigned to the Not-E conditions directed their gaze towards the holding cage containing the focal female (E condition, paired  $t$  test:  $t_{13} = 1.61$ ,  $P = 0.13$ ; Not-E condition:  $t_{17} = 0.33$ ,  $P = 0.75$ ). The former finding is not consistent with the hypothesis that, during the fight phase, losers interacted more with focal females than did winners.

## 3.5 Experiment 2: Do Males Interact Differently When Watched by a Female?

The difference between preferences for winning males shown by focal females assigned to E and Not-E conditions in experiment 1 is open to yet another interpretation. During the fight phase, target males assigned to E and Not-E conditions may have behaved differently depending on whether they could see a female while interacting with one another. For example, target males assigned to the E condition (which saw a female during the fight phase) might have interacted

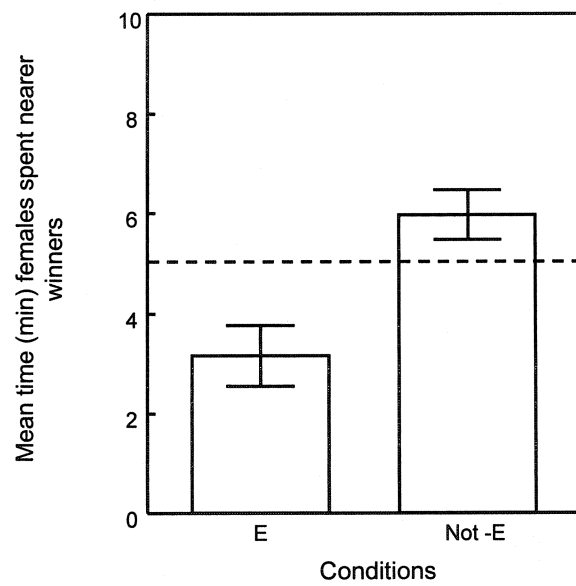


Figure 3.2: Mean ( $\pm$  SE) time during the choice phase that focal females in experiment 1 spent closer to the member of a pair of males that won during the fight phase.

more vigorously than did target males assigned to the Not-E condition (which could not see a female during the fight phase). If so, the difference in behaviour during the fight phase of males assigned to E and Not-E conditions might have affected their subsequent relative attractiveness to focal females during the choice phase. If so, focal females' preferences during the choice phase may have reflected their response to the appearance of males during the choice phase, not information acquired during the fight phase.

We undertook experiment 2 to determine whether differences in the behaviour of males seeing and not seeing females during the fight phase were responsible for differences in the affiliative preferences of females assigned to E and Not-E conditions during the choice phase in experiment 1. In experiment 2, during the fight phase, a one-way mirror either blocked or did not block the females' views of males, without blocking the males' views of the females (e.g. Doutrelant & McGregor, 2000). Keeping the conditions under which males interacted constant while providing or denying females visual access to males provided an opportunity to examine the hypothesis that differences in aggressive interactions of males that either could or could not see a female while fighting were responsible for the outcome of experiment 1.

### 3.5.1 Methods

#### Subjects

Subjects were 47 male and 33 female, sexually mature Japanese quail acquired from Specks Poultry Farm. We randomly assigned trios of subjects to mirror ( $N=18$ ) and no-mirror conditions ( $N=15$ ).

#### Apparatus

We modified the apparatus used in experiment 1 in the following ways. First, we removed the wire-mesh screen separating the ancillary cage and central area and replaced it with a one-way mirror that completely covered the 35 x 40-cm opening between the ancillary cage and central area (Fig. 5.1). Second, we changed the illumination of the experimental room during the fight phase depending on the condition to which a trio of subjects had been assigned.

When subjects assigned to the mirror condition were in the apparatus, we turned off the room lights and illuminated the central area of the main enclosure with 150-W halogen lights. When subjects assigned to the no-mirror condition were in the apparatus, we turned the halogen lights off and turned the house lights on. Consequently, during the fight phase, focal females and target males assigned to the no-mirror condition could see one another, whereas target males assigned to the mirror condition could see focal females, but focal females assigned to the mirror condition could not see target males.

### 3.5.2 Procedure

#### Fight phase

We treated subjects assigned to the mirror and no-mirror conditions exactly as we treated subjects assigned to the E condition of experiment 1 except for illumination of the apparatus

during the fight phase when subjects assigned to the mirror condition were in the apparatus.

### Choice phase

During the choice phase, we treated subjects assigned to both mirror and no-mirror conditions exactly as we treated subjects during the choice phase in experiment 1.

### 3.5.3 Results

#### Interobserver reliability

As in experiment 1, independent observers agreed significantly in their scores of a random sample of videotapes for both number of pecks delivered by each target male during the fight phase (Pearson's correlation:  $r_{18} = 0.91, P < 0.001$ ) and time focal females spent nearer to each target male during the choice phase ( $r_{18} = 0.99, P < 0.001$ ).

#### Fight Phase

Winning and losing target males assigned to mirror and no-mirror conditions pecked the Plexiglas partition separating them for a mean  $\pm$  SE of  $488.9 \pm 74.5$  times (winners assigned to the mirror condition),  $227.9 \pm 41.6$  times (losers assigned to the mirror condition),  $608.4 \pm 33.2$  times (winners assigned to the no-mirror condition) and  $335.6 \pm 81.7$  times (losers assigned to the no-mirror condition). Taken together, winners assigned to mirror and no-mirror conditions pecked more than twice as often as did the losers with whom they interacted. As in experiment 1, we found no difference in the number of pecks delivered to the Plexiglas partition by winners (two-sample Student's  $t$  test:  $t_{27} = 1.11, P = 0.28$ ), losers ( $t_{27} = 1.20, P = 0.24$ ), or pairs of subjects ( $t_{27} = 1.24, P = 0.26$ ), as a function of the condition to which we had assigned subjects.

#### Choice phase

We discarded data from four trios when females failed to move within 3 min of release from the holding cage.

We found a significant effect of group assignment on focal females' preferences for males that won and lost during the fight phase (two-sample  $t$  test:  $t_{27} = 2.05, P < 0.05$ ; Fig. 3.3). During the choice phase, focal females assigned to the no-mirror condition spent significantly more time nearer the loser than the winner (one-sample  $t$  test:  $t_{13} = 3.92, P < 0.01$ ; Fig. 3.3). In contrast, focal females assigned to the mirror condition were indifferent to winning and losing males (one-sample  $t$  test:  $t_{14} = 0.01, P = 0.99$ ).

### 3.5.4 Discussion

The results of experiment 2 are consistent with the prediction that whether focal females can see target males is important and whether target males can see focal females is not important in determining whether focal females prefer to affiliate with losers of aggressive



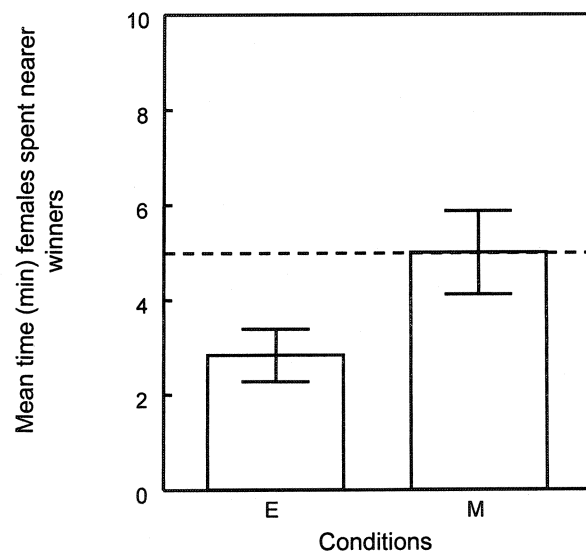


Figure 3.3: Mean ( $\pm$  SE) time during the choice phase that focal females in experiment 2 spent closer to the member of a pair of males that won during the fight phase.

encounters. However, using a one-way mirror to allow males to see females without permitting females to see males turned out to be a less than ideal procedure. The mirror degraded visual stimuli passing between the ancillary cage and the central area throughout both phases of the experiment and, during the fight phase, required use of potentially distracting bright lights and provided the focal female with a mirror image of herself.

