SOCIAL INFLUENCES ON MATE CHOICE

SOCIAL INFLUENCES ON MATE CHOICE IN JAPANESE QUAIL, *COTURNIX JAPONICA*

By

DAVID J. WHITE, B. A. (HONS)

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AUTHOR: David J. White, B. A. Hons (University of Western Ontario)

SUPERVISOR: Professor B. G. Galef, Jr.

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Abstract

Classical theories of how animals make mate choices have focused on each sex's inherited preferences for the other sex's traits or behaviours. The present thesis was undertaken to investigate how social factors play a role in determining an animal's choice of mate. In the series of experiments reported here, 'focal' female and male Japanese quail were given the opportunity to observe another quail (a 'model') of the same sex mating with a conspecific of the opposite sex (a 'target'). Results of experiments described in chapters 2 and 3 revealed that focal females: (1) displayed an increased tendency to affiliate with male targets that they had observed mating with model females, and (2) found a target male more attractive if he had been observed just standing near another female. In Chapter 4, social influences on male mate choice were investigated. Focal males: (1) exhibited a decrease in their preference for female targets that they had observed mating with model males, and (2) showed a decrease in preference for a female target only if she had been seen mating with or being courted by a model male, not simply standing near him. Finally, in chapter 5, it was determined that for quail of both sexes, affiliation time was a reliable predictor of focal subjects' actual choice of a mate. Taken together, these results are consistent with the hypothesis that females gain benefits from attending to the mate choices of other females, whereas for males there is a cost associated with mating with a female that had recently mated with another male.

Preface

This thesis is comprised of four papers (chapters 2 through 5) previously published in Animal Behaviour. Each paper was a collaborative effort co-authored by B. G. Galef, Jr. I was involved extensively in all aspects of each of the works, including formulating the experimental paradigm, creating the major research questions, conducting all experiments, and preparing manuscripts for publication.

To my father

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Chapter 1

INTRODUCTION

In this thesis I investigate how information acquired socially can influence animals' mate choice decisions. Mate choice, particularly female mate choice, has a long history in evolutionary biology (Darwin 1871; Wallace 1891; Cronin 1991). In classical mate choice models, however, researchers have ignored the possibility that social experience acquired in adulthood can modify heritable mate preferences. More recently, theoretical researchers have begun to take into account the possible impact of learning from others on animals' immediate mate choices. Empirical support for these new models, documenting the conditions and stimuli critical for social information to modify mate choice, is limited. Studies of free-living animals lack the control of variables necessary to exclude alternative explanations for concordance in mate selection, and few laboratory studies have found definitive effects of social factors on mate choice. Furthermore, the validity of many laboratory procedures used to measure mate choice has never been tested. In four published papers (chapters 2-5), I undertook a series of experiments to determine, under controlled laboratory conditions, exactly how information acquired socially could influence mate choices of female (chapters 2 and 3) and male (chapter 4) Japanese quail, *Coturnix japonica*. Finally, in chapter 5, I tested whether the laboratory preparation I used was a reliable predictor of sexual preference.

In this first chapter, I provide an introduction to the literature relevant to the important aspects of the thesis: mate choice by females, mate choice by males, and social influences on mate choice. First, I review theories of female mate choice and of social learning and discuss theoretical and empirical investigations undertaken to ascertain how social information might influence female mate choice, addressing fundamental issues and describing relevant investigations in both field and laboratory. I then extend the discussion to male mate choice. Next, I provide a review of past investigations into the natural history and mating behaviours of *Coturnix japonica*, my study species. I conclude with a brief description of the general protocol used in the 16 experiments that comprise chapters 2 through 5.

Female Mate Choice

As part of his theory of sexual selection, Darwin (1871) proposed that female mate choice could be a selective force. Non-random mate choice exercised by females, Darwin argued, could select male traits, if those traits affected the reproductive success of their bearers. Thus, if female preferences for some male trait led females to prefer to mate with certain males, those males would reproduce more frequently, even if the traits that increased males' attractiveness decreased their longevity. Indeed, work since Darwin's time has shown that females of many species do prefer males with characteristics that appear to interfere with survival (Andersson 1994; Andersson and Iwasa 1996; Bateson 1983b; Bradbury & Andersson 1987; Gould & Gould 1997; Jennions & Petrie 1997; Kirkpatrick 1987; Kirkpatrick & Ryan 1991), but the reasons why females should choose mates that are at risk have been actively debated.

Why be Choosy?

Darwin (1871) suggested that females had an aesthetic sense and desired beautiful, elaborately adorned males. This proposition, however, did not explain how such preferences might have evolved. For any model of mate choice to be informative, it must provide an explanation of how benefits of mate choice outweigh potential costs to individuals of being choosy. Such costs of mate choice include time and energy lost in search (Sullivan 1994), increased risk of predation during search or during mating (Travers & Sih 1991; Magnhagen 1991), aggressive responses of rejected males (Manson 1994), and metabolic demands of developing and maintaining the neural circuitry to make comparisons (Dawkins & Guilford 1996). Explanations for the existence of female mating preferences have focused on the benefits females accrue by being choosy.

Direct benefit models of female choice suggest that females gain immediate benefits by preferring particular types of males. By being choosy, females may: (1) acquire nutritious courtship meals from a potential suitor (Gwynne 1984), (2) choose a mate that will engage in parental duties (Downhower, Brown, Peterson & Staples 1983), (3) mate with a male that holds a territory rich in resources (Alatalo, Lundberg & Glynn 1986), or (4) mate with a high ranking male and thus reduce aggressive responses from other males (Horne & Ylönen 1996).

In mating systems where males provide no resources to females, few direct benefits of female choice exist. It has been argued that in such situations, females with preferences might gain benefits for their offspring. Such *indirect benefits* to a female may take several forms. Fisher (1930) proposed that by having preferences for males with specific traits, females could produce male offspring that would inherit the preferred trait and would, therefore, be particularly attractive to other females. These 'sexy sons' would gain reproductive advantage by bearing traits attractive to females even if those traits interfered with survival. Fisher's model provided a way in which female preferences could become linked genetically with male traits and produce 'runaway' selection for trait elaboration, until the sexual selection benefit of the elaborate trait was outweighed by the natural selection cost of the trait (see also O'Donald 1980).

Alternatively, female preferences could lead females to mate with males of high genetic quality, thus producing better-adapted offspring. Such 'good genes' models suggest that elaborate male traits are honest indicators of male quality (Zahavi 1975) so females can use traits to evaluate males' genes. Maintenance of additive genetic variance in populations where females consistently select males of highest genetic quality has been a problem for such models. It is generally proposed that genetic value is moderated by environmental variability (see Hamilton & Zuk 1982 for an example of host-parasite interactions maintaining genetic variance; see also Charlesworth 1988).

A third explanation for the evolution of female choice is that preferences are pleiotropic by-products of the sensory system of females. On sensory-bias models, females are sensitive to particular stimuli as a result of requirements in other functional contexts. For example, sensitivity to moving objects assists in prey detection in anolis lizards (Fleishman 1992), and selection could produce male traits that exploit such sensitivity in females (Arak & Enquist 1993; Basolo 1990; Ryan & Rand 1990; Stamp Dawkins & Guilford 1996).

Preference vs. Choice. One difficulty in studying functions of mate choice is that preference and choice are not synonymous terms. Female preferences bias females' responses to males bearing preferred traits. Female choice is the outcome of behaviour that can be influenced by mate preferences. However, in natural populations female preferences will not fully determine female mate choice. Female choice may be affected by other factors including, but not limited to search strategy, past mating experience, and random environmental events (Gibson & Langen 1996; Janetos 1980; Real 1990, 1991; Wagner 1998; Wiegman, Real, Capone & Ellner 1996).

Summary

Currently, there is no consensus about the critical functions favouring the evolution of mate choice. In fact, in vertebrates there are few data demonstrating that mate choice is actually adaptive (see Boake, 1986, 1998 for a research paradigm investigating this question in insects). Each model detailed above has strengths and weaknesses in dealing with existing empirical data on female choice (Kirkpatrick & Ryan 1991). There is, however, no theoretical reason to suppose that only one model is correct. In many instances, proposed models are complementary, not contradictory; different models could be correct for different species evolving under different ecological circumstances, or even for the same species at different times. Variation in choosiness among conspecifics within sexes and within individuals has begun to be investigated, but this research is in its infancy (Gross 1996; Jennions & Petrie 1997).

One commonality of classic models of the evolution of mate choice is the assumption that once reaching adulthood, females have inherent, unmodifiable preferences for male phenotypic traits and these preferences along with other factors internal to the female (such as sampling strategies) determine female mate choice. Relatively little research has been conducted on whether adult experience can modify inherited preferences.

Social Learning

Mechanisms that promote phenotypic plasticity can benefit organisms living in environments varying in temporal and spatial distribution of resources (Boyd & Richerson 1985). Learning allows individual animals to modify their behaviour in response to reinforcement contingencies, permitting them to exploit fluctuating environments efficiently. One dynamic component of an organism's environment is the presence of conspecifics. Many animals interact with their social environment on a daily basis, both when acquiring information about (Galef 1993) and when competing for (Lefebvre & Palameta 1988) resources. By learning from others, a naïve animal can potentially, at least, save the effort and avoid the costs of learning individually about its environment (Boyd & Richerson 1985). The social learner can thus rapidly produce a behavioural repertoire that is locally adaptive in novel or particularly harsh environments (Galef 1995). Investigations into mechanisms that promote social learning provide evidence of a variety of socially learned processes in diverse taxa including rodents (*Rattus norvegicus*; Galef & Wigmore 1983), birds (*Zonotrichia leucophrys*; Petrinovich 1988), primates (*Macaca mulatta*; Mineka & Cook, 1988), and fishes (*Poecilia reticulata*, Laland & Reader 1999).

Social learning can influence both the rates and the trajectories of evolution (Boyd & Richerson 1985; Laland, Richerson & Boyd 1996), permitting non-heritable factors to produce selection pressures on individuals, thus creating and maintaining between-population differences in behaviour (for laboratory examples see Aisner & Terkel 1992; Freeberg 1998; Galef & Allen 1995, Laland & Plotkin 1990). Studies of social influence on mate choice can cast light on gene-culture interactions, because behavioural traditions that modify mate choice can influence assortative mating and thus change gene frequencies within a population.

Social Learning and Female Mate Choice

Evidence is accruing suggesting that social information, whether acquired throughout development or even during a single mating season, can modify animals' mate choices.

In infancy. Learning about characteristics and behaviours of conspecifics in early stages of development can influence sexual preferences later in life. Such *sexual imprinting* has been used to explain: (1) species divergence, (2) sexual dimorphism, and (3) optimal outbreeding. The hypothesized mechanism is similar for all three of these diverse results; during a critical period in development, young animals learn from observation of parents or siblings critical features of their species, sex, or kin. When adult, animals use traits of others as cues: (1) to identify conspecifics, [individuals may prefer mates with species-specific traits, functioning to avoid hybridization (Kirkpatrick 1987)], (2) to discriminate males from females [females may prefer elaborate traits of males as different as possible from the traits of females (ten Cate & Bateson 1988; Weary, Guilford & Weisman 1993)], or (3) to choose a genetically compatible mate [individuals may choose as mates conspecifics that are different enough from themselves to avoid inbreeding, but similar enough not to break up adaptive gene complexes (Bateson 1978, 1982, 1983a)]. Theoretical models of sexual imprinting support ten Cate and Bateson's (1988) contention that asymmetrical mating preferences resulting from sexual imprinting may influence sexual selection of male characteristics (Laland 1994a).

Further, sexual imprinting could act as a barrier to gene flow among populations, increasing opportunities for speciation (Laland 1994a).

There is some empirical evidence that information gained through oblique or horizontal transmission (i.e. from unrelated conspecifics; Boyd & Richerson 1985) in infancy can influence mating preferences later in life. Gallagher (1976) exposed male Japanese quail chicks to either albino conspecifics or conspecifics with normal plumage. When given a choice, in adulthood, between albino females and females with normal plumage, males housed as chicks with albinos for the first 25 days post hatch copulated more frequently with albino females than with normal females, whereas males housed with albinos from 16 to 25 days post hatch were indifferent about the type of females with whom they copulated, and males housed as chicks with normal plumed conspecifics never mated with albino females in adulthood (see also Gallagher & Ash 1978). Clearly, learning about conspecifics in infancy can play a role in modifying mate preferences later in life.

Throughout development. Listening to the song of father in the nest (Mann & Slater 1994), or interacting with peers (West & King 1996), can provide reinforcements that shape male courtship song and produce different local song dialects. For example, juvenile male cowbirds, *Molothrus ater*, learn which songs are most effective in eliciting behavioural responses by singing to females before the breeding season starts. Then, in the breeding season, males sing only those songs to which females had previously responded positively (West & King 1988). Furthermore, juvenile males learn what songs not to sing by interacting with mature males. Mature males attack and kill juvenile males whose songs are most attractive to females (King & West 1983). Thus interacting with adults, juvenile males learn to use a repertoire of songs that are socially appropriate.

Into adulthood: Social interactions in the breeding season can also provide important information to animals making mate choice decisions. Animals sensitive to this public information may be able to modify their behaviour to maximize the probability of successfully reproducing. Evidence exists consistent with the hypothesis that females gain information about potential mates from sampling males in a breeding season (Real 1991) and observing male competitive interactions (Jennions & Petrie 1997). Also, evidence from both field and laboratory studies is accruing indicating that animals change their mate choices based on the mating behaviours of conspecifics. Theoretical modelers have begun to establish the impact that socially modified mate choice can have on sexual selection. It is these immediate changes to mating decisions based on information about the mating behaviours of others that will be the focus of the work in following chapters.

Social Mate Choice: A Framework

Pruett-Jones (1992) has distinguished two different ways in which the mate choices of an animal can be changed socially; animals can change their mate choice based on direct observation of the behaviour of others (*non-independent choice*) or as a byproduct of the behaviour of others (*independent choice*).

Independent choice: Following Pruett-Jones (1992), if a female makes an independent mate choice, then the conditional probability of her choice when she has information about the mate choices of other females is equal to her probability of choice based on her own assessment of males. In other words, under independent choice, a female's mate choice may be modified by social factors but her mate preferences remain unchanged. For example, female 'A' may engage in independent choice and still preferentially mate with a male due to her observation of his courtship display directed at female 'B'. In this case the male's increased attractiveness to female A is a result of her observation of his courtship display, which is a byproduct of the female B's presence. Nothing about the behaviour of female B is taken into account by female A when choosing a mate.

Non-independent choice: Females making non-independent mate choices mate with particular males based on the actions of other females, *per se* (Pruett-Jones 1992). To date, two major types of non-independent mate choice have been distinguished: *conspecific cueing* (or female aggregation), and *mate-choice copying*. While conspecific cueing and mate-choice copying produce similar behavioural responses, they differ in the types of information an observing female gains about a male.

Conspecific cueing (Keister 1979) refers to a female's tendency to attend to and move about with other females. Females may cluster into groups for a number of reasons including reduced risk of predation or increased food-finding efficiency. Conspecific cueing may increase the likelihood that a male who happens to be in the vicinity of a female group will gain more matings than he would if females were moving around independently. The increased success of the male, however, is a result of females' tendency to aggregate, not of females' preference for a particular male.

In *mate-choice copying*, the probability of a female choosing a male increases when she observes other females mating with him (Dugatkin 1996b; Pruett-Jones 1992). The important feature of mate-choice copying, distinguishing it from conspecific cueing, is that females gain information about and an increased preference for a male from observing the behaviour of other females.

Jennions and Petrie (1997) have criticized the distinction between mate-choice copying and conspecific cueing, arguing that there is no dichotomy. The proposed differences in the two models, they suggest, is a result of researchers' confusion between proximate and ultimate explanations of behaviour analogous to the distinction made in the past between passive and active mate choice (Parker 1983; Sullivan 1989, see also Kraak 1996). While it is true that conspecific cueing and mate-choice copying predict similar behavioural responses, and thus are difficult to separate in both the field and laboratory, there is a fundamental difference between the two explanations of behaviour; they have different implications for sexual selection.

Impact of Conspecific Cueing and Mate-Choice Copying on Sexual Selection

Non-independent mate choice can increase variance in male mating success by causing a few males to garner most copulations. Thus, both conspecific cueing and mate-choice copying can increase the opportunity for sexual selection (Wade & Pruett-Jones 1990). Where mate-choice copying differs from conspecific cueing is in the potential for females to modify their preferences through copying. Females using mate-choice copying as a strategy can learn about male behaviours and characteristics, whereas conspecific cueing does not provide females that opportunity. It should be noted, however, that there are few theoretical investigations of the evolutionary consequences of conspecific cueing. Conspecific cueing can influence male traits, for example, by selecting males that best monopolize harems (McComb & Clutton-Brock 1994).

While the impact of conspecific cueing on sexual selection has been understudied, the potential impact of mate-choice copying on sexual selection has been studied intensively. The influence of mate-choice copying on sexual selection depends on the underlying economics of why females copy the mate choice of others. Theoretical models consider two main non-mutually exclusive advantages (Pruett-Jones 1992). First, in situations where asymmetries exist in females' ability to determine high-quality males, naïve females could learn to choose high quality mates by viewing the mating behaviour of more experienced females (referred to as the *information asymmetry hypothesis*). Second, females viewing others mating can copy them, thus mating with a male of no worse quality than did the choosing female, and avoiding some costs of searching independently for their own mate (referred to as the *avoidance of search costs hypothesis*).

Gibson and Höglund (1992) argued that the influence of mate-choice copying on sexual selection would differ depending on the function mate-choice copying served. If females use mate-choice copying as a way of reducing costs of independently searching for a mate, then avoiding costs of search may trade-off against personally evaluating of the quality of males. Here, choice of low quality males could be maintained and could lead to a decrease in intensity of sexual selection on males. If, however, females use mate-choice copying as a strategy to increase their likelihood of choosing a high quality male, copying would reduce the number of errors in choosing quality males and intensity of sexual selection on males would increase. Furthermore, if male traits serve as reliable indicators of male quality, and females gain generalizable preferences for traits of males seen mating, then mate-choice copying can intensify sexual selection on male traits. Gibson and Höglund (1992) also suggest that mate-choice copying can generate unpredictable fads in the male characteristics females find attractive based on information cascades.

Many of the following models of mate-choice copying focus on the benefits of using such a strategy. For mate-choice copying to be favoured, however, these hypothesized benefits to females of copying must be high enough to outweigh potential costs. Potential costs associated with mate-choice copying strategy include aggression from other females (Kempenaers 1994), mating with a sperm-depleted male (Birkhead & Møller 1992), and increased risk of sexually transmitted disease (Sheldon 1993).

Models of Mate-Choice Copying

Losey et al. (1986) used game theory to investigate circumstances under which mate-choice copying could evolve as a mating strategy. They found frequency-dependent selection on a copying strategy in a population where some females were copiers and others were choosers, making mate choices independent of other females. On Losey et al.'s model, copying served as a beneficial strategy only when: (1) information asymmetries existed in females' abilities to choose high quality males, (2) fecundity was relatively low, and (3) costs of incorrect mate choice were high. Furthermore, opportunities for females to observe other females' mate choices had to be available, and the increased preference for a male seen mating had to last long enough for females to use social information when choosing a mate.