### **3.6 Experiment 3: Do Males Interact Differently When Watched by a Female Revisited?**

Rather than persevere with one-way mirrors, we took an alternative approach to determining the effects of seeing a focal female on the males' behaviour during the fight phase. We repeated experiment 1, but added a substitute female (S-F) condition in which, during the fight phase, target males interacted while seeing an observing female, as did target males assigned to both the E condition of experiment 1 and to the no-mirror condition of experiment 2. However, in the S-F condition, a female other than the female that had observed the fight phase chose between target males during the choice phase. If, seeing a female during the fight phase caused males to interact so as to enhance subsequent attractiveness of losers to females, then females assigned to the S-F condition that chose between males, like focal females assigned to the E condition in experiment 1 and the no-mirror condition in experiment 2, should prefer losers to winners during the choice phase.

#### **3.6.1 Methods**

##### **Subjects and apparatus**

Subjects were 66 male and 68 female sexually mature Japanese quail acquired from Speck's Poultry Farm. Nine females served only as models in the S-F condition. We used the same apparatus that we had used in experiment 1 (Fig. 5.1).

##### **Procedure**

We first randomly assigned males to 59 unique pairs, then randomly assigned one female to each of 19 pairs of target males that we assigned to the E condition and each of 20 pairs of target males that we assigned to the Not-E condition. We then assigned a unique pair of females to each of the 20 pairs of target males that we assigned to the S-F condition.

##### **Fight phase**

During the fight phase, we treated both female subjects and target males assigned to E and Not-E conditions just as we had treated subjects assigned to those conditions in experiment 1. We treated subjects assigned to the S-F condition exactly as we treated those assigned to the E condition, except that we removed the female that had observed target males during the fight phase (the model female) and replaced her with a female that had not observed target males interacting (the focal female). Thus, target males assigned to the S-F condition fought

in the presence of a female, as had target males assigned to the E condition. However, focal females assigned to the S-F condition, like focal females assigned to the Not-E condition, had not seen a fight before choosing between target males.

### Choice phase

During the choice phase, we removed model females from the experiment and treated both their replacement focal females and target males exactly as we had during the choice phases of experiments 1 and 2.

## 3.6.2 Results and Discussion

### Interobserver reliability

As in experiments 1 and 2, independent observers agreed significantly on scores from a random sample of videotapes for both number of pecks delivered by each target male during the fight phase (Pearson's correlation:  $r_{16} = 0.88$ ,  $P < 0.001$ ) and time focal females spent nearer to each target male during the choice phase ( $r_{14} = 0.97$ ,  $P < 0.001$ ).

### Fight phase

Winners assigned to E, Not-E and S-F conditions pecked at the partition separating them from losers a mean  $\pm$  SE of, respectively,  $495.9 \pm 60.5$ ,  $511.0 \pm 80.9$  and  $506.22 \pm 62.07$  times. Losers in the same three groups pecked, respectively,  $201.7 \pm 40.0$ ,  $224.0 \pm 27.4$  and  $153.7 \pm 42.7$  times. As in experiment 1, group assignment had no effect on pecking rates of winners, losers (one-way ANOVAs:  $F_{2,47} < 0.90$ , both *NS*), or pairs (one-way ANOVA:  $F_{2,47} = 0.18$ ,  $P = 0.83$ ). As in experiments 1 and 2, because we consistently assigned subjects that pecked more frequently to the group of winners, the pecking rates of winners was greater than that of losers.

### Choice phase

Data from nine focal females were discarded when they either failed to take a first step during the first 3 min of the choice phase or failed to enter both halves of the central area during the choice phase.

We found a significant effect of group assignment on the affiliative behaviour of focal females during the choice phase (one-way ANOVA:  $F_{2,47} = 3.48$ ,  $P < 0.05$ ; Fig. 3.4). Focal females assigned to the E condition, who saw a pair of males fight before choosing between them, preferred losers more than did focal females assigned to either Not-E or S-F conditions (Fisher's positive least significant difference (PLSD) tests, both  $P_s < 0.05$ ; Fig. 3.4).

On the other hand, focal females assigned to S-F and Not-E conditions, who had not seen a pair of males fight before choosing between them, did not differ from one another (Fisher's PLSD test:  $P=0.92$ ; Fig. 3.4). Although none of the three groups showed a statistically significant preference for either winners or losers (one-sample t tests: group E:  $t_{16} = 1.52$ ,  $P$

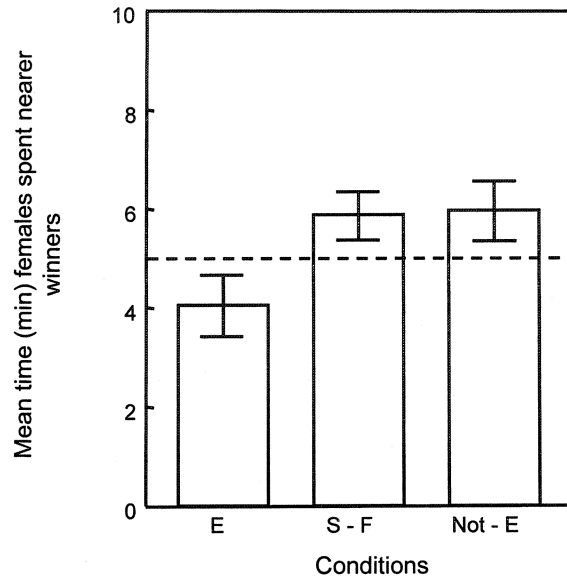


Figure 3.4: Mean  $\pm$  SE time during the choice phase that focal females in experiment 3 spent closer to the member of a pair of males that won during the fight phase.

= 0.15; group S-F:  $t_{17} = 1.79$ ,  $P = 0.09$ ; group Not-E:  $t_{14} = 1.52$ ,  $P = 0.15$ ), both groups E and Not-E deviated from chance in the same direction as in our previous experiments.

The results of experiment 3 replicate the finding in experiment 1 showing that focal females that have watched two males fight prefer the loser of the fight to the winner. The present results, like those of experiment 2, suggest that information garnered by females watching a fight between males determines their subsequent choice of a male with whom to affiliate.

### 3.7 Experiment 4: Why Might Females Prefer Losers?

As discussed briefly in the introduction, on general theoretical grounds, a female quail might be expected to favour the more aggressive or dominant member of a pair of males that she has seen interact (Qvarnström & Forsgren, 1998). Dominant males are generally assumed to have superior access to resources and to be bearers of better genes than submissive males. Consequently, the reproductive success of females mating with dominant males should generally be greater than that of females mating with submissive individuals (Qvarnström & Forsgren, 1998). In fact, females of several species have been shown to prefer dominant to submissive

males (e.g. Brown et al., 1988; Rich & Hurst, 1998; Doutrelant & McGregor, 2000). However, results of experiments 1, 2 and 3 above indicate that female Japanese quail, like females of several other species (reviewed in Qvarnström & Forsgren, 1998), show the opposite effect and prefer to affiliate with submissive rather than dominant males. Why might female Japanese quail prefer losers to winners?

To a human observer, the courting behaviour of male Japanese quail, like that of male horses, *Equus caballus*, (Linklater et al., 1999), fallow deer, *Dama dama*, (Clutton-Brock et al., 1989) and elephant seals, *Mirounga angustirostris*, (Le Boeuf & Mesnick, 1990) seems able to physically damage females of their species. Consistent with this view, results of recent studies in our laboratory show that female Japanese quail find the attentions of at least some male suitors unpleasant and form aggregations in the presence of male conspecifics to reduce the probability of sexual harassment (Persaud & Galef, 2003).

We saw considerable variability in the frequency with which males engaged in potentially injurious behaviours while courting females. However, most courting males chased females, pecked vigorously at their heads and bodies, seized the feathers at the back of females' heads, dragged them around by their feathers and repeatedly jumped onto females' backs while attempting to achieve cloacal contact. If relatively dominant males are more violent when courting females than are relatively submissive males, then females might gain by foregoing whatever benefits might accrue from mating with a dominant male to escape the cost of being courted by him.

Here, we first used a round-robin tournament to establish the relative dominance of a cohort of male quail. We then allowed each male in the cohort to court and mate with three females in succession and scored the potentially punishing aspects of each male's interactions with females that he courted.

### 3.7.1 Methods

#### Subjects and apparatus

Subjects were 17 sexually mature male and 17 sexually mature female Japanese quail. We used the same apparatus that we had used in experiments 1 and 3.

### 3.7.2 Procedure

#### Dominance phase

We determined the dominance of our 17 male subjects over 8 days by allowing each male to interact through the Plexiglas partition in the ancillary cage (Fig. 5.1) with each of the other 16 males. Because we had to score 136 aggressive encounters between males, we reduced the duration of each to 2 min. No male participated in more than two encounters on any one day, and a minimum of 20 min separated any male's participation in two encounters.

Two reviewers independently scored videotapes of encounters to determine how many times each member of a pair of males pecked at the Plexiglas barrier separating them. As in previous experiments, we considered whichever member of a pair of males that pecked the

Plexiglas barrier the most times to be the winner of an encounter. To create a relative ranking of the 17 males, we determined how many times each male won in the 16 encounters in which he was engaged.

### Courtship and mating phase

After we determined the dominance ranking of each male, we allowed him to court and mate for 10 min every third day until he had mated with three females. An experimenter who was unaware of the outcome of the dominance phase scored videotapes of encounters between males and females to determine the number of potentially harmful behaviours and the number of courtship behaviours in which each male engaged. We considered pecks, feather pulls, drags, mounts and single-foot mounts to be potentially damaging to females, and heightened postures, strut/tidbitting, approach, invitations to preen and feather ruffles as courtship behaviours. Each of these behaviours other than ‘single-foot mount’ has been described in the literature (Adkins & Adler, 1972; Wilson & Bermant, 1972; Ramenofsky, 1984; Schleidt et al., 1984). We defined a single-foot mount as any instance in which a male placed only one foot on a female when attempting to mount.

### 3.7.3 Results

#### Interobserver reliabilities

Once again, we found substantial agreement between independent observers scoring videotapes as to the number of pecks delivered by target males during the dominance phase (Pearson’s correlation:  $r_{46} = 0.93$ ,  $P < 0.001$ ). Observers also agreed on the number of female directed pecks ( $r_{15} = 0.83$ ,  $P < 0.001$ ), number of other harmful behaviours males directed towards females ( $r_{15} = 0.86$ ,  $P < 0.001$ ) and number of courting behaviours ( $r_{15} = 0.90$ ,  $P < 0.001$ ) produced by males during the courtship and mating phase.

#### Main results

We found a strong positive relation between the number of wins that a male achieved during the dominance phase and the number of pecks that he delivered to females with whom he interacted during the courtship and mating phase ( $r_{15} = 0.83$ ,  $P < 0.0001$ ; Fig. 3.5a). There was a similar strong positive correlation between the number of wins that a male achieved during the dominance phase and the number of potentially harmful behaviours other than pecking that a male engaged in during the courtship and mating phase ( $r_{15} = 0.71$ ,  $P < 0.001$ ; Fig. 3.5b).

Males winning more encounters during the dominance phase were not just generally more active than males scoring fewer wins during the dominance phase. For example, we found no correlation between the number of wins that a male achieved during the dominance phase and the frequency of his courting behaviours during the courtship and mating phase ( $r_{15} = 0.08$ ,  $P = 0.77$ ; Fig. 3.6).

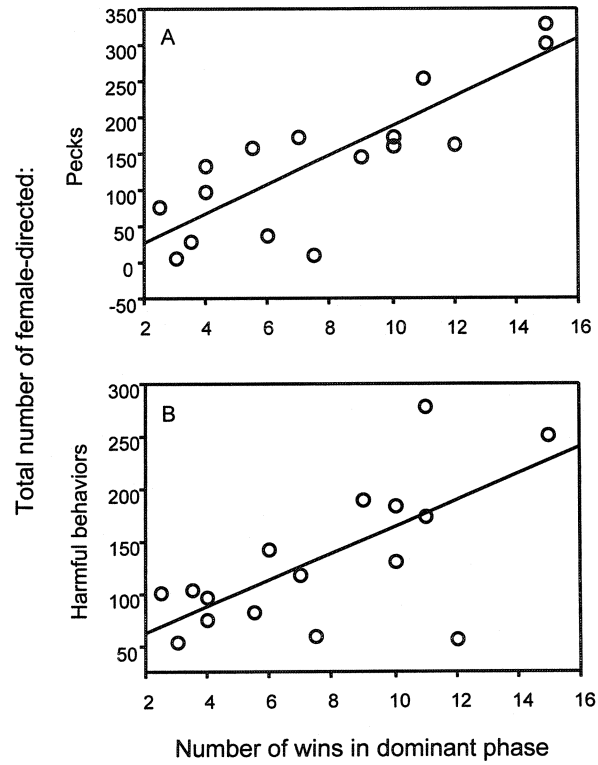


Figure 3.5: Scatter plots of the number of wins that a male achieved during the dominance phase and the number of (a) pecks and (b) other potentially harmful behaviours that he engaged in during the courtship and mating phase in experiment 4. The solid line represents the best linear fit.

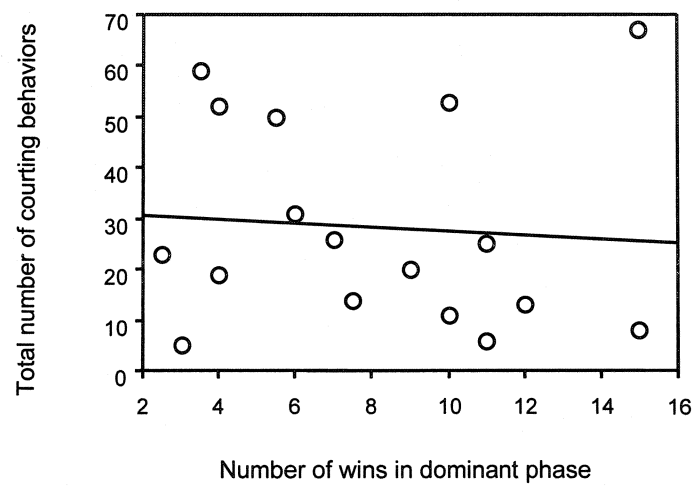


Figure 3.6: Scatter plots of the number of wins that a male achieved during the dominance phase and the number of courtship behaviours that he engaged in during the courtship and mating phase in experiment 4. The solid line represents the best linear fit.