Dugatkin and Höglund (1995) modeled the evolution of mate-choice copying in lekking species. On their model, females used a copying strategy to increase their ability to assess the quality of males observed mating with other females. Time constraint on breeding opportunity, Dugatkin and Höglund argued, was the critical factor favouring evolution of mate-choice copying.

Wade and Pruett-Jones (1990) provided a model showing that female copying would always lead to increased variance in male mating success irrespective of the underlying economics of female preferences. Female copying increased variance in male mating success by enhancing the relative mating success of some males and diminishing that of others. Increasing variance in male mating success increases the opportunity for sexual selection. Wade and Pruett-Jones concluded that female mate-choice copying was a viable strategy because it is an adaptive alternative to random choice when there is either a cost to mate choice or evaluation of males is difficult. The Wade and Pruett-Jones (1990) model differs from models based on game theory, in which females have discreet mating strategies of either copying or choosing (Losey et al. 1986; Dugatkin & Höglund 1995 above). To the contrary, Wade and Pruett-Jones (1990) suggest that all females should have a tendency to copy.

Marks, Deutsch and Clutton-Brock (1994) argued against Wade and Pruett-Jones's (1990) hypothesis that copying always increases intensity of sexual selection. Marks et al. (1994) argued that stochastic events in the lifetime of animals have dramatic effects on female choice, and these effects, combined with female copying, could lead to an increased frequency of errors in mate choice (i.e. females mating with males of lower quality than they would have chosen independently). In these cases, the intensity of sexual selection would be lowered, not increased by female mate-choice copying. Marks et al.'s argument is, however, based on data from lekking ungulates whose behaviour is likely to be explained by conspecific cueing rather than by mate-choice copying. Mating with males in an area where other females are aggregating can reduce the opportunity for sexual selection of male traits below that available if females were to make independent mate choices. There have been no studies of the impact of stochastic events on species that use mate-choice copying, not conspecific cueing, as a mating strategy.

Stöhr (1998) modeled critical conditions under which mate-choice copying could evolve. Stöhr's model suggested that both asymmetries in the ability of females to choose high quality males and time available in the breeding season determine whether mate-choice copying is a beneficial strategy. On Stöhr's model, variance in male genetic quality was not an important determinant of the type of choice strategy females used.

Servedio and Kirkpatrick (1996) presented a model evaluating how a 'copying allele' could become fixed in a population. On their model, copying spreads in a population when it causes females to mate with males of high total lifetime fitness, even if there is no direct selection acting on the copying trait itself (e.g. avoiding search costs). As in Fisherian runaway selection, when females use copying to mate with high quality males, a genetic linkage disequilibrium can develop between the copying trait and phenotypic traits of high quality males.

Kirkpatrick and Dugatkin (1994) attempted to determine how copying could influence the intensity of sexual selection on male characteristics. They showed that unless preexisting female preferences had been established for a novel male trait, copying would reduce the likelihood that a novel trait would become fixed in a population. Kirkpatrick and Dugatkin agrued that because of the initially low frequency of the novel trait in a population, females would be more likely to view and copy females mating with a male that did not have the new trait. However, copying's effect on a novel trait that was independently preferred by females could rapidly fix the trait in a population. In this work, and in Servedio and Kirkpatrick's (1996) model, it is assumed that mate-choice copying leads not only to preferences for the particular male seen mating but also to preferences for traits he expresses. Thus males with traits similar in appearance to those of the male seen mating would be preferred. There is, however, no empirical evidence that mate-choice copying ever entails establishment of an altered preference for male traits as opposed to mere selection of a particular male.

Laland (1994b) provided a model with implications similar to Kirkpatrick and Dugatkin's (1994) and Servedio and Kirkpatrick's (1996) models. While Laland's (1994b) model was not designed to explore the implications of mate-choice copying, Laland noted that a culturally established and transmitted mating preference could provide selection pressure on a male trait that is transmitted genetically, even if that trait impairs the survival of the bearer. The trait can come to fixation in a population rapidly due to a female's culturally-dictated preference.

Empirical support

The above models, though in some cases contradictory, provide a basis to establish the potential import of social influences on mate choice. Empirically, however, few studies have been conducted that determine unambiguously whether social factors available to animals engaged in mate choice do affect choice. One common problem has been controlling for the many variables that may influence a female's choice behaviour. Particularly in field studies, it is difficult to determine why unanimity of mate choice occurs. If, for example, one male is found to be more successful than others, it is hard to determine whether all females independently found him most attractive, or whether the act of some females finding him attractive had an influence on other females. The most notable attempts to determine whether social influences on mate choice occur are discussed below.

Field Studies. Sticklebacks: Ridley and Rechten (1981) showed that male three-spined sticklebacks, *Gasterosteus aculeatus* that had recently mated were particularly successful in attracting other females to their nests. Ridley and Rechten suggested that females preferentially spawned in nests already containing eggs so their offspring would be subject to lower risk of predation. Jamieson and Colgan (1989) conducted a field study on sticklebacks to investigate this egg dilution hypothesis. While they did find that females preferentially laid eggs in nests that already contained eggs, they found no evidence that females actively chose nests because there were other eggs in them. Instead Jamieson and Colgan found that males with eggs in their nests courted more vigorously. Jamieson and Colgan suggested that eggs had a priming effect on the reproductive behaviour of males, which in turn made them more attractive to females.

Goldschmidt, Bakker and Feuth-De Bruijn (1993) determined whether females sticklebacks preferred males that had eggs in their nests or the nests themselves. They found that females showed no preference for males with eggs in their nests when they could not see the eggs, suggesting that it was the eggs themselves that females preferred when choosing a male with whom to mate. Jamieson (1995) and Patriquin-Meldrum and Godin (1998) attempted to determine whether females were depositing eggs in nests that already contained eggs because they were copying the mate choices of other females, but found little evidence of mate-choice copying.

In summary, social influence on mate choice in sticklebacks has been considered independent choice based on Pruett-Jones's (1992) definition since the observation of another female is not required. Such an effect on mate choice behaviour, however, does influence the opportunity for sexual selection, increasing variance in males' reproductive success. Thus the distinction between independent and non-independent mate choice, at least here, may not be a completely heuristic one since this case of independent choice has evolutionary implications very similar to non-independent choice.

Isopodia: Shuster and Wade (1991) suggested that female marine isopod crustaceans, *Paracerceis sculpta*, copy the mate choice of others. In the breeding season, female isopods aggregate in breeding areas and are fertilized by a resident male. Since Shuster and Wade were interested in understanding the influence of female non-independent choice behaviour on the opportunity for sexual selection in males of this species, they made no distinction between conspecific cueing and mate-choice copying. The behaviour of these female isopods, however, seems to be more easily explained by conspecific cueing because females group together primarily to avoid predation. There is no evidence that the female groups take into account the traits of the resident male when choosing a breeding area.

Lekking species: Leks are breeding season aggregations of displaying males in areas that females visit to breed. By definition, in lekking species females and males have no other extensive contact during the breeding season. Males provide no parental care, and thus females receive no direct benefits of mate choice. In most leks sexual dimorphism is pronounced, a large skew in male reproductive success exists, and females seem to display mate choice behaviour (Höglund & Alatalo 1995). The opportunity to observe other females' mate choices is available, and the skew in male reproductive success is difficult to explain based on independent choice models (Bradbury, Vehrencamp & Gibson 1991; Pomiankowski 1990). Field researchers, however, have not been able to demonstrate conclusively that mate-choice copying exists on leks, again due to researchers' inability to control enough variables to rule out other possibilities (Bradbury & Gibson 1983).

Lill (1974) conducted one of the first field studies that suggested that females might be copying the mate choice of others. In his study of lekking white-bearded manakins, *Manacus manacus trinitatis*, he noted that the spatial and temporal distribution of matings seemed non-independent. Lill suggested that these trends imply that females may be visiting a lek and observing others make mate choices, then returning and mating with the males others had chosen. He made no direct tests of this proposition.

Gibson, Bradbury & Vehrencamp (1991) found that in lekking sage grouse, *Centrocercus urophasianus*, the temporal distribution of matings by males suggested that females might be copying the mate choice of others. As the number of female matings per day increased, unanimity of female choice increased. Unanimity of female choice of males did not correlate with variance of any particular male traits they measured. Additionally, when comparing individual matings to matings that occurred in groups, success of particular males did not correlate, suggesting that if copying was occurring it was leading females to mate with males they might not have chosen independently. While mate choice copying could account for Gibson et al.'s findings, other explanations, such as conspecific cueing and increased courtship display of mated males, could not be excluded.

In their field study of black grouse, *Tetrao tetrix*, Höglund, Alatalo and Lundberg (1990) found that females entered lekking areas together, observed other females mating, then later returned to mate. As did Lill (1974), Höglund et al. suggested that mate-choice copying may be occurring, but concluded that controlled experiments were required to discriminate among several closely related hypotheses. Höglund, Alatalo, Gibson and Lundberg (1995) attempted to manipulate social influences on male black grouse experimentally. They found that the females visited in greater numbers those male territories where the resident males had the opportunity to court and mate with four taxidermic dummy females. Males received no increased visitation from females when they could court but not mate with two dummies, nor when there were three duck decoy dummies on the territories. Höglund et al. (1995) suggested that mate-choice copying was a reasonable mechanism explaining their results. Why they used different numbers of decoys across conditions, however, was not explained, which makes interpretation difficult.

Fiske, Kålås and Sæther (1996) investigated how the distribution of matings on a lek of great snipe, *Gallinago media*, compared to a mathematical model of mating distributions under mate-choice copying. Because simulations from their model revealed that the proportion of copiers to choosers was not significantly different from zero, they concluded that mate-choice copying probably did not account for much of the variance in male mating success in great snipe.

Clutton-Brock, Hiraiwa-Hasegawa, and Robertson (1989) undertook a study of lekking fallow deer, *Dama dama*, to determine whether territories or the males on those territories were important to females making mate choices. They experimentally moved males around territories and measured mating success of the displaced bucks. They found that successful males remained successful when moved to other territories, and that the most important factor affecting female choice was the number of females in a male's harem. To determine whether the skew in male reproductive success was due to mate-choice copying or conspecific cueing, Clutton-Brock and McComb (1993) and McComb and Clutton-Brock (1994) conducted experiments using a corral system in which females could observe males in confined areas with or without females. Females preferred areas where males and females were housed together, but also preferred areas where groups of other females were held. Taken together, their results indicate that females tend to aggregate and to move around in groups irrespective of males. Males that could defend areas that females frequented increased their reproductive success.

Further evidence of conspecific cueing in lekking ungulates comes from the Uganda kob, *Kobus kob thomasi*, and the Kafue lechwe, *Kobus kafuensis*. Deutsch and Nefdt (1992) exchanged soil samples from territories that held males that were either successful or unsuccessful in obtaining females. As a result, males on formerly unsuccessful territories became more successful. Deutsch and Nefdt suggested that females were attracted to the urine of other females. Thus in lekking ungulates, females showed both independent choice of mates (Clutton-Brock et al. 1989) and conspecific cueing (Deutch & Nefdt 1992; McComb & Clutton-Brock 1994). Mate-choice copying was never systematically observed.

Laboratory studies. Laboratory experiments designed specifically to investigate mate-choice copying have met with limited success. Slagsvold and Viljurgrein (1999) found no evidence that female pied flycatchers, *Ficedula hypoleuca*, copied other females' mate choices. Even though most females showed consistency in preference for particular males, females independently preferred those males that courted most vigorously. This study used female nest building near particular males as a measure of female's sexual preference for those males. Whether this measure is a valid indicator of female preference remains untested.

Schlupp, Marler and Ryan (1994) studied mate-choice copying in poeciliid mollies under controlled laboratory conditions. Amazon mollies, *P. formosa*, are female gynogens that require sperm from male sailfin mollies, *P. latipinna*, to reproduce. Schlupp et al. hypothesized that mate-choice copying could provide male sailfin mollies with enhanced reproductive success by mating with heterospecific Amazon mollies due to female sailfin mollies increasing their preferences for males seen mating with Amazon mollies. Schlupp et al. provided a female sailfin molly with the opportunity to view two conspecific males at either end of an aquarium. Both males could see and court an Amazon molly, but because an opaque barrier was present on one side of the aquarium, the observing sailfin female could see an Amazon molly interact with only one of the two males. When subsequently given the opportunity to swim near the two males, the observing female spent more time near the male that she had seen with a female Amazon molly. Schlupp et al. controlled for female consistency of choice across trials and for female preferences to school with greater numbers of fish, and concluded that only mate-choice copying could account for their results.

Grant and Green (1996) have shown in Japanese medaka, *Oryzias latipes*, that females would remain near a male that had been observed to spawn with another female rather than near a male paired with a female that had spawned in the past, and therefore was not ready to spawn again. In a similarly designed experiment, Howard, Martens, Innis, Drnevich and Hale (1998) could not replicate this mate-choice copying result in Japanese medaka. Their protocol was less rigidly controlled than that of Grant and Green (1996), so differences in experimental design might account for the discrepant findings.

Most evidence for mate copying comes from the extensive work of Dugatkin and collaborators on Trinidadian guppies. Dugatkin (1992) gave 'focal' female guppies the opportunity to view two males in end chambers of an aquarium. Dugatkin found that significantly more focal females than would have been expected by chance spent the majority of their time near a male that had been observed courting a second 'model' female. Dugatkin went on to determine whether females were merely schooling in areas where there were greater numbers of fish, or whether females were being influenced by the male's increased courtship display. His series of experiments provided evidence that, of the above explanations, only mate-choice copying could be used to explain all observed results.

Dugatkin and Godin (1992) found that social influence was strong enough to reverse a preference for an initially preferred male when the non-preferred male was seen mating with another female. However, researchers attempting to replicate Dugatkin's work with either store bought guppies (Lafleur, Lozano & Sclafani 1997) or guppies from a feral population in Durban, South Africa (Brooks 1996), as opposed to first generation descendants of a wild population from the Quaré and Turure Rivers in Trinidad, failed to yield evidence of female mate-choice copying.

As is apparent, empirical evidence of mate-choice copying is limited. Few studies have produced unambiguous evidence of mate-choice copying, and even fewer explore the underlying economics of mate-choice copying. Using the paradigm for mate choice in guppies described above, Dugatkin and collaborators have attempted to distinguish between the information asymmetry hypothesis and the avoidance of search costs hypothesis.

Dugatkin and Godin (1993) investigated the intensity of mate-choice copying among guppies of different ages. They reasoned that if mate-choice copying were used by naïve females to choose quality mates, then younger females would benefit from copying older, more experienced, females more than older females would benefit from copying younger females. They found that smaller (assumed to be younger) females copied the mate choices of larger (assumed to be older) female models more readily than larger females copied the mate choices of smaller females.

Briggs, Godin and Dugatkin (1996) attempted to increase costs associated with mate choice by having female guppies make mate choices while a predatory fish was present in a nearby aquarium. They found females spent less time near brightly coloured males when: (1) a predator was present or (2) given the opportunity to copy another female's choice of the less brightly coloured of two males whether a predator was present or not. Briggs et al. suggested that these results might be explained either as females tending to choose less brightly coloured males in the presence of a predator or by mate-choice copying irrespective of the presence of a predator. Because Briggs et al. simultaneously tested preferences for brightness and for mate-choice copying, interpretation of the influence of predation on mate-choice copying is difficult.

Dugatkin and Godin (1998) attempted to manipulate costs associated with mate searching, this time by changing female hunger levels. They reasoned that a cost associated with searching for mates is lost foraging time. Thus, a food-deprived female should be more likely to copy another female's mate choice and save time searching for a mate in order to spend more time foraging. Contrary to expectation, food-deprived females were less likely to copy. Dugatkin and Godin stated that this finding was not due to the lack of motivation to mate in food-deprived females because both well fed and food-deprived females spent similar time near males during testing. Whether time spent near a male is a valid indicator of sexual motivation to mate was not tested.

Other studies have shown that manipulating the costs of searching for a mate can have an influence on mate choice behaviour (Slagsvold, Lifjeld, Stenmark & Breiehagen 1988). There are, however, no studies that have shown that search costs have any influence on mate-choice copying. In addition, there is little evidence that there are high costs of search on leks. To the contrary, spatial clustering of males on leks suggests that search costs are low. Reynolds and Gross (1990) and Gibson and Bachman (1992) both report less than one percent daily energy expenditure due to searching. Many theories of the evolution of lekking even implicate as a benefit to females the reduced cost of search on leks (Höglund & Alatalo 1995). Höglund and Alatalo also reported very low predation risks on leks. On many leks there may, however, be limited time in a breeding season when fertilization can take place (Höglund & Alatalo 1995).

Patriquin-Meldrum and Godin (1998) suggested that mate-choice copying would be expected where there is little variability in male secondary sex characteristics, making independent assessment of male quality is difficult (see also Wade & Pruett-Jones 1990). This suggestion has not been well investigated, although recent studies with results that are somewhat applicable to this contention suggest that when it is easy to discriminate between males, social information is not used. For example, Witte and Ryan (1998) found that sailfin molly females would not reverse their mate preferences for a male seen with another female if that male was substantially smaller (on average less than 6.5 mm) than the other male in the choice test. Similarly, Dugatkin (1996a) found that female guppies only copied another female's mate choice when the two males did not differ by more than 24% of total orange body colour. When females had the opportunity to choose between two males differing by more than 40% of total orange body colour, females always chose the more orange coloured male, irrespective of social influences of seeing another female mate with the less orange coloured male. If, however, females could observe two different females choose the dramatically less orange coloured male, they would reverse their preference (Dugatkin 1998). Dugatkin (1996a) discusses these results as evidence of the relative strength of cultural and genetic factors on mate choice.

Galef and Whiskin (1998) conducted a study on limitations on the ability of social information to influence the dietary preferences of rats either fed a very palatable diet or a very unpalatable diet. Their results, along with the results pertaining to limitations on social influences of mate choice discussed above, suggest a general rule that large differences in the response of naïve individuals to two stimuli are correlated with reduced social induction of preference for one of those stimuli (see also Galef 1995). While this limitation on the effect of social information does not help to distinguish between the information-asymmetry and avoidance-of-search-costs hypotheses, it does suggest that mate-choice copying is more likely in populations when variability of male traits is low.

In sum, there is little empirical evidence conclusively establishing whether mate-choice copying occurs. Furthermore there is not a consensus on the purpose mate-choice copying serves if it does occur. Some support exists for the two main explanations for the benefits of mate-choice copying, either increasing the accuracy of naïve females learning to choose quality mates (Losey et al. 1986; Dugatkin & Höglund 1995; Servedio & Kirkpatrick 1996; Dugatkin & Godin 1993) or decreasing costs of independent search (Dugatkin & Höglund 1995; Wade & Pruett-Jones 1990; Stöhr 1998). However, no empirical data unambiguously support the avoidance-of-search-costs hypothesis.