### 3.7.4 Discussion

Females eavesdropping on a pair of males engaged in an aggressive interaction could predict which male would be more likely to peck at them and to engage in other potentially harmful behaviours. Consequently, by affiliating with less dominant males, females could avoid contact with males more likely to engage in potentially injurious behaviour when courting and mating.

## 3.8 General Discussion

Evidence shows that females of many, but not all, species prefer to mate with relatively dominant males (Qvarnström & Forsgren, 1998). Female preference for winners of intrasex competitions would be expected on the hypothesis that dominant males have greater access to resources or better genes than do subordinate males, and females could, therefore, acquire direct or indirect benefits from mating with dominant individuals (Qvarnström & Forsgren, 1998).

The finding in experiments 1, 2 and 3 indicate that female quail prefer the less aggressive of two males that they have seen interact. The results of experiment 4 suggest that the relatively less dominant males that females prefer as affiliative partners are less likely than are more dominant males to court in ways that could be harmful to females.

Ideally, we would be able relate our laboratory findings to the behaviour of free-living Japanese quail. Unfortunately, Japanese quail are difficult to observe in the wild, and there is contradictory information as to both their social organization and sexual behaviour (Wetherbee, 1961; Nichols, 1991). Opportunistic observations of mating in wild Japanese quail have produced reports of both monogamy and polygyny (Kawahara 1967, cited in Nichols, 1991).

Studies of both domestic and feral quail in large flight cages (Nichols, 1991) suggest that females bond with one or two males, but that most engage in extrapair copulations. Most important for studies of female mate choice, Nichols (1991) reported that female Japanese quail solicit copulations from some males by walking in front of them and crouching, thus apparently inviting particular males to mount, and female quail prevent apparently undesired copulations by resisting males or fleeing 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 the male’, behaviours quite similar to those that we used in the present studies as indices of female preference. Whether females in natural circumstances would have an opportunity to observe males fighting or defending territories is difficult to know.

Taken together, the results of all four experiments suggest that female quail can use information that they acquire while eavesdropping on males engaged in aggressive interactions to reduce their own probability of sustaining injury while mating. Theoretically, reproductive costs to female Japanese quail of mating with dominant conspecific males should be greater than the direct and indirect reproductive benefits that such males might provide (Qvarnström & Forsgren, 1998). Unfortunately, empirical tests of that hypothesis are difficult to envision in a species such as *Coturnix japonica*, where whatever physical damage that males inflict on females is not readily observed.

### **3.9 Acknowledgments**

This research was supported by Natural Sciences and Engineering Research Council of Canada operating and equipment grants to B.G.G., Jr. We thank Jeanine Johnson, Nav Mangat and Rebecca Lee for their devotion in scoring videotapes, Kamini Persaud for technical assistance, and Martin Daly for suggesting experiment 3.

## Chapter 4

# Are female quail attracted to location or the individual?

It's not my house that women desire.

*Anonymous*

### 4.1 Preface

This chapter is an unpublished study that controls for the possibility that female quail are attracted to specific sites where where less aggressive males were previously observed rather than to a less aggressive males per se.

### 4.2 Introduction

Previous experiments on the mate preferences of Japanese quail, *Coturnix japonica*, have provided evidence consistent with the view that female quail prefer to affiliate with the less aggressive of two “target” males that they have watched interact (Ophir & Galef, 2003b). Unfortunately, in the Ophir and Galef (2003b) experiments, the identity of target males and their locations were confounded. Consequently, it was impossible to determine whether female quail preferred the less aggressive of two males or the general area where the less aggressive male had been observed while engaged in an agonistic interaction.

In the present experiment, undertaken to determine whether females preferred less aggressive males or the locations where less aggressive males had been seen, we allowed females to observe a pair of males interact and to then choose between those males after we had reversed their usual locations in the apparatus.

### 4.3 Experiment 1: Does location affect how female quail prefer to affiliate with males?

#### 4.3.1 Methods

##### Subjects

Eleven female and 14 male Japanese quail, acquired from Speck's Poultry Farm (Vineland, Ontario) when 52 days of age, served as subjects. After transporting subjects to our laboratory (Hamilton, Ontario), we placed them in individual cages, measuring 55 x 55 x 110 cm, housed in a single temperature- and humidity-controlled colony room illuminated on a 16:8 light:dark cycle, with light onset at 0700 h. All subjects had ad libitum access to water and Mazuri Pheasant Breeder (PMI Feeds, St. Louis, Missouri) for the duration of their stay in the laboratory.

Experiments began only after subjects had achieved sexual maturity. We considered females to be sexually mature when they began to lay at least one egg every other day. To determine whether a male was mature, when he started to call regularly (at about 70 days of age), we placed him together with a succession of sexually mature females, for 5 min/day for 7 consecutive days, in alternating end chambers of the apparatus illustrated in Figure 4.1. We observed the behavior of pairs on closed-circuit television, and when a male mounted and made cloacal contact with females on 2 successive days, we considered him to be sexually mature.

##### Apparatus

We performed experiments in an apparatus constructed of painted plywood, transparent Plexiglas and wire mesh (Fig. 4.1) that rested on an aluminum tray lined with absorbent paper pads (Tray liners, Lilo Products, Hamilton, Ontario, Canada). The apparatus was divided into four sections: a "central area," measuring 61 x 61 x 30 cm, two "end chambers," each measuring 61 x 30 x 30 cm, and an "ancillary cage," measuring 44 x 30 x 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 x 26 cm, located in the center of the roof of the central area, allowed a transparent Plexiglas "holding cage," measuring 25 x 25 x 40 cm, to be raised and lowered using a pulley system. A vertical line drawn at 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.

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

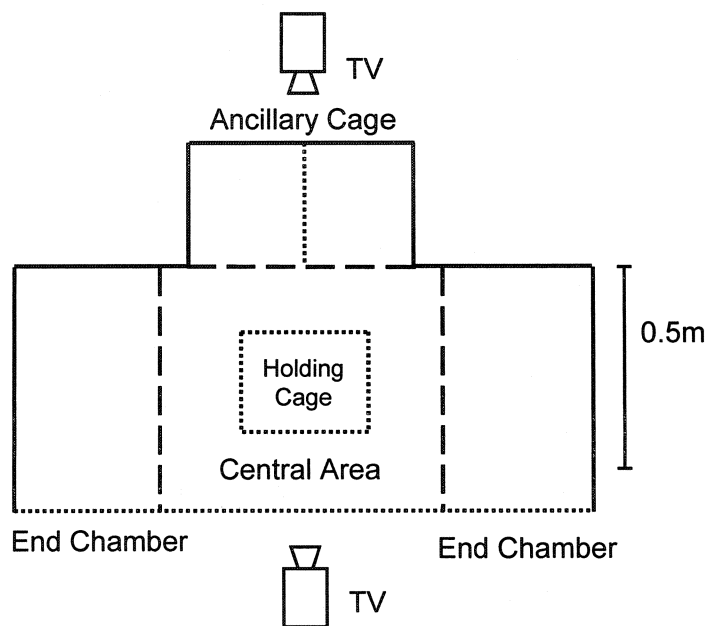


Figure 4.1: Overhead schematic of the apparatus. Solid lines = opaque walls; dotted lines = transparent Plexiglas; dashed lines = wire mesh. The camera viewing the ancillary cage was mounted directly above its midpoint, facing down, and the camera viewing the central area was located at its midpoint and was oriented horizontally.