Problems with Previous Investigations

A major problem with studies of mate choice pertains to the laboratory testing paradigm most often used. Mate choice is only of evolutionary interest if male and/or female reproductive success is changed as a result of their mate choice behaviour. Many studies of mate choice use affiliation time as a surrogate for mating preferences in order to control for factors such as intra- or intersexual dominance that may influence assortative mating. That affiliation time reliably predicts mate choice is an untested assumption in a variety of species where this type of procedure is common (see chapter 5). Other than for mate choice purposes, for example, females could avoid being near highly aggressive males (Krupa, Leopold & Sih 1990).

Additionally, search strategies used by females may influence which male a female chooses in any given experiment. Different search strategies can lead to female choice of different males, sometimes irrespective of male quality (Janetos 1980; Real 1990). Real (1990) also indicated that a female might prefer one male in an experiment, but not show repeatable preferences for him upon re-testing. Because repeatability is a measure of variability in female mate choice, it can provide an estimate of heritability of female preferences. If females do not show repeatable preferences for males, there can be no heritable component of female preferences (Falconer 1981; Boake 1989; Brooks 1996). Few researchers have studied repeatability of mate choice (Godin & Dugatkin 1995; Boake 1998;

Møller 1994) and these studies do not necessarily bear upon repeatability of female preferences.

In summary, there are a number of evolutionarily important effects that social influences may have on mate choice. In attempting to study them, however, researchers must take into account the fact that mate choice is an important selective force if and only if females reliably choose males and mate discriminatively with them. These factors remain untested assumptions in great numbers of laboratory studies of mate choice.

Male Mate Choice

Male mate choice has rarely been studied. The common notion that the sex incurring the preponderance of costs of reproduction will be the limiting resource, and thus will be the sex that is most choosy (Trivers 1972, 1985), has led the majority of researchers on assortative mating to focus on female choice and male intrasexual competition. It is true that in most species males do not incur the majority of costs of reproduction, and it is also true that as requirements of paternal care increase, costs for males of reproductive failure also increase. However, even in species that do not provide paternal care, males may incur a significant cost of any particular episode of reproductive failure.

In mating systems where there is variability in male mating success, a major component of reproductive success for males is determined by fertilizations achieved per unit time invested (Andersson 1994). Males can incur opportunity costs by spending too much time on any mating opportunity or by engaging in mating when fertilization is unlikely. As skew in male mating success increases, so does the intensity of sexual selection on males (Wade & Pruett-Jones 1990). It is plausible then that males have been subjected to strong selection pressure to behave so as to maximize their likelihood of fertilization during any given mating opportunity. In general, males should behave in a choosy manner in any species in which: (1) males have the opportunity to mate with more than one female, (2) there is predictable variation in the fecundity of females, or (3) there is predictable variation in the fertilizability of females (Andersson 1994). There is, in fact, evidence that males do behave in a choosy manner when making mate choices, for example in birds (Clayton 1987), reptiles (Tokarz 1992), fishes (Grant, Casey, Bryant & Shahsavarani 1995) and mammals (Schwagmeyer & Parker 1990).

One example showing that males can attend to cues that predict probability of successful fertilization when making mate choice decisions comes from a laboratory investigation of male mate choice in fish. Grant et al. (1995) found that male Japanese medaka, a species in which males contribute no parental investment, show mating preferences for females that are larger than average. Larger females are more fecund than smaller ones, and males that mate with larger females achieve a reproductive advantage by producing more fry.

Social Influences on Male Mate Choice

The behaviour of males in response to social information about females could vary depending on the purpose such information serves. Models of partner choice (Dugatkin & Sih 1995) and territory settlement (Gibson 1992) suggest that males can benefit by being near other males that are attractive to females. By being near successful males, other males can use alternative mating strategies (Reynolds, Gross & Coombs 1993) to steal some reproductive opportunities from females attracted to the successful males. Alternatively, in some situations, males may be more successful by avoiding other males. In many species if two males mate with a female within a short amount of time, the first male will fertilize the majority of that female's eggs (e.g. Birkhead 1996; Birkhead & Møller 1992). Consequently, one way to predict probability of fertilizing a female is to attend to her recent mating history. If in the recent past a female had been observed to mate with another male, the likelihood of her being fertilized by the observing male would be low and avoiding mating with a female seen with another male might be the best reproductive strategy for an observing male. For example, Schwagmeyer and Parker (1990) showed that male thirteen-lined ground squirrels, *Spermophilus tridecemlineatus*, avoid copulating with females that had copulated with another male. Using a model of behaviour dictated by sperm competition, they predicted 73% of observed male rejections of females on the basis of females' past mating behaviour.

Erickson and Zenone (1976) showed that male ring doves, *Streptopelia risoria*, directed less courtship behaviour and more aggressive behaviour toward females displaying behaviours indicating that they were in advanced stages of breeding with another male. Erickson and Zenone suggested that this behavioural reaction by males might be a mechanism that reduced their likelihood of being cuckolded.

There are, however, few laboratory studies concerned with whether males use information gained from observing other males' behaviour to influence their immediate mate choice. An experiment by Schlupp and Ryan (1997) showed that male sailfin mollies copy the mate choice of other males. Schlupp and Ryan suggested that males may benefit from mate-choice copying because attending to past reproductive behaviour of females can assist them in determining whether females are in breeding condition. There have been no studies of mate-choice copying by males in species with mating systems more common than the gynogenetic system of sailfin and Amazon mollies.

Social Influences on Mate Choices of Females and Males

To the extent that females and males both benefit from information acquired from their social environments, I proposed that both sexes would attend to social information when making mating decisions. To the extent that the interests of the sexes differ with respect to mating, I proposed that males and females would use social information differently in learning about a potential mate's quality.

Females in species acquiring few direct benefits from mates may gain indirect benefits by choosing as a mate a male that had been observed with another female, while males may benefit from avoiding a female that had been observed with another male. To test these hypotheses, I undertook a series of laboratory experiments to investigate the role information acquired socially could have on mate choice in Japanese quail, *Coturnix japonica.*

Coturnix japonica

There has been debate on the taxonomic status of the Japanese quail. Initially considered a subspecies of the common quail, *Coturnix coturnix*, the Japanese quail was given the designation *Coturnix coturnix japonica.* More recently, however, due to differences in vocalizations, sympatry, and hybrid inviability, it has been considered a distinct species *Coturnix japonica* (Mills, Crawford, Domjan & Faure 1997). In chapters 2 and 3, I use the older designation and change to the newer designation for chapters 4 and 5.

The Japanese quail is well-suited for laboratory investigations of mating behaviour. It has been used extensively in the past for studies of hormonal influences on sexual behaviour (Watson & Adkins-Regan 1989), studies on stimulus control of sexual behaviour (Domjan 1992; Gutierez & Domjan 1997; Hilliard, Nguyen & Domjan 1997; Köksal & Domjan 1998), and in studies of mate choice (Bateson 1978, 1982, 1983a).

Natural History...?

The Japanese quail is a terrestrial bird native to Japan, China, Korea and Indochina and was introduced to Hawaii in 1921 (Mills et al. 1997), where it has established a small feral population (Nichols 1991). Unfortunately, little is known about the natural history of this species. The quail's preferred habitat of grasslands, croplands, riversides, alpine meadows and grass steppes, their small size, secretive habits and aposematic colouration make them difficult to study in the wild (Nichols 1991), which may account for the few ethograms available.

The species was domesticated in Japan in the 11th century originally for song, then for meat and egg production (Mills et al. 1997). The majority of knowledge about Japanese quail comes from this domesticated stock and from field studies on the closely related common quail. Reports suggest that wild Japanese quail still exist in parts of Japan and in Eastern Asia as far west as India, but their numbers are dramatically decreasing (Nichols 1991).

The species is sexually dimorphic in size and colouration, with males of the common strain being slightly smaller than females and having rusty red breast plumage. Females have a more speckled brown colouration on their breast feathers (although several mutations of feather colour variations exist for both sexes; Cheng & Kimura 1990). Both female and male quail can discriminate the sex of conspecifics visually (Domjan & Hall 1986a). The head and neck regions of quail hold most of their sexually dimorphic features and are the most salient stimuli to the opposite sex (Domjan & Nash 1988; Domjan Green & North 1989).

Both sexes call; males make a loud guttural 'coturnix' call while females make a quieter 'cricket' call (Wetherbee 1961). The function of these calls is not clear, but some researchers have suggested that they assist in individual mate recognition and facilitation of pair-bonding (Guyomarc'h, Aupiais & Guyomarc'h 1998).

Japanese quail become sexually mature at a young age (approximately 42 days; Cooper 1987) and can be maintained in breeding status by keeping them throughout the year on long photoperiods (Cooper 1987). Parental behaviour has not been well studied in the domesticated strain because they do not readily engage in any sort of parental behaviour in most housing situations. The proper conditions, however, will elicit parental behaviour (Hess, Petrovich & Goodwin 1976; Nichols 1991). Males never engage in any parental duties other than to sit near an incubating female and defend her from the aggressive mating attempts of other males (Nichols 1991).

Mating System and Behaviour

Male sexual behaviour is forceful and aggressive. Males will approach females (and stimuli associated with females) and repeatedly attempt to mate with them in almost any environment. Females display less obvious forms of courtship behaviour, including remaining near a male, crouching, and pecking the ground near a male (Nichols 1991). Female sexual receptivity varies across the day, peaking 11 to 13 hr after light onset (Delville, Sulon & Balthazart 1986). Copulation consists of a rapid sequence of actions in which the male approaches, grabs the head of the female, mounts, and makes cloacal contact with her. Gamete exchange can be completed rapidly depending on female receptivity (Adkins-Regan 1995). A single brief insemination can fertilize, on average, 75 percent of a female's clutch (Adkins-Regan 1995).

Both sexes play an active role in mate choice (Nichols 1991). Male quail pursue and attempt to mount preferred females and remain near mates (Domjan and Hall 1986b). Females can either remain near a preferred male or flee and hide from an aggressive male to avoid copulation. Males can force copulations upon females, but unreceptive females are less likely to be fertilized (Adkins-Regan 1995). Females can expel male sperm but the effect of sperm expulsion on fertilization is not clear (Adkins-Regan 1995). Males produce a foamy substance from their proctodeal gland. This foam may function to reduce passive sperm loss in the female by maintaining sperm in the oviduct (Atkins-Regan 1999; Birkhead & Møller 1992), but currently there exists no consensus on the foam's function (Adkins-Regan 1999; Cheng, Hickman & Nichols 1989; Cheng, McIntyre & Hickman 1989; Domjan 1987).

Debate exists about the mating system of Japanese quail. Some researchers have considered them monogamous because they pair-bond and have been known to flush in pairs (Weatherbee 1961). Other studies suggest that they are more likely to be polygamous. Field studies investigating the mating system of the common quail revealed some degree of polygamy. In one recent field study, 72 percent of females switched mates at least once over a breeding season

(Rodrigo-Rueda, Rodríguez-Teijeiro, Puigcerver & Gallego 1997). In feral and domesticated Japanese quail, Nichols (1991) reported cases of mate switching during the breeding season and of individuals engaging in extra-pair copulations. Domjan & Hall (1986b) suggested that the Japanese quail mating system falls near polygyny because: (1) males do not show parental behaviour (Nichols 1991), (2) males engage in mate guarding (Domjan & Hall 1986b), and (3) novel females can induce increased sexual response from males (Domjan & Kurth 1986).

In summary, *Coturnix japonica* has characteristics that make it an excellent model species for experiments studying social influences on mate choice: (1) both sexes have some control of mate choice, (2) there seems to be little variability in plumage and behaviour among same sex individuals, (3) evidence suggests that quail can attend to and use social information in other contexts (Akins & Zentall 1996), (4) there is extensive literature on their sexual behaviour, (5) they will mate in any environment, and (6) they are hardy and easy to maintain under laboratory conditions.

General Protocol

All experiments used the same methods designed to: (1) isolate the role of choice behaviour from intrasexual competition or intersexual dominance in assortative mating, (2) use each choosing animal as its own control to determine both independent mate choice and the influence social factors could have on that choice, and (3) determine the proximal mechanisms critical for social factors to moderate mate choice decisions. The general procedure for each experiment consisted of three phases: a pretest, an observation phase, and a post-test. During the pretest, a 'focal' subject had the opportunity to affiliate with two opposite sex conspecific 'targets' confined at either end of a test chamber. In the observation phase, the focal subject could view a same-sex conspecific 'model' interact with one of the two targets. Finally, in the post-test the focal subject could once again affiliate with the two targets. I measured the change from pretest to post-test in the time focal subjects spent near each target, one of which had been seen with a model during observation phase.

I investigated how social information impacted female preferences for male targets (chapter 2) and distinguished the critical stimuli required to influence a female's preference (chapter 3). These experiments were designed to isolate the mechanisms involved in modifying the female's behaviour, so as to distinguish among the different models of independent and non-independent mate choice. I then investigated whether social information had an impact on male mate choice and determined the stimuli that were critical in moderating males' behaviour (chapter 4). Finally, I conducted a series of experiments to determine whether affiliation time is a valid and reliable measure of sexual preference (chapter 5).

Chapter 2

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

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BENNETT G. GALEF, JR & DAVID J. WHITE

Department of Psychology, McMaster University

Abstract

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

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

Although field data are often consistent with the hypothesis that female birds copy one another's choices of males, it is difficult, under field conditions, to exclude alternative explanations for observed concordance in female selection of mates. For example, some males may simply be more attractive to females or occupy more attractive territories than do their competitors. Or, a tendency of females to move about in groups (Pruett-Jones 1992), rather than mate-choice copying *per se*, might be responsible for observed differences in the mating success of males in lekking species (Clutton-Brock & McComb 1993). Alternatively, engaging in mating behaviour may change the appearance or behaviour of males making them more attractive to females (Goldschmidt et al. 1993).

The strongest experimental evidence of mate-choice copying has been provided by Dugatkin and co-workers using guppies, *Poecilia reticulata*, as subjects. In a series of experiments, Dugatkin (1992) carried out a series of experiments in which he offered a confined female guppy (a 'focal' female) the opportunity to observe two confined males, one of which was courting a second female (the 'model' female). Shortly after the model female was removed from the vicinity of the male that had been courting her, the focal female was released and allowed to choose between males. Focal females spent more time near a male that they had seen courting than near a male that they had seen alone, even if the locations of the two males were reversed before a focal female was released to choose between them. In subsequent studies particularly relevant to the experiments reported here, Dugatkin and his colleagues provided evidence that the tendency of female guppies to copy the mate choices of others was sufficiently powerful to reverse prior preferences for one male over another (Dugatkin & Godin 1992; Dugatkin 1996).

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

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

General Methods

Subjects

Ten male and 10 female Japanese quail acquired from a commercial breeder (Speck's Poultry Farm, Vineland, Ontario) at 48 days of age served as subjects in all four of the experiments reported here. After we transported subjects to the laboratory, we placed them in individual, stainless-steel cages, (45.7 x 61.0 x 40.6 cm), and gave them ad libitum access to water and Purina Game Bird Startena 5419 (Ralston-Purina Canada, Woodstock, Ontario).

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

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

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

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

Apparatus

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

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

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

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

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

Procedure

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

Pre-test

To begin an experiment, we placed a sexually proven male quail in each of the end chambers of the apparatus and a focal female in the holding cage in the centre of the apparatus and left them undisturbed for 30 s. We then raised the holding cage approximately 15 cm, allowing the focal female to move into the larger enclosure.

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

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

Observation

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

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

Post-test

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

Inter-observer reliability

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

Testing schedule

To ensure that we did not repeatedly use the same males and females, before beginning each experiment, we randomly assigned two females to each of the 28 combinations of males that we could create using our eight sexually active male subjects. We then randomly assigned one of the two females in each quartet to serve as a focal female and the other to serve as a model female within that quartet.

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

EXPERIMENT 1: EFFECTS OF OBSERVATION ON CHOICE

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

Methods

Subjects

We randomly assigned the 28 quartets of quail to experimental and control groups (N = 14 quartets each). We discarded data from three quartets when non-preferred males failed to mount the model female placed with them during the observation phase. All other non-preferred males vigorously courted and copulated with any females to whom they were given access. We also lost the data from an additional quartet due to equipment failure.

Procedure

At the end of the pre-test, we placed a model female in the end chamber of the enclosure containing the non-preferred male of each focal female that we had randomly assigned to the experimental condition. We treated each focal female that we had assigned to the control condition exactly as we treated focal females assigned to the experimental condition, except that we did not place a model female in the apparatus during the observation phase.

Results and Discussion

Pre-test

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

Post-test

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

The change between pre-test and post-test in amount of time spent by focal females assigned to the experimental group with their respective non-preferred males was significantly greater than was the change between pre-test and post-test in the time spent with non-preferred males by focal females assigned to the control group (Mann-Whitney U-test, $U = 24$, $N_1 = 13$, $N_2 = 11$, $P < 0.01$; Fig 2).

Also consistent with the hypothesis that focal females increased their tendency to affiliate with males after they had seen those males mate was the observation that 8 of 11 experimental focal females spent more than half of the 10-min post-test phase on the side of the cage containing the male that they had not preferred during the pre-test, but none of the 13 control focal females showed a comparable change in preference between pre-test and post-test (Fisher's exact test, $P < 0.0002$).

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

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

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

Methods

Subjects and Procedure

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

Results and Discussion

Pre-test

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

Post-test

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

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

There was a significantly greater increase in the time spent with a male seen mating when that male was the non-preferred male rather than the preferred male in the pre-test ($U = 44$, N_1, $N_2 = 14$, $P < 0.01$; Fig. 3). This result could reflect a greater effect of seeing mating by a non-preferred than by a preferred male on the tendency of females to affiliate with that male. We suspect, however, that this result instead reflected an upper bound on the possible increase in the amount of time that focal females assigned to the preferred-male condition could spend with their preferred male during the post-test. Focal females assigned to the preferred-male condition had spent an average of almost 75 % of the pre-test closer to their preferred male. There was not much room for increase during the post-test.

EXPERIMENT 3: CHOOSING MALES OR CHOOSING LOCATIONS

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

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

Methods

Subjects

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

Procedure

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

Results and Discussion

Pre-test

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

Post-test

Focal females increased the time that they spent on the side of the enclosure to which the non-preferred male they had observed mating had been moved (mean ± SE = 4.36 ± 1.08 min; $T = 7$, $P < 0.005$). The results are consistent with the view that females remain near males they have seen mating, not near locations where they have seen males mate.

EXPERIMENT 4: CHANGES IN FEMALE PERCEPTION OR MALE BEHAVIOUR?

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

Methods

Subjects

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

Procedure

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

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

We placed experimental focal females in the holding cage with its opaque walls facing the end enclosures holding preferred and non-preferred males, so that these females could not see the other birds in the test enclosure during the observation phase, although they could hear them.

Results and Discussion

Pre-test

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

Post-test

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

The data are consistent with the hypothesis that females are attracted to males that they see mating, not to males that have undergone some change in behaviour or appearance as a result of their having mated.

GENERAL DISCUSSION

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

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

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

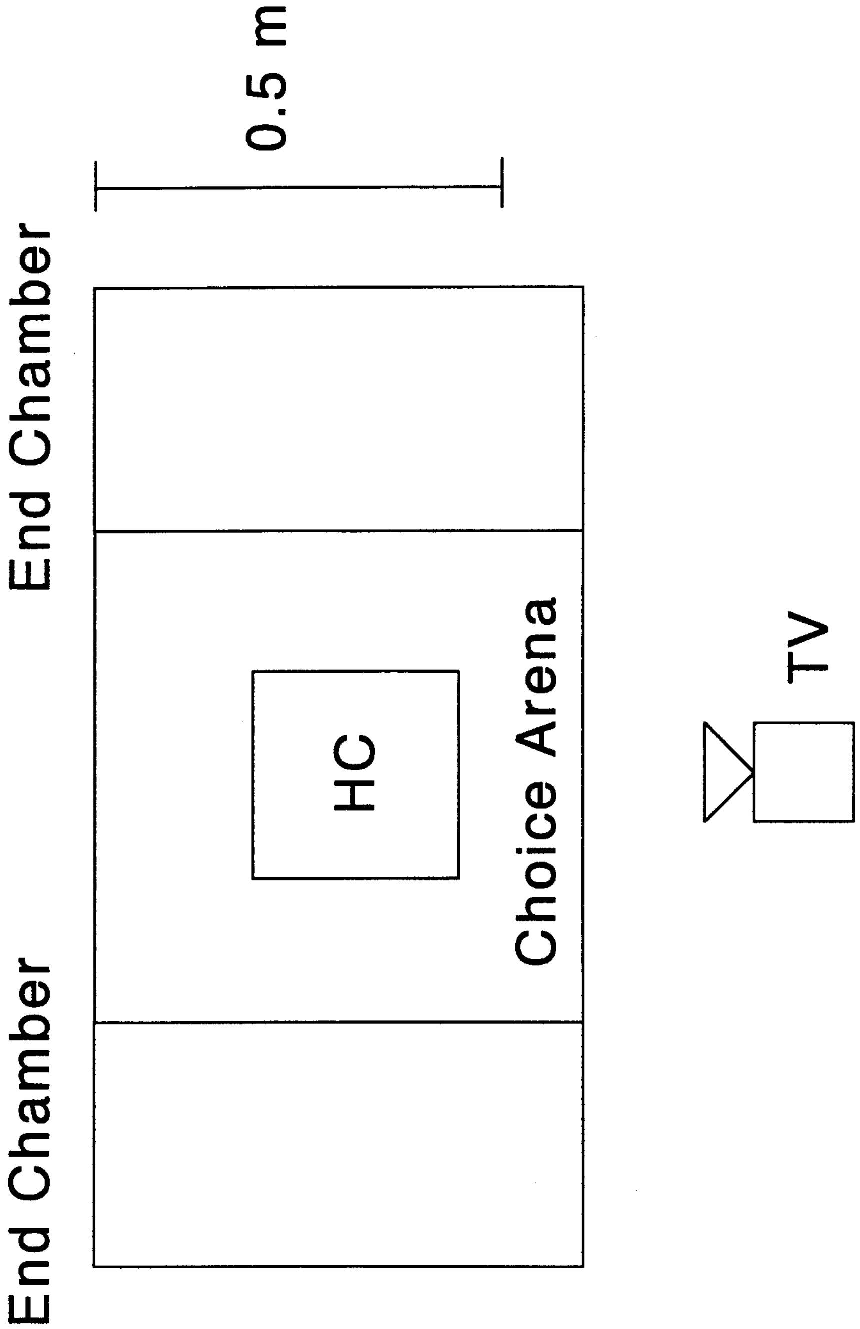
Figure Captions

Figure 1. Overhead schematic of the apparatus. H.C. = holding cage, TV = television camera.

Figure 2. Mean increase from pre-test to post-test in the number of min that focal females assigned to control and experimental conditions in experiment 1 spent on the side of the apparatus containing their respective non-preferred males. Bars = ± 1 SEM.

Figure 3. Mean increase from pre-test to post-test in the number of min that focal females assigned to preferred-male and non-preferred-male conditions in experiment 2 spent on the side of the apparatus containing their respective non-preferred males. Bars = ± 1 SEM.

Figure 4. Mean increase from pre-test to post-test in the number of min that focal females assigned to control and blind conditions in experiment 4 spent on the side of the apparatus containing their respective non-preferred males. Bars = ± 1 SEM.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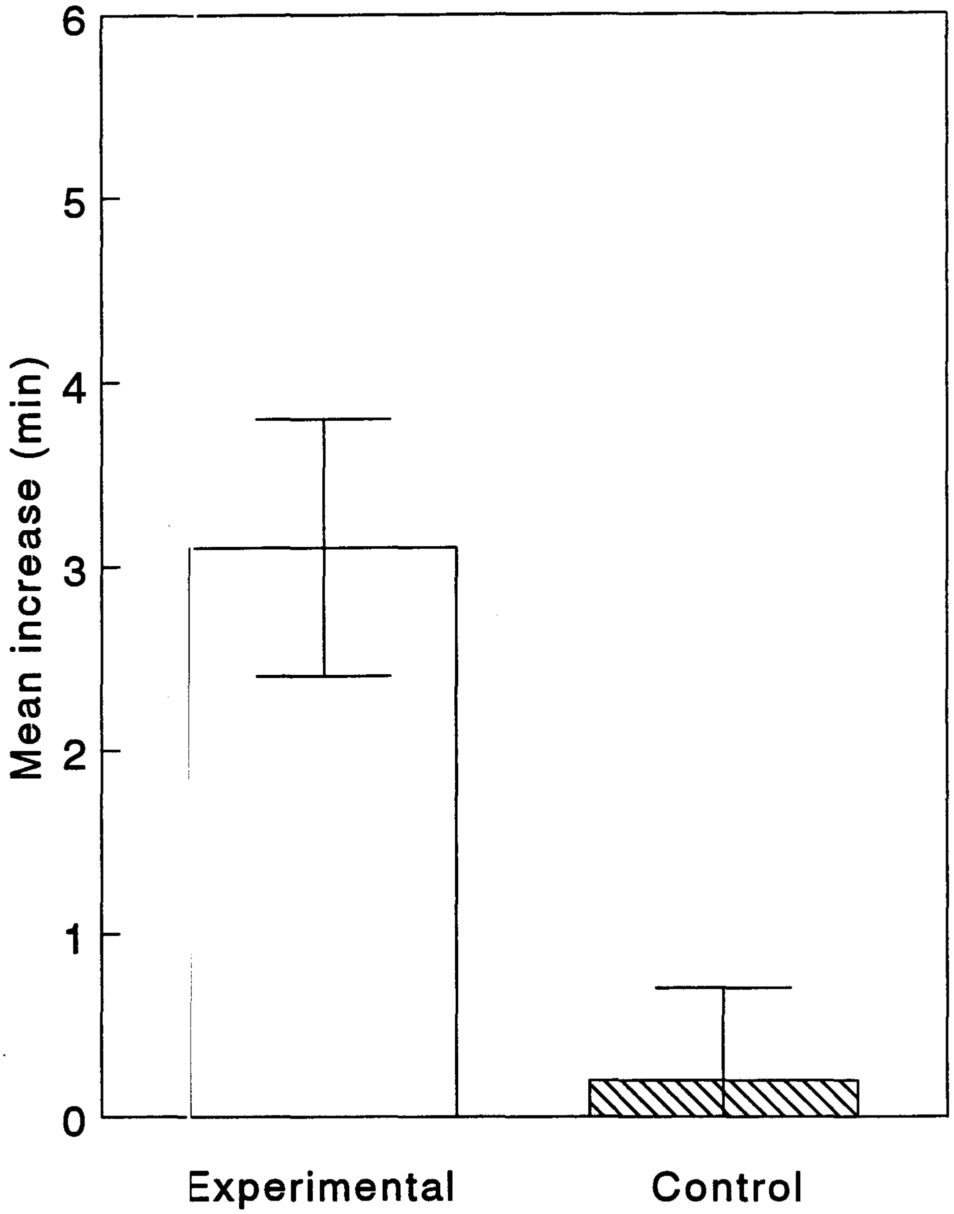
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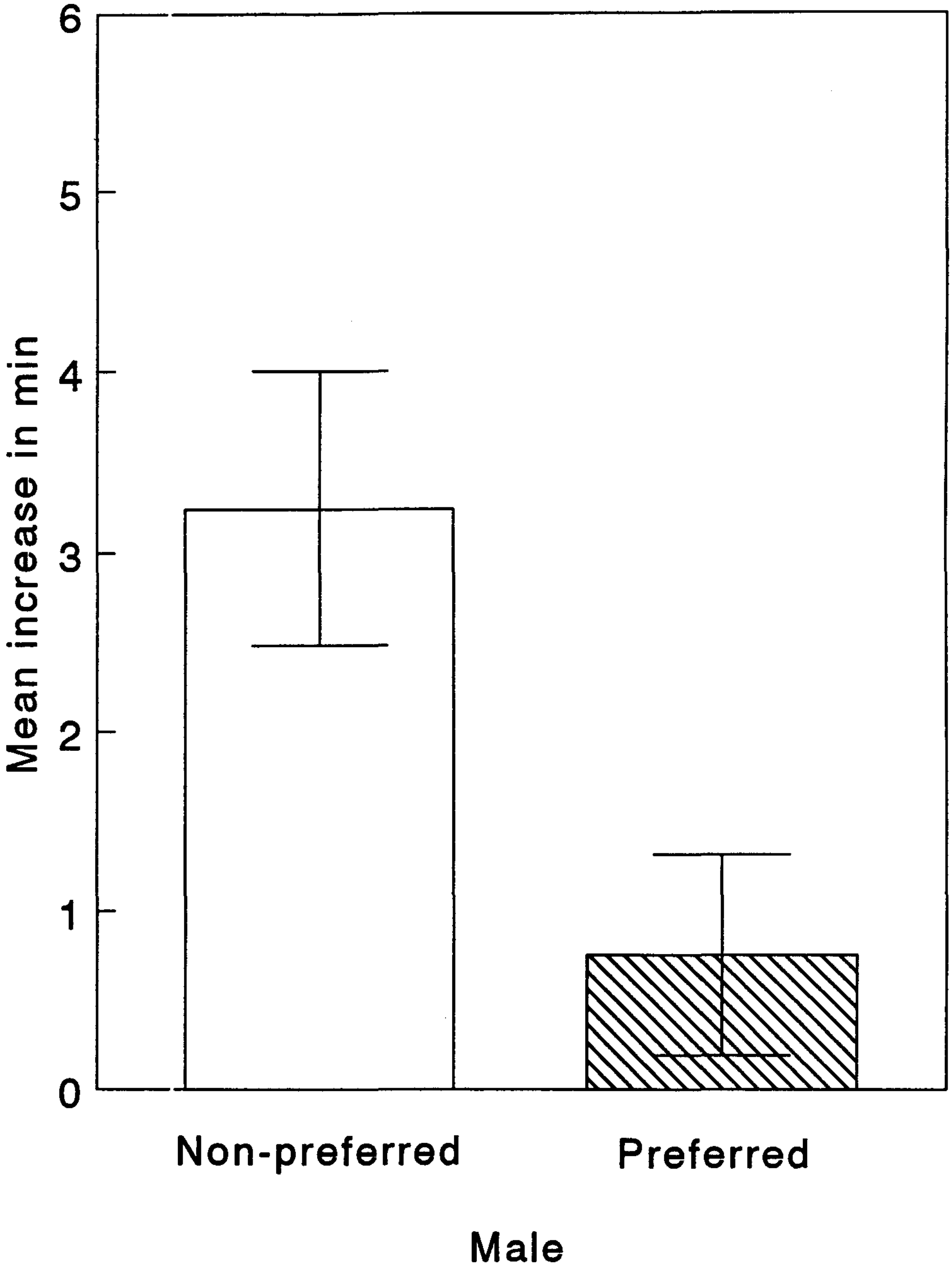
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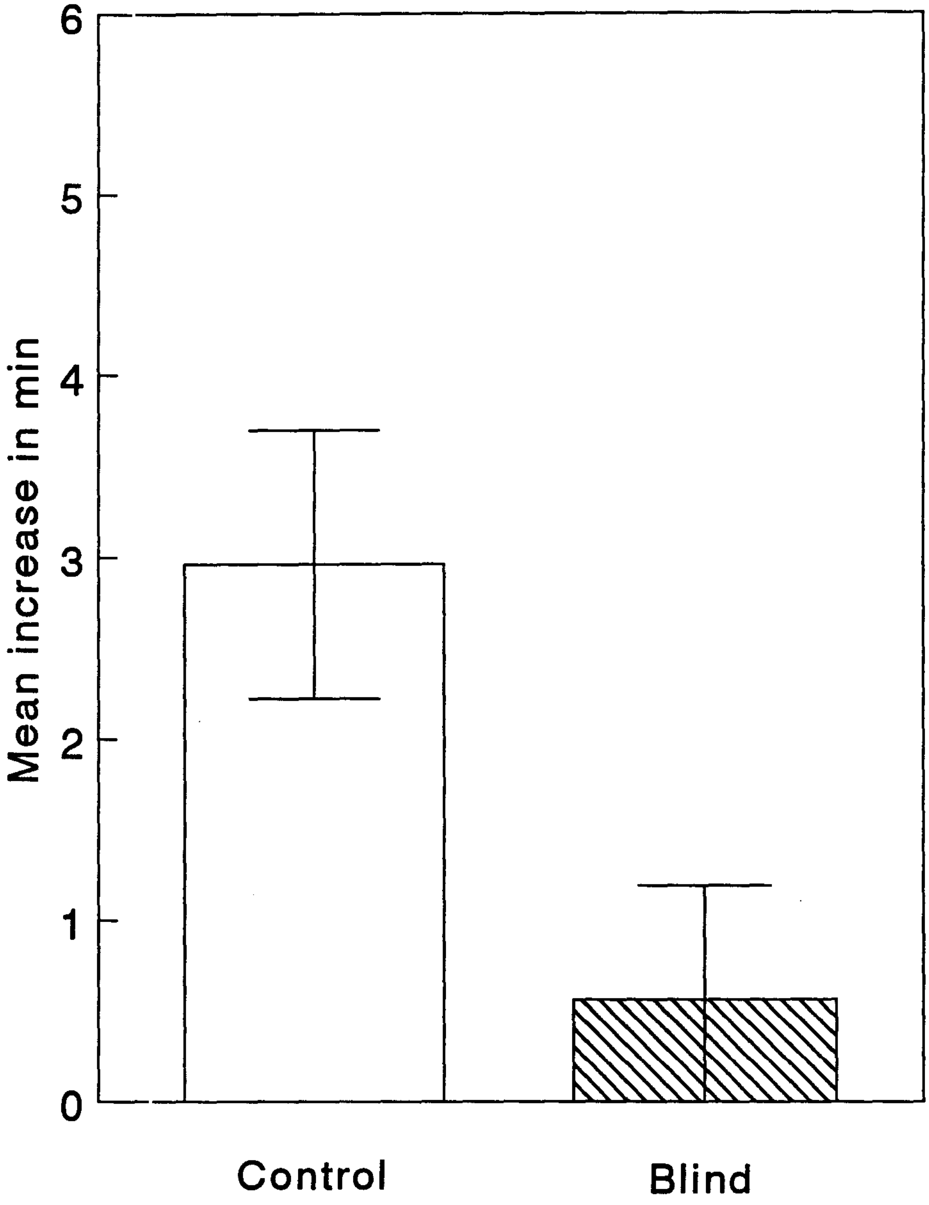
Preferred
Male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Control
Blind

Chapter 3

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

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DAVID J. WHITE & BENNETT G. GALEF, JR

Department of Psychology, McMaster University

Abstract

In five experiments, we examined the effects on the affiliative preferences of 'focal' female Japanese quail given the opportunity to watch a conspecific male interact with a 'model' female. Experiments were conducted in three, 10-min phases: (1) a pretest during which a focal female chose between two males; (2) an observation phase, when each focal female watched the male she had spent less time near during the pretest (her 'non-preferred' male) interact with a model quail; and (3) a post-test, during which each focal female again chose between her non-preferred and preferred males. Focal females increased their preferences for non-preferred males after seeing them together with a model female (but not a model male), even if the non-preferred male and model female were separated by an opaque barrier that prevented them from interacting. A focal female's preference for the end of the enclosure containing her non-preferred male was not increased when she either watched him court a concealed model female or watched a model female that was being courted by him. Taken together, the present results suggest that a simple tendency for females to approach areas where they have previously seen a male and female quail, in preference to locations where they have seen only a male quail, can explain some of the effect of watching a non-preferred male mate on a female's tendency to affiliate with him. However, focal females also showed enhanced preferences for non-preferred males they had seen mating after we both moved those males and controlled for effects of transposition. Thus, processes akin to both 'mate-choice copying' and

‘conspecific cueing’ remain viable explanations for the increase in a focal female quail’s tendency to affiliate with a male she watched mate with another female.

The results of recent experiments examining social influences on preferences of female Japanese quail, *Coturnix coturnix japonica* (Galef & White 1998: chapter 2) demonstrate that a 'focal' female's tendency to remain near a previously non-preferred male increases significantly after she has watched that male mate with another female (a 'model'). Focal females often reverse their preference after watching the non-preferred member of a pair of males mate with a model female (Galef & White 1998: chapter 2, exp. 1).

Such findings are consistent with the hypothesis that female quail copy one another's mate choices. However, as Pruett-Jones (1992, page 1000) and others have indicated, the fact that females increase their tendency to remain near males they have seen mating is not, in itself, sufficient to show that they copy one another's mate choices. The important characteristic of copying behaviour that separates it from other similar processes is that the change in the probability of choice is strictly because of the actions of other females and not the consequences of those actions. Heyes (1993) has made a parallel distinction between imitative and nonimitative forms of social learning of motor acts, defining imitation as involving learning about behaviour (responses, actions, etc.), and nonimitative social learning as resulting from observers' learning socially about stimuli, objects, or events in the environment.

On Pruett-Jones's (1992) definition of mate-choice copying, if mating changed the appearance or behaviour of males, thus increasing their attractiveness to females (Goldschmidt et al. 1993), or if females preferred males they had seen courting other females (Grant & Green 1996), such increase in attractiveness would not be a result of mate-choice copying. Similarly, if females tended to move about in groups (a tendency that has been labeled 'conspecific cueing'; Keister 1979), a solitary female might move into an area where she had previously seen a female consorting with a male, although she would not be copying the behaviour of the other female.

The results of our previous experiments on social influences on affiliative tendencies of female quail (Galef & White 1998: chapter 2) were not consistent with the hypotheses that either enhanced male attractiveness following mating or a tendency to stay near other females produced the observed increases in preferences of female quail for males seen courting and mating; (1) female quail showed increased preferences for males they had seen mating, but not for males that had mated while out of sight, and (2) female quail preferred a male they had seen mating even after his location was exchanged with that of another male that a female had not seen mating (Galef & White 1998: chapter 2, exps. 4 and 3, respectively). While these results suggest that female Japanese quail do copy one another's mate choices, they are obviously not sufficient to exclude alternative explanations of the observed increase in female quail's tendency to affiliate with males seen courting and mating.

We undertook the present series of experiments to further define the stimuli that alter female quail's preferences for conspecific males they have seen engage in courtship. We hoped to determine whether 'copying' need be invoked to explain observed increases in the tendency of female quail to affiliate with males they have seen engage in reproductive behaviour.