## Procedure

**Group assignment.** We assigned subjects to trios each composed of a “focal” female and two “target” males. To construct trios, we first assigned males to 11 unique pairs and then randomly assigned a focal female to each pair.

**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 barrier dividing the ancillary cage. We then lifted the opaque partition separating the males, leaving the transparent Plexiglas partition in place. For the next 10 min, we used a closed-circuit television camera suspended directly above the midpoint of the ancillary cage and a videocassette recorder to make a permanent record of the behavior of the two target males. Two independent observers subsequently scored these videotapes to determine the number of times that each target male pecked the transparent Plexiglas partition during the 10-min fight phase.

We considered the target male in each trio that pecked the transparent partition more frequently during the fight phase the “winner” of the fight and the male that pecked it less frequently the “loser” of that fight.

Schlinger et al. (1987) staged direct aggressive encounters between eight pairs of males. They found in all eight cases that the male that had previously pecked more at a Plexiglas barrier separating him from a conspecific target won the aggressive encounter. Because of ethical problems associated with staging aggressive interactions, we used Schlinger et al.’s indirect measure of male aggression.

**Choice phase.** As soon as the fight phase ended, we placed each target male in the end chamber of the main enclosure that was furthest to the side of the ancillary cage he had occupied during the fight phase. We then lifted the holding cage, waited until the released focal female took her first step, and allowed the focal female to move freely about the central area for 10 min, recording her behavior using a video camera located in front of the central area (Fig. 4.1). We considered a female to “prefer” whichever target male she spent more than half of the 10-min choice phase nearer. We excluded data from one trio in which the focal female failed to take a first step within 3 min of our lifting of the holding cage.

### 4.3.2 Results and Discussion

#### Interobserver reliability

Two independent observers’ scoring random selections of videotapes for both the number of pecks delivered by each target male during the fight phase (Pearson’s correlation:  $r_{12} = 0.95$ ,  $P < 0.001$ ) and time focal females spent nearer to each target male during the choice phase ( $r_5 = 0.99$ ,  $P < 0.001$ ) agreed closely in their assessments.

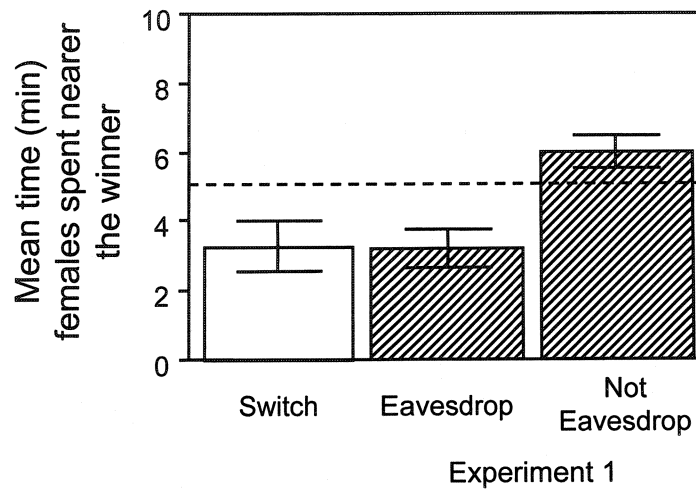


Figure 4.2: Mean time ( $\pm$  SE) during the choice phase that focal females spent closer to the male that won during the fight phase when the location of the target males was switched in the choice phase (white bar). Filled bars represent data presented in Chapter 3; Experiment 1 (Eavesdrop = females could see males fight during the ‘fight phase’; Not Eavesdrop = females whose view of males during the ‘fight phase’ was blocked). Dashed line = chance.

### Fight phase

Winner and loser target males pecked the Plexiglas partition separating them an average ( $\pm$  SE) of: (winners)  $499.8 \pm 95.7$  times, and (losers)  $234.1 \pm 64.7$  times. The number of pecks winners and losers produced in the present experiment is comparable to that of subjects in previous experiments (Chapter 3).

### Choice phase

During the choice phase, focal females spent significantly more time nearer to losers than to winners (one sample  $t$  test:  $t_9 = 2.30$ ,  $P < 0.05$ ; Fig. 4.2).

For comparison purposes, we have provided results from Chapter 3 (Experiment 1) and analyzed those data together with those from the present experiment. We found a significant effect of treatment on females’ preferences for males (one-way ANOVA:  $F_{2,40} = 7.70$ ,  $P <$

0.01:Fig. 4.2). Both females assigned to the eavesdrop condition in Chapter 3 (i.e. females that observed an agonistic interaction between males before choosing between them) and females in the present experiment (switch condition) spent significantly less time with winning males than did females assigned to the blocked condition in Chapter 3 (i.e. females that did not observe the aggressive interaction of a pair of males before choosing between them (Bonferroni-adjusted  $t$  test:  $t_{26} = 3.08$ ;  $P < 0.01$ ). Females assigned to eavesdrop and switch conditions did not differ from one another (Bonferroni-adjusted  $t$  test:  $t_{23} = 0.079$ ;  $P = 0.94$ ).

The present data are entirely consistent with the view that female quail prefer the less aggressive of a pair of males seen interacting aggressively, not the general area where that male was seen engaged in aggressive interaction.

#### 4.4 Acknowledgements

This research was supported by Natural Sciences and Engineering Research Council of Canada operating and equipment grants to B. G. G., Jr. We thank Jennifer Malowney for assistance scoring videotapes. The research is described in Animal Utilization Proposal 99-05-26 approved by the McMaster University Research Ethics Board in May of 1999.



## Chapter 5

# The influences of sexual experience on mate choice

Good judgment comes from experience, and a lot of that comes from bad judgment.  
*'Texas' Bix Bender*

### 5.1 Preface

This chapter is reprinted from *Animal Behaviour*, Ophir, A. G. & Galef, B. G. Jr., Sexual experience can affect use of public information mate choice, in press, Copyright 2004, with permission from Elsevier. The paper was first submitted to *Animal Behaviour* on March 23, 2003, and revised and resubmitted on July 8, 2003. It was initially accepted for publication on October 28, 2003, and its final acceptance was December 1, 2003 (MS. number A9582).

### 5.2 Abstract

The mate choices of sexually experienced, female Japanese quail (*Coturnix japonica*) are influenced by public information acquired by observation of potential partners engaged 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 engage in an agonistic interaction. 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. On the other hand, virgin female quail differed from sexually experienced female conspecifics in preferring the more aggressive rather than the less aggressive member of a pair of males that they had seen engage in an agonistic encounter. The results bear on hypotheses as to why females choosing a mate use information acquired by observing potential mates interacting with others.

### 5.3 Introduction

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

Observation of aggressive interactions, 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 engage in aggressive interactions subsequently prefer the winner to the loser.

Female Japanese quail, *Coturnix japonica*, the subjects in the experiments described here, like female Poeciliidae, prefer to affiliate with males they have seen mating with other females (Galef & White, 1998; White & Galef, 1999c, 2000b, 2000a; Ophir & Galef, 2003a), and in quail, affiliative preferences have been shown to predict choice of actual sex partners (White & Galef, 1999b). Female Japanese quail, unlike females in other species examined to date, prefer the less aggressive of two males observed in an aggressive encounter (Ophir & Galef, 2003b).