General Methods

Apparatus

We conducted all experiments in an enclosure, measuring 122.0 x 61.0 x 30.5 cm, constructed of painted plywood, transparent Plexiglas, and hardware cloth (Fig. 1). The enclosure rested on an aluminum tray covered with disposable, absorbent paper pads (Tray Liners, Lilo Products, Hamilton, Ontario, Canada).

Two hardware-cloth partitions placed 30.5 cm from each end of the enclosure, divided it into three compartments: two end compartments and a central compartment. During experiments, each end compartment of the apparatus, measuring 30.5 x 61.0 x 30.5 cm, held a male quail, while the central compartment, measuring 61 x 61.0 x 30.5 cm, held a female quail.

We cut a 25.4 cm^2 opening in the centre of the Plexiglas roof of the central compartment through which we could raise and lower a holding cage, measuring 25.2 x 25.2 x 40.6 cm, that we had constructed of transparent Plexiglas. A pulley system operated from a room adjacent to that housing the enclosure, allowed us to raise the holding cage and release a female from under it without entering the room containing the enclosure.

We drew a line from top to bottom on the Plexiglas front wall of the enclosure, at its midpoint, so that, at all times, we could reliably determine the end of the enclosure to which a female was closer. A television camera (connected to a VHS video-cassette recorder and video monitor) faced the front wall of the enclosure and permitted us: (1) to observe in real time all behaviour occurring within the enclosure, and (2) to determine the location of focal females throughout the pre- and post-test.

Results of tests of inter-observer reliabilities in scoring videotapes (Galef & White 1998: chapter 2) revealed a high level of agreement between independent observers ($r_{10} = 0.99$, $P < 0.001$).

Subjects

Six groups, each consisting of 10 male and 10 female Japanese quail that we purchased from a commercial breeder (Speck's Poultry Farm, Vineland, Ontario) when 48 days old, served as subjects. Groups of 20 subjects were randomly selected from a barn containing several thousand quail of similar age. Selected quail were very unlikely to have been either close relatives or social companions.

After we transported each group of 20 subjects to the laboratory, we placed them in individual stainless-steel cages, measuring 45.7 x 61.0 x 40.6 cm, and gave them ad libitum access to water and Purina Game Bird Startena no. 5419 (Ralston-Purina Canada, Woodstock, Ontario).

Before we started experiments, we brought all subjects into breeding condition by keeping them for 30 days on a 16:8 light:dark cycle. We considered females to be ready to breed when they began to lay eggs once every 2 or 3 days.

To establish the readiness of males to breed, we repeatedly placed each male together with a female in breeding condition in one end chamber of the apparatus we subsequently used for experiments (Fig. 1). We thus accustomed subjects to mating in the experimental apparatus at the same time that we determined when males were ready to breed. We paired each male with a different, randomly selected female in breeding condition twice per day until he either mounted two females in succession or 2 weeks passed without his showing interest in the females.

We did not use as subjects any males that failed to mount females 6 weeks after arrival in the laboratory.

Procedure

Each of the experiments described below consisted of three, distinct, 10-min phases: (1) a pretest used to determine a 'focal' female's initial preference between two males, (2) an observation period, during which a focal female could observe one of the two males she had chosen between during the pretest interact with a female and the other remain alone, and (3) a post-test that determined for a second time each focal female's preference between the same two males she had seen during the pretest. Experiments differed only in manipulations carried out during the observation phase.

Pretest

To begin an experiment, we placed a sexually proven male in each end chamber of the apparatus and a focal female in the holding cage in the centre of the apparatus and left them undisturbed for 30 s. We then raised the holding cage approximately 20 cm to allow the focal female to leave the holding cage.

During the 10 min following the first step that a focal female took after we had raised the holding cage, we recorded the time that she spent on each side of the midline of the enclosure. We considered the male on the side of the enclosure where a focal female spent the majority of the 10-min pretest to be her 'preferred' male and the other male to be her 'non-preferred' male.

Observation

To begin the observation phase, we again placed the focal female in the holding cage, then placed a second female (a model female) in the end compartment that held the focal female's non-preferred male. We then left the four birds undisturbed for 10 min so that the focal female could observe: (1) her non-preferred male court and mate with the model female, and (2) her preferred male remaining alone. While in the holding cage, focal females could both see and hear both males.

Post-test

At the end of the observation phase, we removed the model female from the apparatus and repeated the procedure we had used during the pretest (i.e. we released the focal female from the holding cage and, once she had started to walk, recorded the time that she spent on each side of the midline of the enclosure).

Testing schedule

To be sure that we were not repeatedly using the same males and females in any experiment, before beginning each experiment, we randomly assigned two females to each of the combinations of males that we could create using the sexually active male subjects in each group. We then randomly assigned one of the two females in each quartet to serve as a focal female and the other to serve as a model female within that quartet. No two focal females ever chose between the same pair of males, no focal female ever saw any male twice, and no female ever served twice as the model female for the same focal female.

We conducted five trials/day, and allowed no female or male to participate in more than two trials on the same day. On those days when a female participated in the experiment twice, she never served twice as either a focal or model female and always served as a focal female before she served as a model female.

EXPERIMENT 1: EFFECTS OF OBSERVATION OF MATING ON MATE CHOICE

To establish the reliability of social influences on preference for males in Japanese quail, in experiment 1 of the present series, we simply repeated our basic experiment (Galef & White 1998: chapter 2, exp. 1), in which, during the observation phase, non-preferred males of focal females assigned to the experimental group courted and mated with model females, while non-preferred males of focal females assigned to the control group did not interact with a model female.

Methods

Subjects

We randomly assigned each of 24 quartets of quail to experimental (N = 14 quartets) and control (N = 10 quartets) conditions.

Procedure

At the end of the pretest, we placed a model female in the end chamber of the enclosure containing the non-preferred male of each focal female that we had assigned to the experimental condition. We treated each focal female assigned to the control condition exactly as we treated focal females assigned to the experimental condition except that we did not place a model female in the apparatus during the observation phase of the experiment.

Results and Discussion

Pretest

During the pretest, focal females assigned to the experimental group spent an average (± SE) of 7.32 ± 0.44 min on the side of the cage containing their preferred males. Focal females assigned to the control group did not differ from those assigned to the experimental group in the time (7.38 ± 0.51 min) that they spent close to their respective preferred males (t_{22} = 0.08, NS).

Observation

During the observation phase, all 14 males assigned to the experimental group mounted their respective model females.

Post-test

Focal females in the experimental group spent significantly more time with their non-preferred males during the post-test than during the pretest (paired t test, $t_{13} = 5.59, P < 0.001$; Fig. 2). On the other hand, there was no change between pre- and post-tests in the time focal females assigned to the control condition spent on the side of the enclosure containing their respective non-preferred males (Paired t test, $t_9 = 1.03$, NS; Fig. 2).

The change in time spent with non-preferred males between the pre- and post-tests was significantly greater for focal females assigned to the experimental group than for focal females assigned to the control group (t test, $t_{22} = 2.98, P < 0.01$; Fig 2). During the post-test, nine of the 14 subjects assigned to the experimental group spent more time affiliating with the male they had not preferred during the pretest, while only two of the 10 subjects assigned to the control group did so (Fisher's exact test $P < 0.04$).

The results of experiment 1 confirmed the main findings of Galef and White (1998: chapter 2). Female Japanese quail show an enhanced tendency to affiliate with non-preferred males after seeing non-preferred males court and mate with model females.

EXPERIMENT 2: DEFINING NECESSARY CONDITIONS

FOR CHANGES IN FEMALE PREFERENCE

We undertook experiment 2 to determine whether a focal female had to observe a non-preferred male actually court and mate with a model female in order for her attraction to that male to increase. If seeing a non-preferred male court and mate is, in fact, necessary to enhance his attractiveness, then mate-choice copying would seem a likely explanation for the changes in preferences of focal females in experiment 1. Copying would seem an unnecessarily elaborate explanation for the effects on focal females of watching males and model females mate if either seeing a male and model female in the same area without seeing them interact or simply seeing a model female in an area later increased the attractiveness of that area to focal females (Grant & Green 1996). Indeed, in the latter case, 'conspecific cueing' would seem an appropriate explanation of the phenomenon.

Methods

Subjects

We used as subjects 16 male and 20 female Japanese quail assigned to 41 quartets as described in the General Methods. We randomly assigned quartets to the male-court (14 quartets), male-court-female-no copulation (14 quartets and isolate (13 quartets) conditions.

Apparatus

We used the same apparatus we had used in experiment 1 with the addition of a second holding cage into which we placed model females during the observation phase of the experiment. We made this second holding cage, measuring 18.8 x 18.8 x 30 cm, of transparent Plexiglas, and then made one of the walls opaque by attaching to it a piece of white Bristol board measuring 30 x 30 cm. By confining the model female in her holding cage, placing it in the middle of the end compartment (so that non-preferred males could not walk around the holding cage), and facing the opaque wall of the cage in various directions, we could change the visual stimuli available both to the focal females and to the non-preferred males during the observation period, while holding everything else constant.

Procedure

The procedure was identical to that of experiment 1, except that, during the observation phase of the experiment, we confined model females, as well as focal females, in holding cages. We labeled the various experimental groups in terms of what focal females could see during the observation phase. If, during the observation phase of the experiment, the opaque wall of a model female's holding cage faced away from the focal female, she could see her non-preferred male court but not mate with a model female (the male-court-female-no-copulation group). If the opaque wall was between the model female and the non-preferred male, the focal female could see both the non-preferred male and the model female, but the non-preferred male and model female would not be visible to each other (the isolate group), and thus the male could not court or mate with the model female. If the opaque wall faced the focal female, the focal female could both see and hear a male courting (the male-court group), but she could not see the object of his attention.

Results and Discussion

Pretest

During the pretest, focal females assigned to male-court, male-court-female-no-copulation and isolate groups spent, respectively, an average (± SE) of 7.49 ± 0.39 min, 7.41 ± 0.43 min, and 7.70 ± 0.40 min on the side of the enclosure containing their preferred males. There were no significant differences between groups in the time focal females spent with their preferred males during the pretest ($F_{2,38} = 0.13$, NS).

Post-test

A one-way ANOVA performed on the change between pre- and post-tests in the time that each focal female assigned to male-court, male-court-female-no-copulation and isolate groups spent with her non-preferred male revealed a significant effect of group assignment on affiliation ($F_{2,38} = 3.41$, $P < 0.05$; Fig 3). Focal females assigned to both male-court-female and isolate groups showed a significant increase between the pre- and post-tests in the time they spent with their non-preferred males (paired *t* tests, both *t*s > 3.23, both *P*s < 0.01; F .Uig. 3), while focal females assigned to the male-court condition did not ($t = 0.43$, NS; Fig. 3).

The finding that focal females were attracted to areas where they had seen non-preferred males and model females simply standing near one another (isolate group) suggests that much of the apparent increased attractiveness to focal females of non-preferred males seen courting and mating may have resulted not from 'copying' of the behaviour of model females by focal females, but from the focal females' attraction to areas where they had previously seen either two quail or a male and female quail.

EXPERIMENT 3: TWO QUAIL OR A MALE AND FEMALE QUAIL?

During the observation phase of experiment 2, focal females assigned to the isolate group saw two quail, one male and one female, at one end of the test enclosure. It is impossible to know whether the focal female's increased attraction to that end of the enclosure during the post-test was the result of her having seen her non-preferred male in the vicinity of a female quail or of her having seen her non-preferred male in the company of another quail, whose sex was irrelevant.

In experiment 3, we both repeated the isolate group of experiment 2 and added a new condition (the male-male-isolate group) in which the focal female saw her non-preferred male standing near a model male during the observation phase of the experiment.

Methods

Subjects

As described in the General Methods, we conditioned and assigned eight male and eight female quail to quartets, that we then assigned to two conditions (N = 10 quartets/condition).

Apparatus and procedure

The apparatus and procedure were exactly those of experiment 2, except that we examined the behaviour of 10 quartets treated as we had treated quartets assigned to the isolate condition of experiment 2, and an additional 10 quartets, each consisting of three males and a single female, which we assigned to a male-male isolate condition.

During the observation phase of experiment 3, focal females assigned to the male-male isolate condition were treated exactly like those assigned to the isolate condition of experiment 2, except that they saw their non-preferred male caged in the vicinity of a model male, rather than a model female, but separated from him by an opaque partition.

Results and Discussion

Pretest

During the pretest, focal females assigned to the isolate condition spent an average (± SE) of 7.85 ± 0.51 min on the side of the cage containing their preferred males. Focal females assigned to the male-male isolate condition did not differ from those assigned to the isolate condition in the time (7.34 ± 0.37 min) that they spent close to their respective preferred males ($t_{18} = 0.81$, NS).

Post-test

Focal females in the isolate condition spent significantly more time with their non-preferred males during the post-test than they had during the pretest (paired *t*-test, $t_9 = 4.48$, $P < 0.01$; Fig. 4). On the other hand, focal females assigned to the male-male isolate condition did not show a change between pre- and post-tests in the amount of time they spent on the side of the enclosure containing their respective non-preferred males (paired *t*-test, $t_9 = 0.57$, NS; Fig. 4).

The change in the time spent with non-preferred males between pre- and post-tests, was significantly greater for focal females assigned to the isolate condition than for focal females assigned to the male-male isolate condition (*t* test, $t_{18} = 2.43$, $P < 0.05$; Fig 4). Clearly, a focal female's preference for her non-preferred male increased after she saw him in the vicinity of a model female, not after she saw him in the vicinity of a model male. Consequently, the socially induced change in time that focal females assigned to the isolate condition in experiment 2 spent with their non-preferred males cannot be attributed to a simple tendency of females to prefer areas where they had recently seen two quail over those areas where they had seen only one quail. The presence of a female in the end of the enclosure occupied by a non-preferred male was necessary to increase a focal female's preference for that male.

EXPERIMENT 4: A MALE AND FEMALE QUAIL OR JUST A FEMALE QUAIL?

Of course it is possible, as the conspecific cueing hypothesis suggests, that focal females in experiment 3 were simply attracted to areas of the cage where they had seen a fellow female. In experiment 4, we determined whether simply seeing a female in an area previously occupied by a non-preferred male increased the subsequent attractiveness of that area to focal females.

Methods

Subjects

We used as subjects 20 female and 16 male Japanese quail, conditioned and assigned to 42 quartets as described in the General Methods.

Apparatus

The apparatus used was that used in experiment 1, with the addition of two holding cages into which we placed each male during the observation phase of the experiment. We made these two holding cages, each measuring 17.8 x 17.8 x 30.0 cm, of transparent Plexiglas, and then made one wall of each opaque by attaching a piece of white Bristol board, measuring 30 x 30 cm, to it.

Procedure

The procedure was as described in the General Methods except that during the observation phase of the experiment, we confined both preferred and non-preferred males assigned to experimental conditions in holding cages.

As in experiment 2, we labeled the groups to which we assigned subjects in terms of the view available to focal females during the observation phase of the experiment. If, during the observation phase, the opaque wall of each male's holding cage faced the focal female, she could see only the model female in the area where the non-preferred male was held (model-female group). If the opaque wall of the cages confining preferred and non-preferred males faced away from the focal female, she could see the model female and the non-preferred male courting the model female, but not mating with her (male-court-female group). We treated members of a control group (male-alone group) exactly as we treated members of the male-court-female group except that we did not place a model female in the enclosure with the non-preferred male during the observation phase of the experiment.

Results and Discussion

Pretest

During the pretest, focal females assigned to male-alone, male-court-female and model-female groups spent, respectively, an average (± SE) of 6.81 ± 0.37 min, 7.19 ± 0.36 min, and 7.40 ± 0.36 min on the side of the enclosure containing their preferred males. There was no difference between groups in the time that focal females spent near their preferred males during the pretest ($F_{2,39}$ = 0.67, NS).

Post-test

A one-way ANOVA performed on the change in the time each focal female spent with her non-preferred male during the pre- and post-tests, revealed a significant effect of group assignment ($F_{2,39} = 4.75$, $P < 0.02$; Fig. 5) on affiliation. Tukey's multiple-comparison post-hoc tests revealed that focal females assigned to the male-court-female group showed a significantly greater increase in their tendency to affiliate with their respective non-preferred males than did focal females assigned to either the model female or male-alone groups (both Ps < 0.04). Furthermore, focal females assigned to the male-court-female group also showed a significant increase between pre- and post-tests, in the time they spent with their non-preferred males (paired t-test, $t_{13} = 4.07$, $P < 0.005$; Fig. 5), whereas focal females assigned to the model-female and male-alone groups did not (paired t-tests, both $t\text{s}_{13} < 0.55$, both NS; Fig. 5).

These results show that confined, non-preferred males seen courting model females, like unconfined, non-preferred males seen courting females (experiments 1, 2 and 3) increase in attractiveness to focal females. The results also show that focal females do not show an increase in their tendency to spend time near an area where they have simply seen a female being courted by a male that is invisible to them. Thus, a simple tendency for females to aggregate in the same area cannot explain the effects of seeing model females near males on the affiliative behaviour of focal females.

Taken together the results of experiments 2, 3 and 4 indicate that much of the change in the behaviour of focal females that results from watching a male court and mate with a model female (experiment 1) may have been the result of a tendency for focal females to show an enhanced attraction to areas where they had seen both a male and female quail relative to areas where they had seen only a male quail.

EXPERIMENT 5: THE SWITCH EXPERIMENT

We undertook the final experiment in the present series to determine whether female quail are attracted not only to areas where they have seen a male and female quail, but also to an individual male that they have seen mating.

The standard laboratory technique for disassociating a focal female's attraction to an area where a male and female were seen mating and her attraction to the mating male per se is to move the male to a new area prior to testing the preference of the focal female (Dugatkin 1992, 1996; Dugatkin & Godin 1992; Schlupp et al. 1994; Galef & White 1988: chapter 2).

There is, however, a problem in interpreting results of experiments in which: (1) a focal female watches one male consort with a model female and a second male not consort with a female, (2) the positions of the two males are reversed before testing the preference of the focal female, and (3) it is found that the female prefers the male she saw consorting with the female, not the place where the pair was observed together. In such an experiment, there is no control for the possibility that the disturbance caused by reversing the position of the two males affects the females' preferences. We would not mention such an inherently unlikely possibility except that, as shown below, at least in Japanese quail, such effects of disturbance on mate choice are surprisingly robust.

We have reported (Galef & White 1998: chapter 2, exp. 4) results of an experiment in which: (1) focal female quail watched their respective non-preferred males court and mate with model females during the observation phase of the experiment, (2) the positions of non-preferred and preferred males were reversed, and focal females showed a substantially enhanced preference for their respective non-preferred males, not for the areas that those non-preferred males and model females had previously occupied. Here, we repeat that experiment with appropriate controls.

Methods

Subjects

We used as subjects 10 female and eight male Japanese quail, conditioned and assigned to 28 quartets as described in the General Methods.

Apparatus

The apparatus was the same as that used in experiment 1.

Procedure

The method was essentially the same as that we used in experiment 1 except that, as described below, we reversed the position of preferred and non-preferred males assigned to experimental groups at the end of the observation phase and before starting the post-test. We treated the subjects we assigned to the mating condition (N = 9 quartets) exactly as we had treated subjects in the experimental condition of experiment 1 (i.e. during the observation phase, the non-preferred male courted and mated with a model female). We treated subjects assigned to the mating-switch condition (N = 9 quartets) as we treated subjects assigned to the mating condition except that we reversed the positions of preferred and non-preferred males after the observation phase of the experiment and before the post-test. We treated subjects assigned to the control-switch condition (N = 10 quartets) exactly as we treated subjects assigned to the mating-switch condition except that we did not introduce a model female into the enclosure containing the non-preferred male during the observation period before we reversed the positions of preferred and non-preferred males.

In all three groups, in order to reduce the disturbance resulting from the switch process to a minimum, at the end of the observation phase, we: (1) placed an opaque shell around the holding cage containing the focal female for approximately 1 min (while we reversed the position of males assigned to mating-switch and control-switch groups), and (2) then waited 5 min before releasing the focal female from her holding cage to start the post-test.

Results and Discussion

Pretest

During the pretest, focal females assigned to control-switch, mating-switch, and mating groups spent, respectively, an average (± SE) of 7.54 ± 0.52 min, 7.67 ± 0.37 min, and 7.64 ± 0.44 min on the side of the enclosure containing their preferred males. There was no significant difference between groups in the time that focal females spent near their preferred males during the pretest ($F_{2,25}$ = 0.03, NS).

Post-test

Focal females in all three groups spent more time affiliating with their non-preferred male during the post-test than during the pretest (paired *t* tests, all $ts_{8 \text{ or } 9} > 3.09$, all $Ps < 0.02$.; Fig. 6). A one-way ANOVA performed on the change in the time between pre- and post-tests that focal females spent with their non-preferred male revealed a significant effect of group assignment on the dependent variable ($F_{2,25} = 4.25$, $P < 0.03$; Fig. 6). Tukey's multiple-comparison post-hoc tests revealed that focal females assigned to the mating-switch group showed a significantly greater increase in the time that they spent affiliating with their non-preferred male than did focal females assigned to the control-switch group ($P < 0.04$; Fig. 6), while focal females in mating and control-switch groups showed virtually identical changes between pre- and post-tests in their responses to non-preferred males ($P < 0.99$; Fig. 6).

The results suggest three conclusions: first, and for reasons unknown, the simple act of switching the positions of two male quail caused an increase in the focal females' preferences for non-preferred males as large as that induced by seeing a non-preferred male court and mate with a model female. This change in female preference for males following reversal of their positions was not a chance outcome. We have repeated experiment 5 twice: once without the 5-min delay at the end of the observation phase before releasing the focal female from her holding cage and once with the lights in the experimental room extinguished while we reversed the positions of preferred and non-preferred males. In both repetitions, switching the position of preferred and non-preferred males reversed the females' preferences.

Second, the finding that simply reversing the positions of males can change females' preferences between those males indicates that experiments in which positions of males are reversed and no controls are used for effects of this reversal on female preference do not provide compelling evidence of mate-choice copying.

Third, although some of the increase in focal females' preferences for non-preferred males in the present experiment could be explained as a result of simple disturbance, the opportunity for focal females to see their non-preferred males court and mate with model females before they were moved induced a further, significant increase in the non-preferred males' attractiveness to their respective focal females. Consequently, the entire observed effect on the mate preferences of female quail of seeing males mate with model females cannot be attributed to a tendency for females to spend time near locations where they have seen a male and model female mate. Focal females increased their preference for non-preferred males they had seen courting and mating.

GENERAL DISCUSSION

Taken together, the results of experiments 2, 3 and 4 are consistent with the view that the increase in attractiveness of non-preferred male quail to focal females that observe them court and mate with model females (experiment 1) may be attributable to a simple tendency of focal females to approach locations where they have seen a male and female quail in preference to locations where they have seen a male quail alone. The results of experiment 5 indicate that female quail increase their tendency to affiliate with non-preferred males after watching such males court and mate with other females.

Of course, it cannot be concluded from the present experiments that the increased attractiveness of non-preferred males seen courting and mating in experiment 5 resulted from females seeing those males actually court and mate. A male might become more attractive to a female that saw him simply standing near another female, but whether this increase in male attractiveness is an example of 'mate-choice copying' is open to debate.

Determining the stimuli sufficient to change a female's attraction either to a given area or to a given male is a relatively straight-forward matter. One can define such stimuli to whatever degree of precision one desires. Determining the underlying psychological process that produces the observed change in behaviour is more difficult. Unfortunately, terms such as 'mate-choice copying' and 'conspecific cueing' refer to psychological processes occurring within the observer, as well as to stimuli in the environment.

Those familiar with the 100-year history of experiments to determine whether animals can learn by imitation (Galef 1988, 1998) will be aware of how difficult it is to of establish that any change in behaviour results from one animal copying the behaviour of another, as Pruett-Jones (1992) has suggested is critical to the definition of mate-choice copying. There are experimental outcomes that might permit the conclusion that imitation or copying of behaviour occurs, if for example, as in the present experiments, focal females showed an enhanced tendency to affiliate with non-preferred males only after they see these males actually court and mate with model females. However, such clear experimental outcomes are rare.

The same 100-year history also demonstrates the limited heuristic value of taxonomies of psychological processes that might underlie social influences on behaviour (e.g. Galef 1976, 1988; Whiten & Ham 1992).

Studies of social influences on behaviour in domains other than mate choice suggest that experiments undertaken to discover the necessary and sufficient conditions for social interactions to affect affiliative behaviour and subsequent choice of a mate are more likely to be informative than are experiments undertaken to demonstrate 'mate-choice copying', or other hypothetical types of social influence on mating behaviour. The results of the present experiments suggest the same conclusion.

Figure Captions

Figure 1. Overhead schematic of the apparatus. H.C. = holding cage, TV = television camera.

Figure 2. Mean change from pre- to post-tests in the number of minutes that focal females spent on the side of the apparatus containing their respective non-preferred males in experiment 1 after seeing their non-preferred male court and mate (experimental condition) or not court and mate (control condition). Cartoons above histograms show treatment of model female (M), focal female (F), preferred male (P) and non-preferred male (NP) during the observation phase of the experiment. Bars = ± 1 SEM.

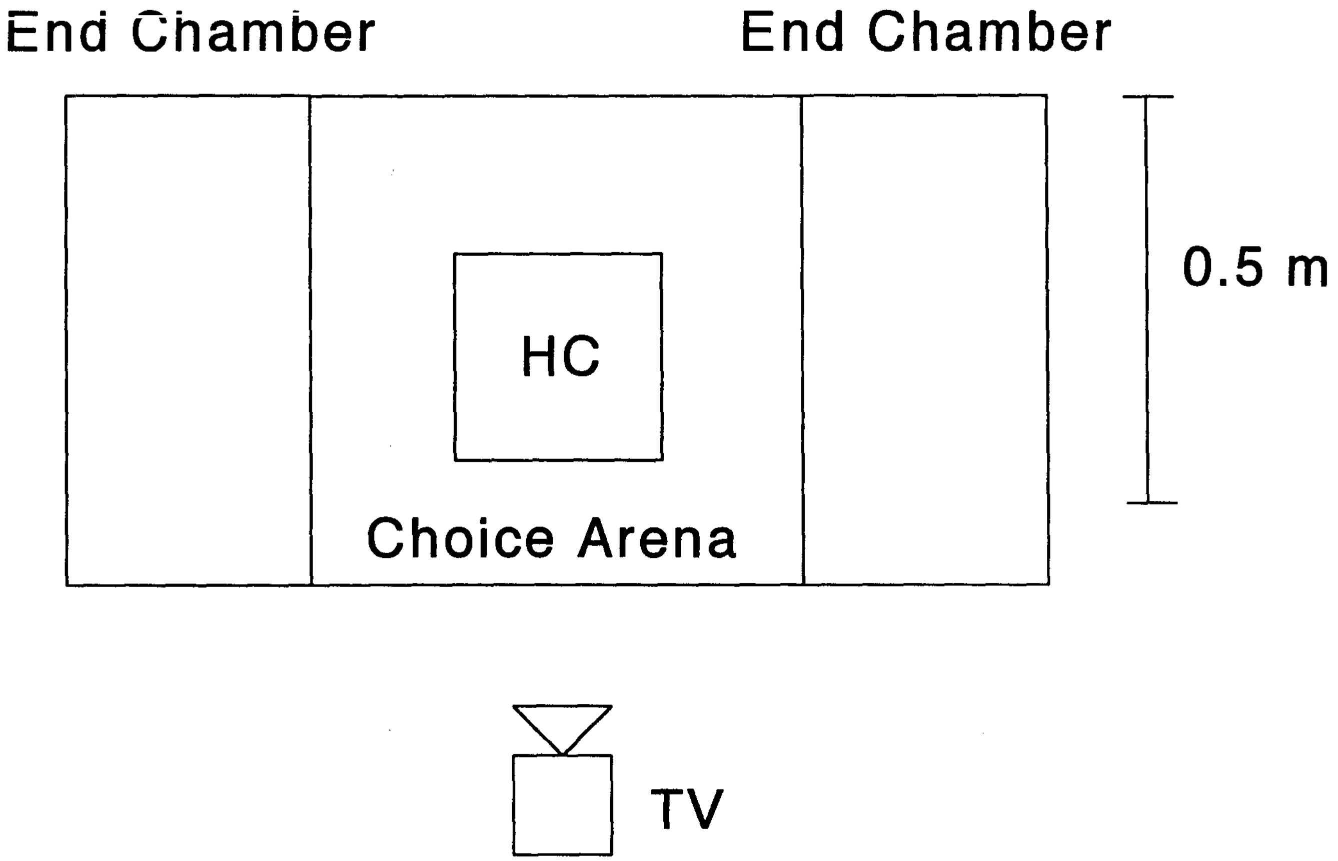
Figure 3. Mean change from pre- to post-tests in the number of minutes that focal females spent on the side of the apparatus containing their respective non-preferred males in experiment 2 for the male-court-female, male-court, and isolate groups. See caption of Fig. 2 for explanation of the cartoons appearing above histograms. Bars = ± 1 SEM.

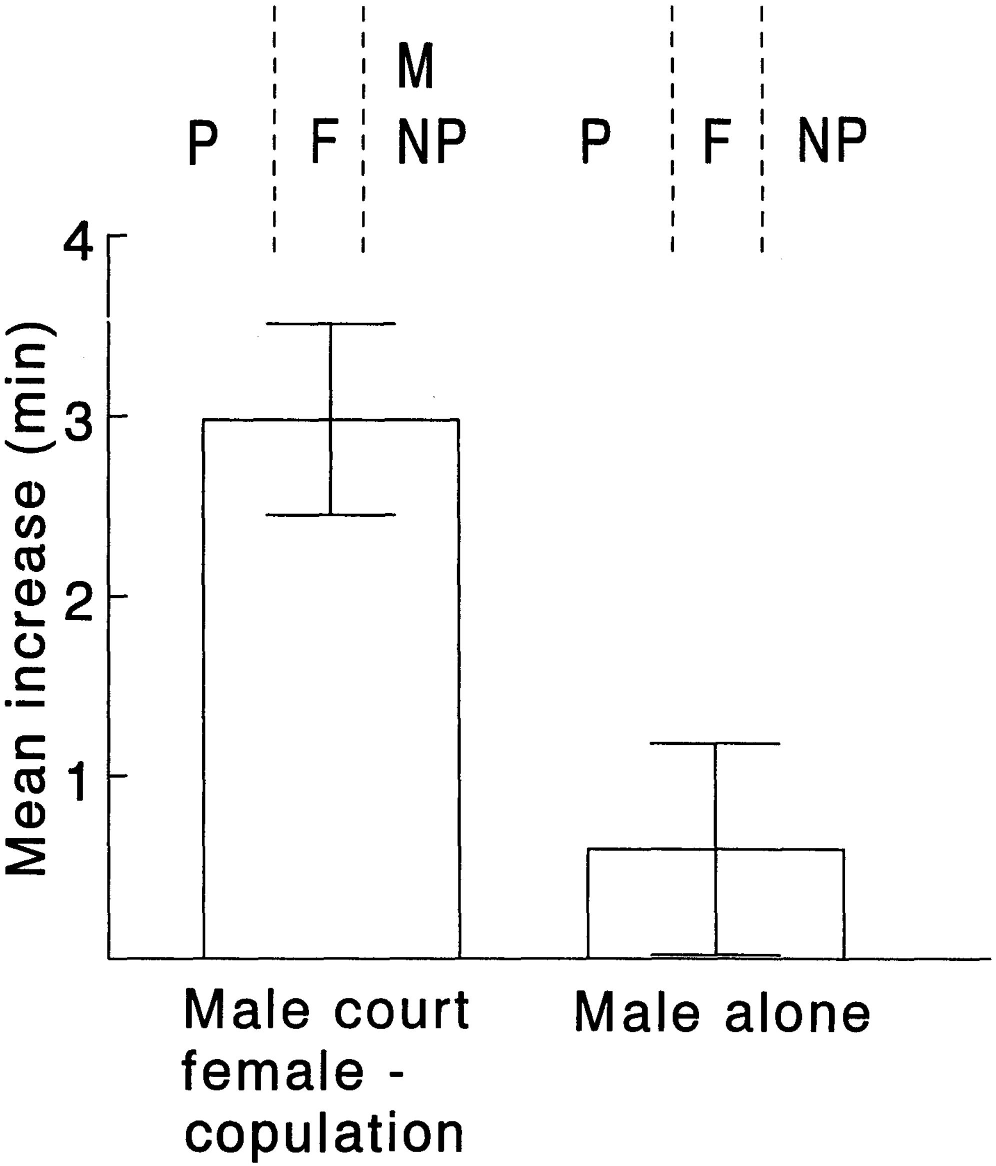
Figure 4. Mean change from pre to post-tests in the number of minutes that focal females spent on the side of the apparatus containing their respective non-preferred males in experiment 3 for the isolate and male-male-isolate groups. See caption of Fig. 2 for explanation of the cartoons appearing above histograms. Bars = ± 1 SEM.

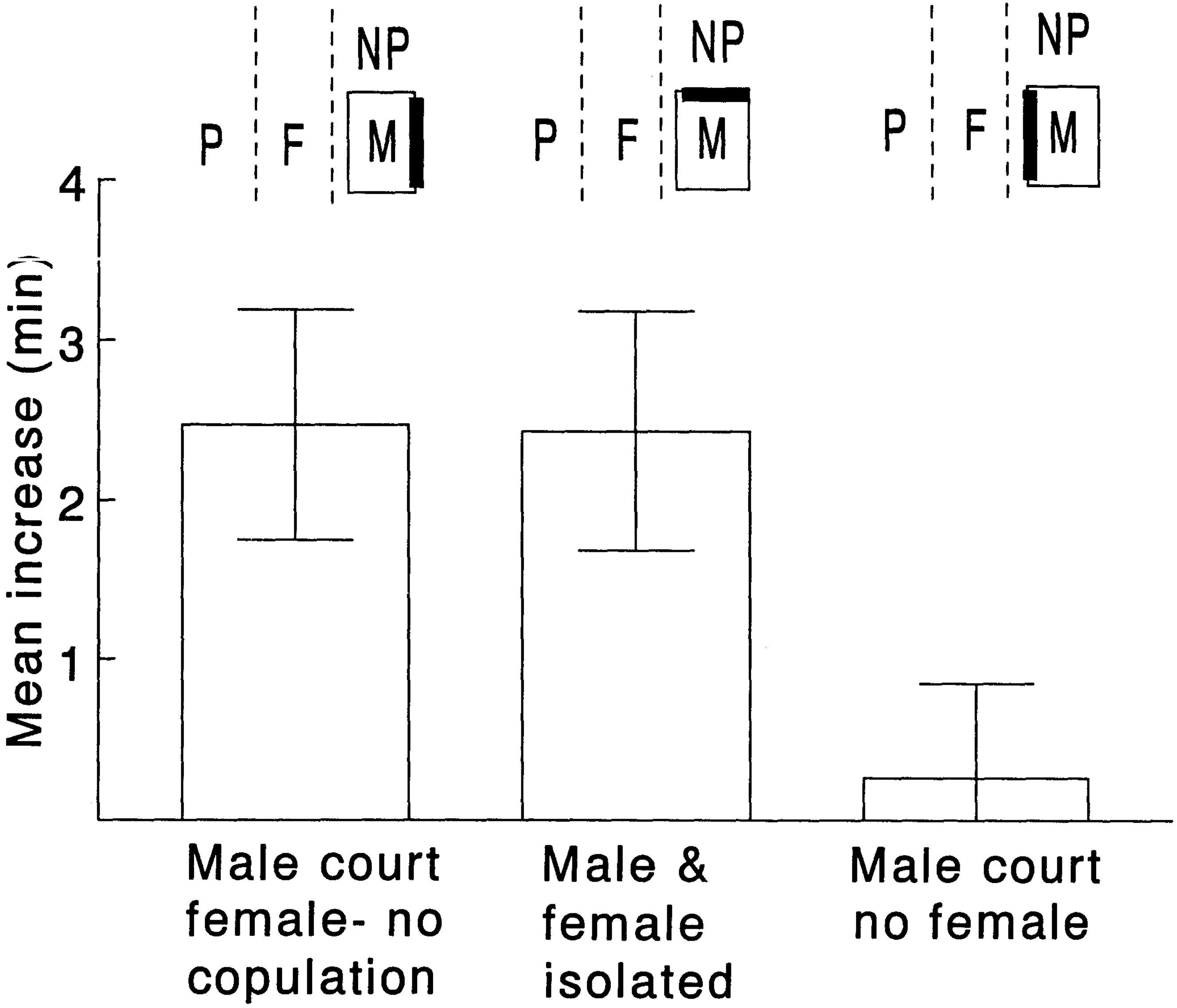
Figure 5. Mean change from pre- to post-tests in the number of minutes that focal females spent on the side of the apparatus containing their respective non-

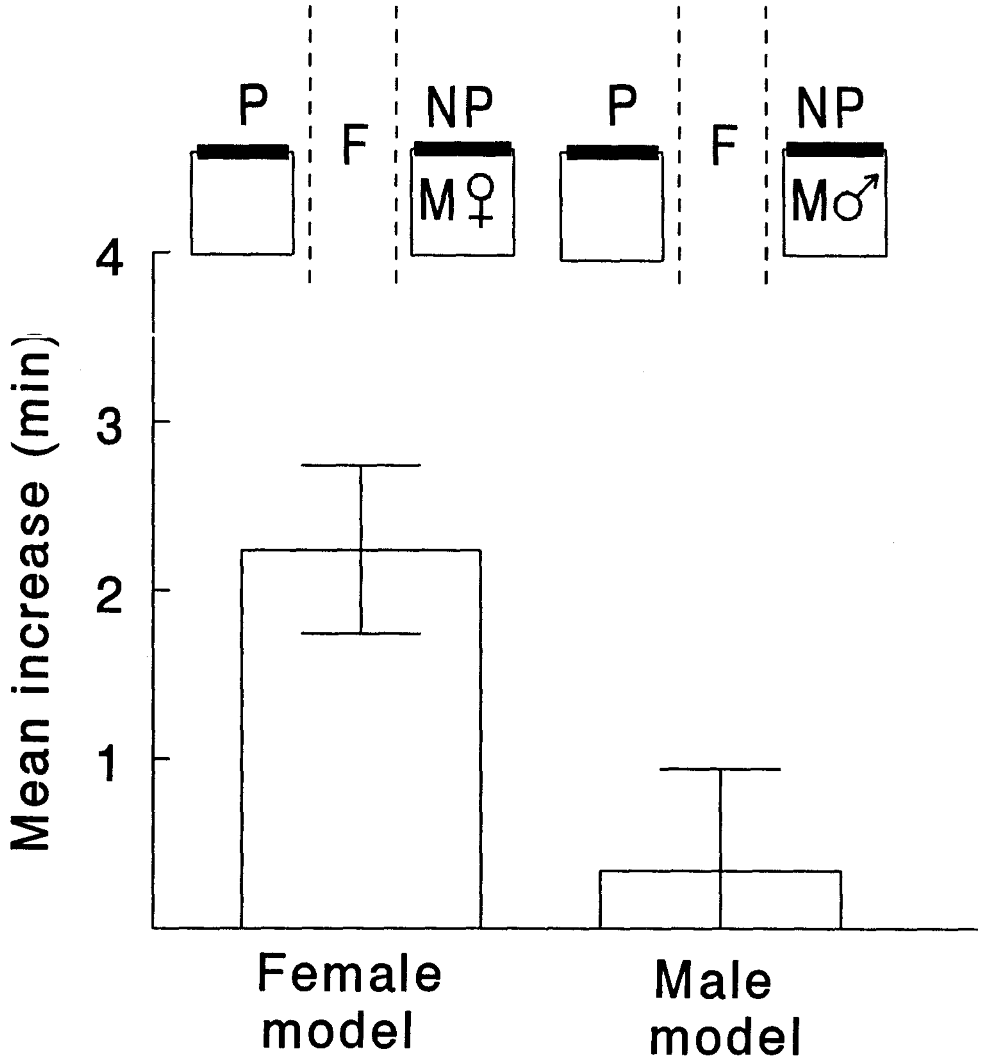
preferred males for the model-female, male-court-female and male-alone groups in experiment 4. See caption of Fig. 2 for explanation of the cartoons appearing above histograms. Bars = ± 1 SEM.