A variety of hypotheses have been proposed to explain females' use of such public information when choosing among males. 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 to 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 and error prone, so inexperienced animals might gain from copying the mate choices of more experienced females that are presumed to be superior assessors of male quality (Gibson & Höglund, 1992; Dugatkin & Godin, 1993). Female quails' preference for the less aggressive of a pair of males has been hypothesized to reflect females' avoidance of male harassment (Persaud & Galef, 2003) together with a tendency for males that are more aggressive towards other males to also be more aggressive towards females (Ophir & Galef, 2003b).

We undertook the present pair of experiments to examine the importance of females' prior sexual experience in mediating dependence on public information when choosing a mate. As indicated below, such developmental analysis can contribute, at least to a limited extent, to an evaluation of the adequacy of the several explanations in the literature of females' use of public information when selecting a sex partner.

### 5.4 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. On the other hand, if mate-choice copying serves simply to reduce sampling costs associated with mate assessment, then prior female sexual experience should have relatively little effect on females' use of public information when selecting a mate.

### 5.4.1 Methods

#### Subjects

Seventeen female and 15 male Japanese quail acquired when 52 days old from Speck's Poultry Farm (Vineland, Ontario) served as subjects. After we transported subjects to our laboratory (Hamilton, Ontario), we placed them in individual cages, measuring 55 x 55 x 110 cm, maintained in a single temperature- and humidity-controlled colony room illuminated on a 16:8 light:dark cycle, with light onset at 0700 h. All subjects had *ad libitum* access to water and Mazuri Pheasant Breeder (PMI Feeds, St. Louis, Missouri).

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. To determine whether a male was sexually mature, when he started to call regularly (at about 70 days of age), we placed him in an end chamber of the apparatus (Fig. 5.1) with a succession of sexually mature females for 10 min/day for 7 consecutive days. We observed the behavior of pairs on closed-circuit television, and after a male had mounted and made cloacal contact with females on 2 successive days, we considered him sexually mature.

#### Apparatus

We performed experiments in an apparatus constructed of painted plywood, transparent Plexiglas and wire mesh (Fig. 5.1) that rested on an aluminum tray lined with absorbent paper pads (Tray liners, Lilo Products, Hamilton, Ontario, Canada). The apparatus was divided into four sections: a "central area," measuring 61 x 61 x 30 cm, two "end chambers," each measuring 61 x 30 x 30 cm, and an "ancillary cage," measuring 44 x 30 x 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 x 26 cm, located in the center of the roof of the central area, allowed a transparent Plexiglas "holding cage," measuring 25 x 25 x 40 cm, to be raised and lowered using a pulley system. A vertical line drawn at 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 color CCTV video cameras (Panasonic WV-CP230; one facing the transparent front wall of the apparatus and the other mounted directly above the ancillary cage and both connected to VHS videocassette recorders (Panasonic AG-1240) allowed experimenters to both record and observe behavior of subjects without disturbing them.

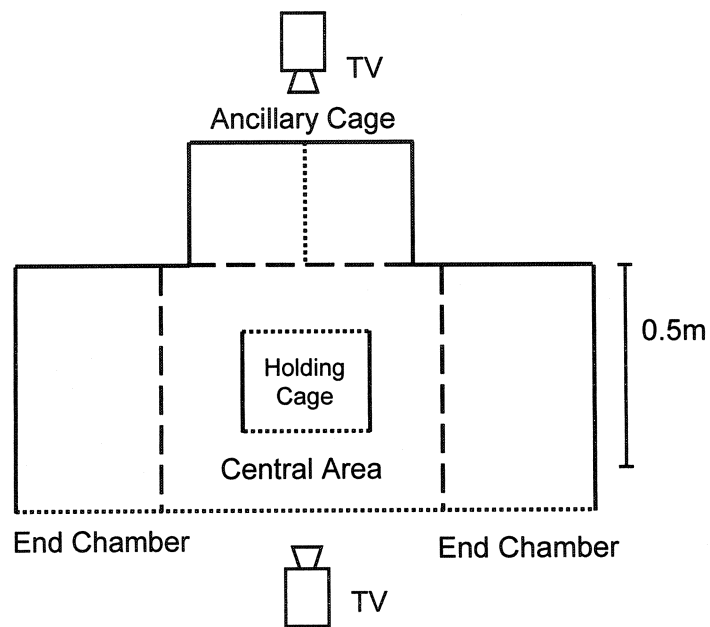


Figure 5.1: Overhead schematic of the apparatus used in all experiments. Solid lines = opaque walls; dotted lines = transparent Plexiglas; dashed lines = wire mesh. The camera viewing the ancillary cage was mounted directly above its midpoint, facing down, and the camera viewing the central area was located at its midpoint and oriented horizontally.

## Procedure

The experiment consisted of three 10-min phases: (1) a pre-test, 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 pre-test (her non-preferred 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 pre-test.

To begin, we randomly assigned females to either virgin ( $N = 7$ ) or experienced ( $N = 7$ ) conditions, or to serve as “model” females ( $N = 3$ ). For 10-min/day for 8 days, we placed each virgin female assigned to the experimental condition in the central area of the apparatus (Fig. 5.1) with a sexually experienced male. We treated females assigned to the virgin condition as we treated females assigned to the experienced condition, 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 three model females both to test males for sexual maturity and as “models” during the observation phase of the experiment described below.

Before testing subjects assigned to virgin and experienced conditions, we assigned them to groups of four, each composed of a “focal female”, a “model female”, and two “target” males. To construct groups, we first assigned males to the 105 unique pairs that can be constructed using 15 male subjects. We then randomly selected 14 of these 105 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.

**Pre-test.** To begin a pre-test, we placed a target male in each end chamber of the apparatus, and a focal female in the holding cage (Fig. 5.1). 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 whichever male the focal female spent more than half of the 10-min pre-test closer to her “preferred male” and the other male her “non-preferred male.”

**Observation phase.** At the end of the pre-test, we returned each focal female to the holding cage and placed a model female in the end chamber that contained the focal female’s non-preferred male. We then left the non-preferred 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, permitting her to move freely about the central area of the apparatus for 10 min. As in the pre-test, we recorded the time that each focal female spent closer to each target male.

## Data Analysis

To determine the effect of the observation phase on a female's preference for her non-preferred target male, we subtracted the time she spent closer to her non-preferred male during the pre-test 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 non-preferred males by focal females assigned to virgin and experienced conditions.

### 5.4.2 Results and Discussion

#### Interobserver reliability

There was substantial agreement between two independent observers scoring a random selection of videotapes for the change between pre- and post-test in the time that females spent closer to their non-preferred males ( $r = 0.94$ ,  $N = 14$ ).

#### Pre-test

During the pre-test, focal females assigned to virgin and experienced conditions spent a mean ( $\pm$  SE) of, respectively,  $7.0 \pm 0.8$ , and  $8.0 \pm 0.5$  min closer to their preferred than non-preferred target males (*t* test;  $t_{12} = 1.05$ , *NS*).

#### Observation phase

During the observation phase all non-preferred target males courted and achieved cloacal contact with their model females.