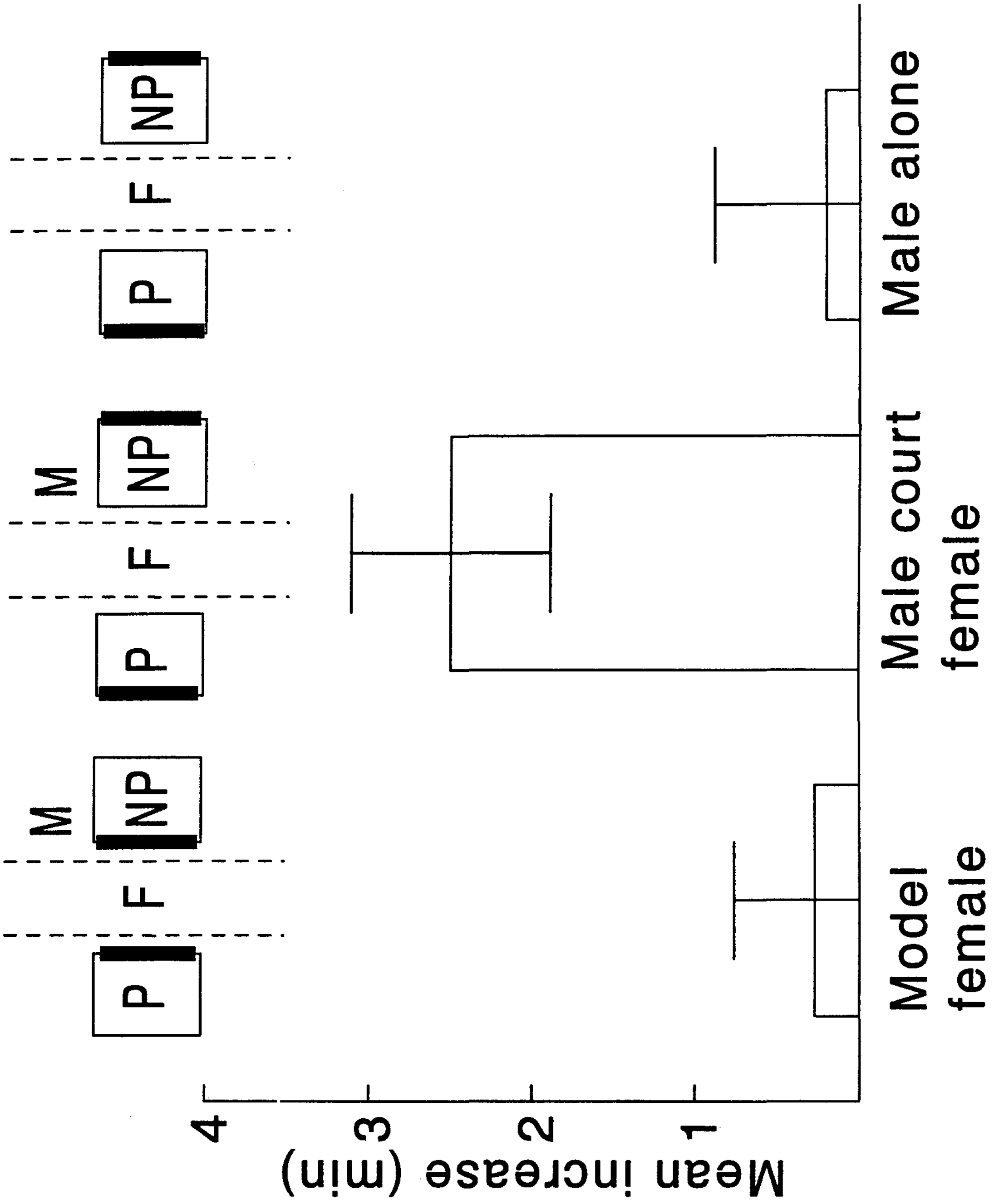
Figure 6. Mean change from pre- to post-tests in the number of minutes that focal females spent on the side of the apparatus containing their respective non-preferred males for the mating, mating-switch and control-switch groups in experiment 5. Bars = ± 1 SEM.

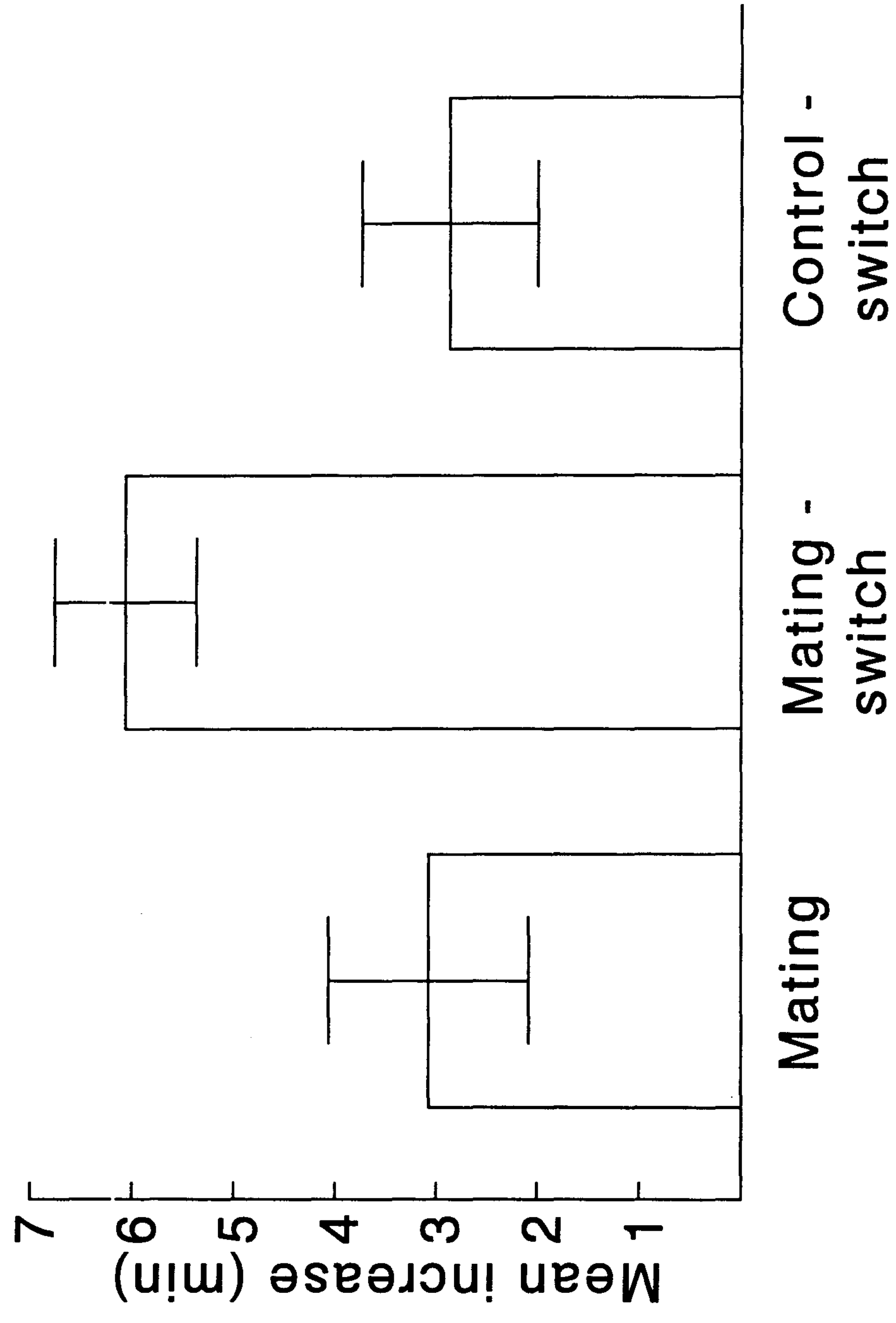

End Chamber
End Chamber
0.5 m
HC
Choice Arena
TV


P
F
M
NP
P
F
NP
4
3
2
1
Mean increase (min)
Male court female - copulation
Male alone


P
F
NP
M
P
F
NP
M
P
F
NP
M
4
3
2
1
Mean increase (min)
Male court female- no copulation
Male & female isolated
Male court no female


P
F
NP
M♀
P
F
NP
M♂
4
3
2
1
Mean increase (min)
Female model
Male model


Mean increase (min)
1
2
3
4
P
F
M
NP
P
F
M
NP
P
F
NP
Model female
Male court female
Male alone


Mean increase (min)
7
6
5
4
3
2
1
Mating
Mating - switch
Control - switch

Chapter 4

Social effects on mate choices of male Japanese quail, *Coturnix japonica*

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DAVID J. WHITE & BENNETT G. GALEF, JR

Department of Psychology, McMaster University

Abstract

In four experiments, we examined effects on affiliative preferences of 'focal' male Japanese quail of seeing a conspecific female interact with another male. Each experiment was conducted in three, 10-min phases: (1) a pre-test during which a focal male chose between two females; (2) an observation phase, when each focal male watched the female he had spent more time near during the pre-test (his 'preferred' female) interact with another male (referred to as a 'model' male); and (3) a post-test, during which each focal male again chose between his non-preferred and preferred females. Focal males decreased their preferences for preferred females after seeing them together with a model male, even when preferred females and model males were separated by a transparent barrier that prevented them from mating, but allowed them to court. A focal male's preference for his preferred female was not decreased when she mated with a model male when out of sight of the focal. These first results could reflect a tendency for males simply to avoid areas where they saw conspecifics courting. However, focal males also showed reduced preferences for preferred females they had seen mate when the locations of preferred and non-preferred females were reversed between observation and post-test phases of the experiment and effects of transposition were controlled for. We concluded that male quail tend to avoid areas that recently contained courting pairs as well as particular females seen courting.

Results of recent experiments have shown that mate choices of female Japanese quail, *Coturnix japonica*, can be influenced by their observation of the behaviour of conspecific females (Galef & White 1998: chapter 2; White & Galef 1999: chapter 3). When given a choice between males, female quail spend more time affiliating with males they have seen standing near, courting, or mating with other females. Such use of social information in selecting a sex partner could, under some circumstances, reduce the cost to females of identifying desirable partners (for review, see Gibson & Höglund 1992; Dugatkin 1996b).

In most species, females incur the preponderance of costs of reproduction, and reproductive failure is less costly for males than for females. Consequently, males would, in general, be expected to be less discriminating than females when choosing sexual partners. Still, as Andersson (1994) has argued, one might expect males to be selective in choosing mates whenever: (1) there is predictable variation in the reproductive potential of females, (2) males have the opportunity to mate with more than one female, and (3) mating with any one female reduces a male's chances of fertilizing other females. Indeed, there are several species of vertebrate in which males are known to be choosy (Erickson & Zenone 1976; van den Berghe & Warner 1989; Sargent, Gross & van den Berghe 1986; Berven 1981; Grant, Casey, Bryant & Shahsavarani 1995). In avian species examined to date (unfortunately, there are no *Corturnix* species among them), the first of two males to mate within a brief period with a female fertilizes the majority of her eggs (Birkhead 1988; Birkhead & Møller 1992), though this first-male advantage is gradually reversed over hours or days. Males of such species might be expected to show a brief decrease in interest in females seen mating with other males. Predicting the effects of observation of females mating on mate preference of male Japanese quail is complicated by females' ability to exert some control over fertilization of their eggs (Adkins-Regan 1995), and it is not known how this active sperm selection interacts with effects of sperm precedence.

In the present experiments, we asked whether the affiliative preference of male Japanese quail, like those of females of their species, might be influenced by seeing potential mates engage in sexual behaviour.

General Methods

Subjects

Groups of 10 male and 10 female Japanese quail purchased from a commercial breeder (Speck's Poultry Farm, St. Mary's, Ontario) when 48 days of age served as subjects in each of the experiments reported below. After transport to our laboratory in Hamilton, Ontario, we placed each bird in an individual, stainless-steel cage, measuring 45.7 x 61.0 x 40.6 cm, housed in a colony room illuminated for 16-hr/day, with light onset at 0600 h.

We maintained all birds on ad libitum Mazuri Pheasant Starter 5637 (PMI Feeds, St. Louis, MO) and water and, at the insistence of our University veterinarian, gave each bird biweekly access to a handful of autoclaved hay that was intended to "enrich" their maintenance environment.

We did not start experiments for 30 days, waiting until the birds had come into breeding condition in response to exposure to light for 16 hr/day. We considered females ready to breed when they started to lay eggs once every 2 days.

To determine when males were ready to breed, we placed each male with females in breeding condition in the apparatus we subsequently used for experiments. We paired each male with a randomly selected female each day until he either mounted females on 2 successive days or 2 weeks passed without his mounting a female. We, thus, accustomed both males and females to mating in the experimental apparatus before we started experiments. We used as subjects only those males that reliably mounted females. We left those males that reached criterion sexual performance in isolation for 7 to 10 days, before we started experiments.

Testing schedule

To be sure that we did not repeatedly use the same males with the same females, before beginning each experiment, we randomly assigned males and females to quartets with the restriction that no male was in more than one quartet with any female. We then randomly assigned one of the two males in each quartet to serve as a 'focal' male and the other to serve as a 'model' male (i.e. a mate for one of the females) in that quartet. Although it would have been preferable if no animal ever participated twice in our experiments, practical constraints made it impossible to maintain the hundred or more sexually active quail needed to do so. We did ensure that in each experiment: (1) no focal male ever saw any female twice, (2) no two focal males ever chose between the same pair of females, (3) no male ever served twice as the model male for the same focal male, and (4) on those days when scheduling required that a male participate in the experiment twice on the same day, he never served twice as a model male or twice as a focal male and always served as a focal male before serving as a model male.

Each male served as a focal male once and only once in each condition in an experiment, and within each experiment, we counter-balanced the order in which males served in conditions.

Apparatus

We conducted all experiments in an enclosure, measuring 121.9 x 61.0 x 30.5 cm, constructed of painted plywood (Fig. 1). The enclosure had a Plexiglas roof and front wall, two hardware-cloth partitions, and rested on an aluminum tray covered with disposable, absorbent paper pads (Tray Liners, Lilo Products, Hamilton, Ontario, Canada).

The two hardware-cloth (1/2-in (1.27-cm) mesh) partitions, placed 30.5 cm from opposite ends of the enclosure, divided it into three compartments. We cut a 25.4 x 25.4 cm opening in the centre of the transparent Plexiglas roof of the central compartment through which we could raise or lower a transparent Plexiglas holding cage measuring 25.2 x 25.2 x 40.6 (Fig. 1) using a pulley system operated from a room adjacent to that housing the enclosure.

We also drew a line from top to bottom of the front wall of the enclosure, at the midpoint of the central compartment. This line enabled us to determine reliably, at any time, the end of the enclosure to which a male was closest.

A colour CCTV video camera (Panasonic WV-CP412) attached to a video-cassette recorder (Panasonic AG-1240) and colour video monitor (CT 1331Y) faced the transparent Plexiglas front wall of the enclosure permitting us both to observe in real time all behaviour occurring within the enclosure and to record that behaviour for later scoring.

Procedure

Each of the experiments described below consisted of three 10-min phases. Phase 1 was a pre-test we used to determine a 'focal' male's initial preference between two females. Phase 2 was an observation period during which each focal male had opportunity to observe one of the two females that he had seen during the pre-test together with another male. Phase 3 was a post-test used to again determine a focal male's preference between the same two females that he had seen during the pre-test.

Experiments differed only in manipulations carried out during phase 2, the observation phase of the experiment.

Phase 1: Pre-test.

To begin an experiment, we placed a reproductively active female quail in each of the two end chambers of the apparatus and a focal male in the holding cage in the center of the apparatus and left all three animals undisturbed for 30 s.

We then raised the holding cage approximately 15 cm thus permitting the focal male to move freely about the central compartment of the enclosure.

We began to take data as soon as the focal male took his first step after we had raised the holding cage that had restrained him. For the next 10 min, we recorded the amount of time the focal male spent on each side of the mid-line of the enclosure. During the pre-test, males moved between the two ends of the central compartment, often orienting towards females and occasionally displaying to them. We labeled the female held on the side of the enclosure where the male spent the majority of the 10-min pre-test as that male's 'preferred' female and the other female as his 'non-preferred' female.

Phase 2: Observation

To begin the observation phase, we returned the focal male to the holding cage and then placed a second 'model' male in the end compartment that held the focal male's preferred female. We then left the four birds undisturbed for 10 min so that the focal male could observe his preferred female with the model male and his non-preferred female alone in her end of the enclosure. We recorded whether the preferred female mated with the model male.

Phase 3: Post-test

At the end of the observation phase, we removed the model male from the enclosure and repeated the procedure we had used during the pre-test (i.e. we released the focal male from the holding cage and, once he had started to walk, recorded the time that he spent on each side of the mid-line of the enclosure).

Inter-observer reliability

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

Data Analysis

To control for each male's serving as a focal male in each condition in an experiment, we analyzed the data using either paired t tests (when there were only two conditions in an experiment) or repeated-measures ANOVAs (when there were more than two conditions in an experiment).