#### Post-test

Sexually experienced and virgin females did not differ in their use of information acquired during the observation phase (*t* test;  $t_{12} = 0.05$ , *NS*; Fig. 5.2). Females assigned to both conditions in the present experiment, like females with extensive previous sexual experience observed in our laboratory (e.g. Galef & White, 1998), showed a mean increase of approximately 2 min between pre-test and post-test in the time that they spent with their respective non-preferred target males. Consequently, it cannot be argued that the lack of difference between females assigned to virgin and experienced conditions was due to insufficient experience by females assigned to the latter.

Equal use of public information by virgin and experienced female quail is not consistent with the hypothesis that public information serves primarily to improve mate assessment by naïve females choosing a partner. Equal use of public information by virgin and experienced female quail is also not consistent with Dugatkin and Godin's (1993) interpretation, in terms of information asymmetry, of the of their finding that small female guppies are more likely to copy the mate choices of large conspecific females than vice versa. In Dugatkin and Godin's (1993) experiment, all females had sexual experience, but larger females were assumed to be more experienced than smaller ones. The present result in quail suggests that although small

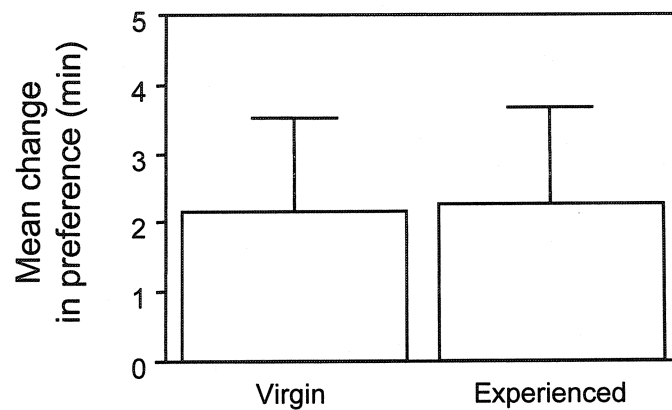


Figure 5.2: Mean ( $\pm$ ) SE change in time (min) between pre-test and post-test that virgin and experienced focal female subjects spent nearer to the target subject they had not preferred during the pre-test.

female guppies may be more likely to copy the mate choices of large ones than the reverse, this asymmetry may not be a result of differences in prior sexual experience and consequent ability to assess males.

## 5.5 Experiment 2: Observing Male Aggression

Ophir and 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.

### 5.5.1 Methods

#### Subjects

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

#### Apparatus

We used the same apparatus that we used in experiment 1 (Fig. 5.1), 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 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 behavior of target males.

Two independent observers reviewed the 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 when pairs of males pecked at one another through a glass partition that separated them, the male that pecked more frequently also won a subsequent unrestrained fight with that conspecific.



### **Ethical note**

Ethical problems associated with staged aggressive interactions led us to use an indirect measure of male aggression rather than 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 occupied during the fight phase. We then lifted the holding cage, waited until the released focal female took her first step, and allowed the focal female to move freely about the central area for the next 10-min, recording her behavior using the video camera located in front of the transparent front wall of the central area (Fig. 5.1). 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.

## **5.5.2 Results and Discussion**

### **Interobserver reliability**

Independent observers largely agreed on the number of pecks delivered by each target male during the fight phase (Pearson's  $r = 0.94$ ,  $N = 20$ ) and the time focal females spent nearer to each target male during the choice phase ( $r = 0.996$ ,  $N = 10$ ).

### **Fight Phase**

Winning and losing target males assigned to virgin and experienced conditions pecked the Plexiglas partition separating them an average (SE) of: (1) winners assigned to the virgin condition  $541.9 \pm 70.2$  times, (2) losers assigned to the virgin condition  $293.1 \pm 39.4$  times, (3) winners assigned to the experienced condition  $588.4 \pm 99.7$  times, (4) and losers assigned to the experienced condition  $239.3 \pm 71.9$  times. There were also no significant differences between the number of pecks delivered by winners (Two-sample Student's  $t$  test,  $t_{25} = 0.39$ ,  $NS$ ) or losers ( $t$  test,  $t_{25} = -0.71$ ,  $NS$ ) assigned to the two conditions, or total pecks by both members of a pair (winner's pecks + loser's pecks;  $t$  test,  $t_{25} = -0.05$ ,  $NS$ ).

### **Choice phase**

We found a significant effect of group assignment on focal females' preferences for winning and losing males ( $t$  test,  $t_{25} = -4.15$ ,  $P < 0.001$ ; Fig. 5.3). During the choice phase, focal females assigned to the experienced condition spent more time nearer losers than winners (One-sample  $t$  test,  $t_{10} = -3.33$ ,  $P < 0.01$ ; Fig. 5.3). On the other hand, focal females assigned to the virgin condition preferred winners to losers ( $t$  test,  $t_{15} = 2.35$ ,  $P < 0.05$ ; Fig. 5.3).

The results of experiment 2 are consistent with the hypothesis that female quail need to learn from personal experience that conspecific males can be hurtful, and once they have,

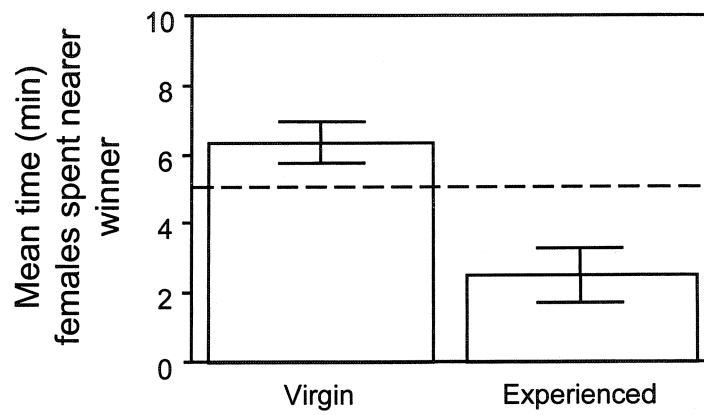


Figure 5.3: Mean time ( $\pm$  SE) during the choice phase that virgin and sexually experienced focal females in experiment 2 spent closer to the member of a pair of males that won during the fight phase. Dashed lines = chance

they will use public information concerning males' relative levels of aggression when choosing a mate.

## 5.6 General Discussion

Taken together, the results of experiments 1 and 2 suggest that female quails' use of public information in mate choice reflects an interaction between the type of public information to which a female has access and her own life experiences. Only females with a prior history of sexual activity use public information about the relative aggressiveness of two males when selecting a mate. Both sexually experienced and sexually inexperienced females will copy mate choices of other females. These findings suggest, both that females must learn either about the potential harmfulness of males or to identify aggressive males before public information about males' aggressiveness becomes useful, and that mate-choice copying functions more to reduce costs of assessment than to redress any informational asymmetries between naïve and knowledgeable individuals. Study of the role of individual experience in development of use of public information provides a potential means of examining proposed functions of social learning.

## 5.7 Acknowledgements

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## Chapter 6

# General Conclusions

This thesis is one of a small number of investigations under controlled conditions of the interaction between inter-male competition and female choice. It also provides data that contribute to our understanding of how socially acquired information and individual experience interact to influence mate choice. Taken together the findings that sexually experienced female quail prefer less aggressive males, and that sexual experience is necessary for development of this preference are both unique and unexpected.

The thesis also contributes to a growing body of experimental data that are consistent with the hypothesis that females choosing a mate must weigh the benefits of consorting with dominant males against the costs of interacting with them (Persaud & Galef, 2003, in press). It demonstrates for the first time that female birds can identify video images of individual conspecific males and will respond to observation of such video images as they would respond to direct observation of male behavior.

The success of the experiment using video sequences of behavior described in Chapter 2 led me to attempt a further experiment in which I used video sequences to avoid problems associated with one-way glass in studying audience effects. I describe below the first of a proposed series of experiments the goal of which was to use video technology to determine whether interactions between males engaged in a fight and a female observing them influenced the outcome of the experiments described in Chapters 3, 4 and 5. As also discussed below, the ambiguous outcome of this first experiment led to termination of the entire series.

### 6.1 Audience effects

After viewing agonistic interactions between pairs of conspecific males, female Japanese quail (*Coturnix japonica*) prefer to affiliate with the less aggressive member of an interacting pair (Chapter 3). This result is consistent with the hypothesis that female quail use information acquired by observing inter-male aggression (see Chapter 1) to select a mate that is relatively unlikely to injure them (Chapter 3).

However, in the experiments reported in Chapter 3, I did not control for the possibility that a female's presence during a fight between a pair of males might cause changes in the behavior

of contesting males, possibly even influencing the outcome of their agonistic interaction. In fact, male quail peck somewhat more frequently during agonistic interactions when females are present (Chapter 3). Consequently, presence of an observing female might cause differences in the behavior of interacting males that influence which member of an interacting pair she comes to prefer.

### 6.1.1 Potential solutions

One way to determine whether presence of a female influences the outcome of agonistic interactions between males and subsequent female preference is to separate interacting males from observing females with either transparent or one-way glass. When one-way glass is interposed between a female and interacting males, the female has visual contact with the males while the males' view of the observing female is obscured. However, one-way glass is far from perfect. It produces a mirrored surface in which interacting males see themselves reflected, and one-way glass requires extensive use of very strong lighting to make it transparent in only one direction.

In Chapter 2, I demonstrated that female quail respond to video images as they respond to live conspecifics. Female quail identified individual males seen on video and, when making mate choices, used information garnered from observation of the behavior of males observed on video screens.

### 6.1.2 Methods and Results

The first experiment was undertaken to determine whether a female quail would prefer the less aggressive member of a pair of males that she had watched interact aggressively on video. I created a series of 6-min videotapes (for a detailed account of how video clips were filmed and edited, see Chapter 2) of pairs of males separated by either clear or opaque Plexiglas partitions so that pair members were either interacting or not interacting. In the experiment, I first presented a video clip showing either interacting or non-interacting pairs of males to a focal female, and then allowed her 10 min to choose between the pair of males she had seen on video. To determine which member of a pair of males that females saw not interacting in a video clip was more aggressive, I allowed them to interact while separated by a transparent Plexiglas partition after a female had observed the videotape of those males not interacting and had chosen between them.

I found that females that had observed a video clip of two males, separated by a transparent Plexiglas partition, and therefore interacting aggressively, spent less time with the more aggressive male than did females that had observed two males separated by an opaque partition and therefore standing passively near one another (Unpaired Student's  $t$  test:  $t_{16} = 2.31$ ;  $P < 0.05$ ; Fig. 6.1). This result was consistent with those reported in Chapter 3 suggesting that female quail prefer to affiliate with the less aggressive of a pair of males. The result also suggested that audience effects were not important in causing a female to prefer the less aggressive of two males she has watched interacting aggressively (see Chapter 1).

Although the results of the study of females watching males interact on television were consistent in some ways with the results I obtained when I allowed females to watch males

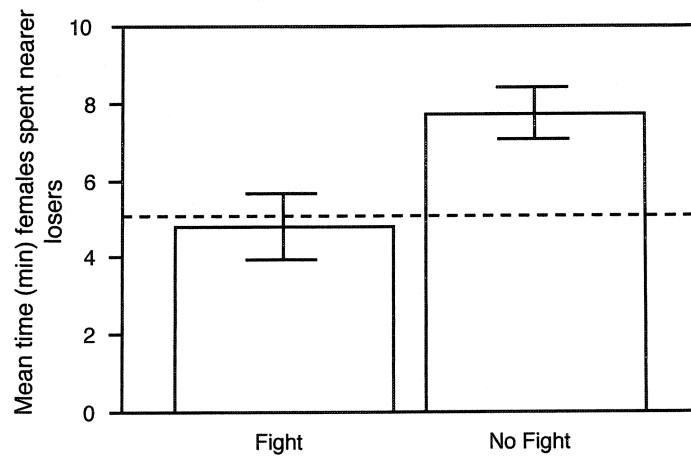


Figure 6.1: Mean ( $\pm$  SE) time during the choice phase that females spent closer to the member of a pair of males that was more aggressive during the fight phase females saw on video.

interact directly (Chapters 3, 4 and 5), there were some problems. In Chapter 3, I found that female quail preferred the less aggressive male, whereas females that did not observe interacting males were indifferent when choosing between more and less aggressive individuals. In contrast, when using video stimuli of the interacting males rather than live interacting males, I found that females were indifferent when choosing between males they had seen interacting in an aggressive manner (One-sample  $t$  test:  $t_{10} = 0.22$ ; *NS*; Fig. 6.1), and preferred the less aggressive member of a pair of male when the videotape they saw depicted non-interacting males (One-sample  $t$  test:  $t_6 = 4.17$ ;  $P < 0.01$ ; Fig. 6.1).

### 6.1.3 Discussion

It is not clear how to resolve the differences in the results of Chapters 3, 4 and 5 and the results of the experiment just described. Possibly, females use information acquired from observing video clips of mating males but not of fighting males. However, if females do not use information they acquired from video clips of interacting males, then subjects that saw males either interacting or not interacting on video should have behaved similarly, and they did not.

There was one major difference in the methods of the experiment described above and those I used in the experiment described in Chapter 3 that might explain their different outcomes. Although females in all relevant experiments observed an agonistic interaction between a pair of males before choosing between them, males depicted on video had interacted days before females saw the tapes and chose between them. Females that saw live males interacting chose between males that had interacted immediately before a female chose between them. Thus, male arousal as a result of involvement in an agonistic interaction at the time of female choice differed markedly between pairs of live and video-taped males. Possibly, the perceived threat to a female posed by winning males differs when males have or have not just completed an agonistic interaction. Such an explanation could be tested by either allowing or not allowing videotaped pairs of males to fight in private for a second time immediately before a female that had watched a videotape of them interacting aggressively chose between them.

## 6.2 Conflicting pressures acting on male and female quail

The experiments presented here have shown that female Japanese quail evaluate potential mates by observing them engage in aggressive interactions and prefer to affiliate with less aggressive males. These data are consistent with the view that males are subjected to conflicting selection pressures, one arising from the demands of inter-male competition for resources and the other arising from female sexual preferences. More aggressive males would be expected to be more successful in acquiring desirable feeding or nesting sites and in guarding mates, but less successful in acquiring mates. Female quail are forced to choose between aggressive males able to provide greater resources and less aggressive males that pose a lesser threat to females' somatic condition.

The data in this thesis suggest that, if female quail are able to indulge their mate preferences under natural conditions, selection might favor less aggressive males. However, domesticated male Japanese quail are highly aggressive animals, and feral quail are even more aggressive than their domesticated relatives (Nichols, 1991). Thus, in the competition between more and less aggressive male quail, more aggressive males appear to be winning. Either female quail are unable to rebuff the advances of more aggressive males or the direct and indirect benefits to females of mating with more aggressive males outweigh the phenotypic costs of being courted by them.



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