EXPERIMENT 1: EFFECTS ON FOCAL MALE MATE CHOICE OF OBSERVING A PREFERRED FEMALE MATE WITH A MODEL MALE

We undertook experiment 1 to determine whether, during the post-test, a focal male Japanese quail would spend less time near the female he preferred during the pre-test, if he had seen her mate with a model male during the observation period.

Methods

Subjects

We, first, randomly assigned 15 males and 18 females from two shipments to 30 quartets. Then we assigned each quartet to either mating or control conditions (N = 15 quartets/condition) with the restriction that each male serve only once in each condition.

Procedure

We treated focal males when assigned to the mating condition as described in General Methods. They first chose between two females, then saw their preferred female mate with a model male, and during the post-test, chose between the same two females that they had chosen between during the pre-test.

We treated focal males when assigned to the control condition exactly as we treated focal males when they were assigned to the mating condition except that we did not place a model male in the apparatus during the observation phase of the experiment.

Results

Pre-test

During the pre-test, male subjects while in the mating condition spent a mean (± SE) of 7.31 ± 0.42 min near their respective preferred females. When the same subjects were in the control condition, they spent 6.42 ± 0.31 min near their respective preferred females (paired *t* test: $t_{14} = 1.64$, NS).

Observation phase

All model males mounted females when given the opportunity to do so.

Post-test

When in the mating condition (i.e. when they had the opportunity to see their respective preferred females mate during the observation phase of the experiment), focal males spent significantly less time with their preferred females than they had during the pre-test (paired *t* test: $t_{14} = 3.34$, $P < 0.005$; Fig. 2). To the contrary, focal males when in the control condition (i.e. when their preferred females did not mate with model males during the observation phase), did not show a change between pre-test and post-test in the time that they spent on the side of the enclosure containing their respective preferred females ($t_{14} = -1.78$, NS; Fig. 2).

Further, when males were focal subjects in the mating condition, they showed a significantly greater change from pre-test to post-test in the time they spent near their preferred female than when they were focal subjects in the control condition. (paired *t* test, $t_{14} = 3.45$, $P < 0.01$).

Also, when we examined each male's first experience as a focal subject, we found that 5 of the 8 focal males assigned first to the mating condition spent less than half of the 10-min post-test on the side of the enclosure containing the female that they had preferred during the pre-test, while 0 of the 7 focal males assigned first to the control condition showed a similar change in affiliative behaviour between pre-test and post-test (Fisher's exact test: $P < 0.05$). This finding, like the results of the paired *t* tests is consistent with the hypothesis that focal males should decrease their tendency to affiliate with females after seeing them mate with other male.

When, for symmetry, we repeated experiment 1 with a new set of subjects (n=9) but placed the model male with each focal males' non-preferred female, rather than with his preferred female, we found a non-significant change between pre-test and post-test in the time focal males affiliated with their respective non-preferred females (-0.58 ± 1.10 min; paired *t* test: $t_8 = 0.53$, NS). During the pre-test, focal males had spent 7.66 ± 0.51 min in contact with their preferred females, and it therefore seems likely that a ceiling effect prevented us from seeing any statistically significant effect of focal males observation of their respective non-preferred females mating with model males.

Discussion

The results of experiment 1 are consistent with the hypothesis that male Japanese quail tend to avoid affiliating with females that they have seen mating. The proximal cause of this change in preference remains to be determined.

EXPERIMENT 2: DOES MATING CHANGE A FEMALE'S ATTRACTIVENESS TO MALES?

The changes in males' behaviour towards preferred females seen in experiment 1 may have been a result not of focal males seeing their respective preferred females mate, but of changes in the behaviour or appearance of females after mating. In the present experiment, we compared the behaviour of focal males towards their respective preferred females when those females mated during the observation phase of the experiment and focal males either saw (visible condition) or did not see (blind condition) their preferred females in the act of mating.

Methods

Subjects

We, first, randomly assigned 9 male and 11 female quail to 18 quartets as described in General Methods. We then randomly assigned these quartets to visible and blind conditions (N = 9 quartets/condition).

Procedure

The procedure was identical to that described in General Methods except that, in the present experiment, we modified the holding cage in which we placed focal males during the observation phase of the experiment. We made two opposite walls of the holding cage opaque by attaching to them pieces of white Bristol board, measuring 30 x 30 cm.

During the observation phase, we placed focal males when assigned to the visible condition in the holding cage with the opaque walls facing the front and back of the enclosure, so that the focal males could see both their preferred and non-preferred females. When the same males were in the blind condition, we treated them as we treated them when they were in the visible condition, except that, during the observation phase, we oriented the holding cage so that its opaque walls prevented focal males from seeing either their preferred or non-preferred females.

Results

Pre-test

During the pre-test, focal males when in the visible and blind conditions spent a mean (± SE) of, respectively, 7.77 ± 0.62 min and 7.81 ± 0.56 min closer to their preferred than to their non-preferred females. There was no statistical difference between groups in the time focal males spent near their respective preferred females (paired *t* test: $t_8 = 0.06$, NS).

Observation phase

All model males mounted females when given the opportunity to do so.

Post-test

Focal males when in the visible condition showed a significantly greater decrease between pre-test and post-test in the time that they spent near their preferred female than they did when in the blind condition ($t_8 = 3.42$, $P < 0.01$; Fig. 3). Only when focal males were in the visible condition did they show a significant decrease between pre-test and post-test in the time that they spent on the side of the enclosure that held their preferred female (paired *t* tests: visible group, $t_8 = 3.23$, $P < 0.02$; blind group: $t_8 = -1.57$, NS; Fig. 3).

Discussion

The results indicate that males are less attracted to females they have seen mating because they saw mating occur, not because of some change in the appearance or behaviour of females that resulted from mating.

EXPERIMENT 3: WHAT DO MALES HAVE TO SEE PREFERRED FEMALES DO IN ORDER TO LOSE INTEREST IN THEM?

In experiment 3, we determined the type of interaction between model male and preferred female that a focal male had to observe, if he were to show a reduced tendency to affiliate with a preferred female. Perhaps a focal male had to see his preferred female actually copulate with another male, if his preference for her was to be reduced. Perhaps seeing a preferred female simply standing near another male would suffice to reduce her attractiveness.

Methods

Subjects

We, first, assigned 10 male and 10 female quail to 30 quartets, and then assigned each quartet to one of the three groups described in Procedure (N = 10/group).

Apparatus

The apparatus that we used in experiment 3 was identical to that described in General Methods except that during the observation phase of the experiment we confined the model male in a transparent Plexiglas holding cage, measuring 25.2 x 25.2 x 40.5 cm, with one wall made opaque by attaching to it a piece of white Bristol board measuring 30 x 30 cm. To control for effects of presence of a holding cage in the end compartment of the enclosure containing a focal male's preferred female, we placed an identical holding cage, in the same orientation, in the end compartment of the enclosure containing each focal male's non-preferred female, but placed no model male in it.

Procedure

The procedure of experiment 3 was identical to that described in General Methods except that, during the observation phase, we confined model males, as well as focal males in holding cages. The only difference in treatment of focal males when assigned to the different conditions was in the orientation during the observation phase of the experiment of the opaque wall of the holding cage containing the model male. When focal males were assigned to the female-alone condition, the opaque wall of the cage holding the model male was located between the focal male and the model male so that, during the observation phase, the focal male saw his preferred female standing alone. When focal males were assigned to the male-female-isolated condition, during the observation phase of the experiment, we placed the opaque wall of the cage holding the model male between the model male and the focal male's preferred female, so that each focal male saw his preferred female and a strange male standing near one another, but not interacting. Last, when we assigned males to the male-court condition we placed the model male in the holding cage with its opaque wall facing away from the focal male. Consequently, during the observation phase of the experiment, each focal male when in the male-court condition saw a model male actively courting, but not mating with, his preferred female.

Results and Discussion

Pre-test

During the pre-test, when focal males were assigned to female-alone (Mean ± 1 SEM = 7.43 ± 0.50 min), male-court (7.53 ± 0.42 min) and male-female isolated conditions (7.59 ± 0.35 min), they did not differ in the time that they spent closer to their preferred females than to their non-preferred females (repeated-measures ANOVA, $F_{2,18} = 0.03$, NS).

Post-test

We found a significant effect of condition on the change between pre-test and post-test in the time that focal males spent nearer their preferred than non-preferred females (repeated-measures ANOVA: $F_{2,18} = 4.76$, $P < 0.03$; Fig. 4), and only when focal males were assigned to the male-court condition did they show a significant decrease between pre-test and post-test in the time that they spent on the side of the enclosure that held their preferred females (male-court condition: paired *t* test, $t_9 = 2.98$, $P < 0.02$; male-female isolated and female-alone conditions: both $t\text{s}_9 > 0.10$, NS; Fig. 4). Post-hoc tests revealed that when assigned to the male-court condition focal males decreased the time that they spent with their respective preferred females significantly more than they did when assigned to either male-female isolated or female-alone conditions (Tukey's tests, both $P\text{s} < 0.05$).

The results indicate that a focal male has to see a model male actively court his preferred female, if the focal male's attraction to that female is to be reduced. This result differs from that obtained by White and Galef (1999: chapter 3) in studies of social influences on mate choices of female Japanese quail. Attractiveness of a non-preferred male quail to a focal female is increased when she sees him simply standing near a model female (White & Galef 1999: chapter 3).

EXPERIMENT 4: CAN FOCAL MALES IDENTIFY AN INDIVIDUAL FEMALE SEEN COPULATING WITH A MODEL MALE?

The results of experiments 1 to 3, while consistent with the hypothesis that a focal male is less attracted to a female after seeing her mate with another male, can also be interpreted as showing that a focal male tends to avoid areas where he has seen another male. We undertook experiment 4 to determine whether the changes in the affiliation of focal males with preferred females seen in experiments 1 to 3 might represent changes in response to individual females seen interacting with model males, rather than changes in attractiveness of places where a female has been seen interacting with a male.

Methods

Subjects

Thirteen male and 19 female quail from two shipments served as subjects. We randomly assigned these 32 animals to 39 quartets, and then assigned these quartets to the three groups described in Procedure.

Apparatus

The apparatus was that used in experiments 1 to 3.

Procedure

We treated focal males when assigned to the mating condition exactly as we treated focal males when assigned to the mating condition in experiment 1 except that at the end of the observation phase, and before starting the post-test, each female was first removed from, then replaced in, the same end chamber that she had occupied since the start of the pre-test. When focal males were assigned to the mating condition, during the observation phase of the experiment, they saw their respective preferred females mate with model males. We treated focal males when assigned to the mating-switch condition exactly as we treated focal males when assigned to the mating condition, except that at the end of the observation period, and before starting the post-test, we reversed the position of the two females. We controlled for possible effects of disturbance caused by moving females in the mating-switch condition (White & Galef 1999: chapter 3, exp. 5), by treating focal males when assigned to the control-switch condition exactly as we treated focal males when assigned to the mating-switch condition with one exception. During the observation phase of the experiment, we did not place a model male with each focal males' preferred female.

Results

Pre-test

During the pre-test phase of the experiment, when focal males were assigned to mating, mating-switch and control-switch conditions they spent, respectively, a mean (± SE) of 8.41 ± 0.34, 7.51 ± 0.40, and 7.79 ± 0.45 min of the 10-min pre-test closer to their respective preferred than non-preferred females (repeated-measures ANOVA: $F_{2,24} = 1.40$, NS).

Post-test

We found a significant effect of condition on the change between pre-test and post-test in the time that focal males spent nearer their preferred than non-preferred females (repeated-measures ANOVA: $F_{2,24} = 3.63, P < 0.05$; Fig. 5); focal males when assigned to both mating and mating-switch conditions showed a significant decrease between pre-test and post-test in the time they spent on the side of the enclosure that held their respective preferred females (paired *t* tests: mating-condition $t_{12} = 3.79, P < 0.01$; mating-switch condition $t_{12} = 3.65, P < 0.01$, Fig. 5), while focal males when assigned to the control-switch condition did not show a change in preference between pre- and post test (paired *t* test: $t_{12} = 0.93$, NS).

Discussion

The results of experiment 4 are consistent with the view that male quail can identify individual females they see copulating with other males, and subsequently avoid contact with such females.

GENERAL DISCUSSION

'Mate-choice copying' by females and social reversal of males' mate choices

Patriquin-Meldrum & Godin (1998, p. 570) have proposed that "A female [should be] considered to have copied the mate choice of another female(s) if the probability of her choosing a specific male as a mate is increased specifically as a result of her observing other females previously choosing that same male, rather than because of any change in that male's behavior due to his prior mating or proximity to females or because of any preference by females for certain sites irrespective of the male or to aggregate with other females" (See also Dugatkin, 1992, 1996b, Pruett-Jones 1992, and Wade & Pruett-Jones 1990). By exchanging the sex of chooser and chosen in Patriquin-Meldrum & Godin's (1998) definition, one could produce a description of 'true' social influence on mate choice in males as well, what we will call 'social reversal of males' mate choices'.

Results of experiment 2 indicate that the change in attractiveness of female quail to conspecific males (like the change in attractiveness of male quail to conspecific females) is not a result of changes in behaviour or appearance caused by mating. Results of experiment 4 indicate that in male, as in female quail (Galef & White 1998: chapter 2; White & Galef: chapter 3), attractiveness of an individual of the opposite sex, not attractiveness of the area that individual occupies, can change after a member of the opposite sex has been seen copulating. Thus, the behaviour of male Japanese quail meets criteria for social reversal of male mate choice analogous to the criteria for mate-choice copying by females proposed by Patriquin-Meldrum & Godin (1998) and met by female Japanese quail.

Choice of a sex partner by male and female Japanese quail

Taken together, the results of experiments 1 to 4 provide compelling evidence that male Japanese quail, like females of their species (Galef & White 1998: chapter 2; White & Galef: chapter 3), change their tendency to affiliate with individuals of the opposite sex seen in compromising situations: female Japanese quail show an increased tendency to affiliate with male they have seen with other females (Galef & White 1998: chapter 2; White & Galef: chapter 3), male Japanese quail showed a decreased tendency to affiliate with females they have seen courted by other males. We also now know that, in both sexes of Japanese quail, affiliative preference is a very potent predictor of actual choice of a sex partner (White & Galef, in press: chapter 5). The opposite direction of the response of males and females to observation of sexual behaviour by potential mates interacting is, therefore, consistent with the hypotheses that: (1) female quail experience costs associated with selection of a sex partner, and (2) male quail experience costs associated with copulation with recently inseminated females.

Figure Captions

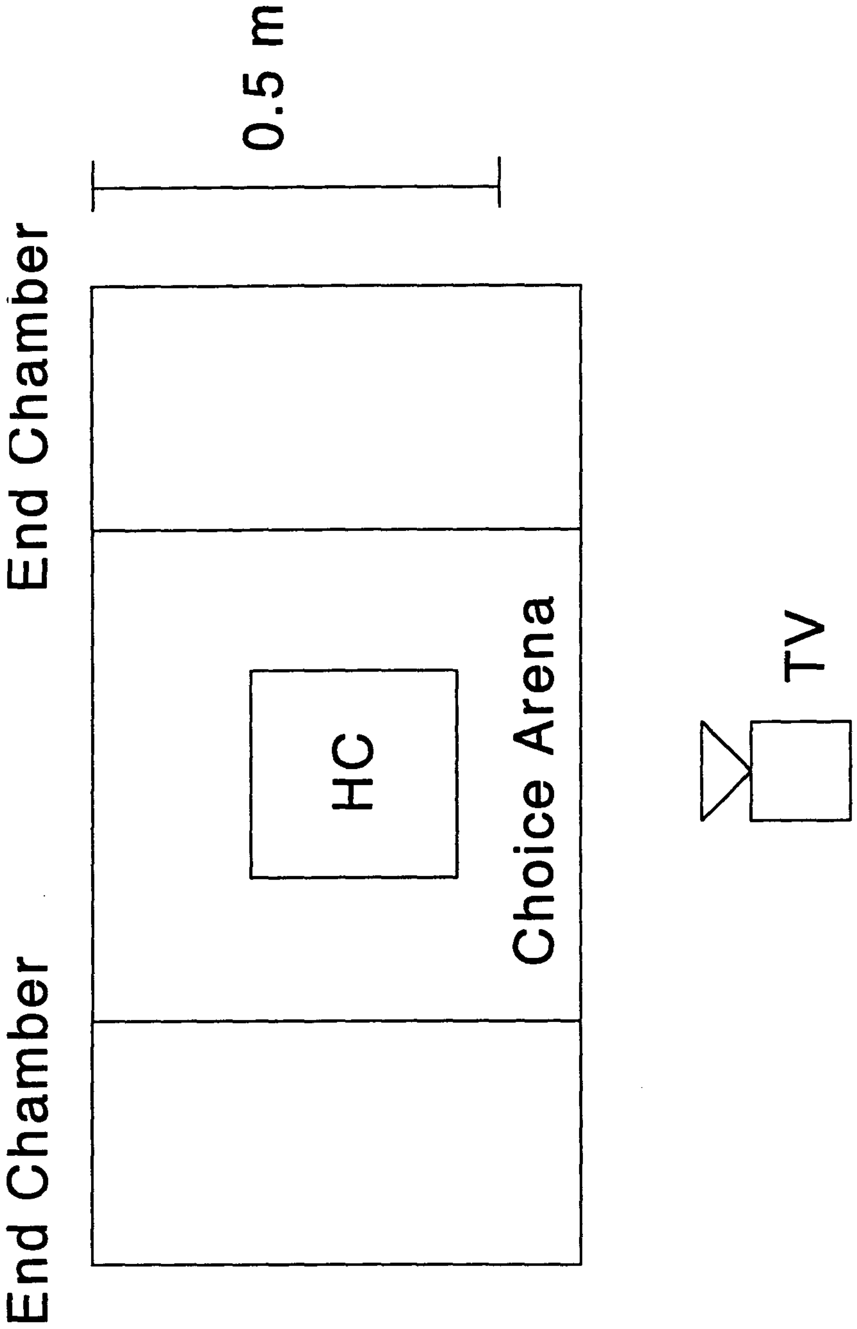
Figure 1. Overhead schematic of the apparatus. H.C. = holding cage, TV = television camera.

Figure 2. Mean change from pre-test to post-test in min that focal males in experiment 1 spent on the side of the apparatus containing their respective preferred females when assigned to mating and control conditions. P = preferred female, F = focal male, M = model male, and NP = non-preferred female. Bars = ± 1 SE.

Figure 3. Mean change from pre-test to post-test in min that focal males in experiment 2 spent on the side of the apparatus containing their respective preferred females when in visible and blind conditions. See caption of Figure 2 for explanation of the cartoons above histograms. Bars = ± 1 SE.

Figure 4. Mean change from pre-test to post-test in min that focal males in experiment 3 spent on the side of the apparatus containing their respective preferred females when in male-court, male-female-isolated, and female-alone conditions. See caption of Figure 2 for explanation of the cartoons above histograms. Bars = ± 1 SE.

Figure 5. Mean change from pre-test to post-test in min that focal males in experiment 4 spent on the side of the apparatus containing their respective preferred females when in mating, mating-switch, and control-switch conditions. Bars = ± 1 SE.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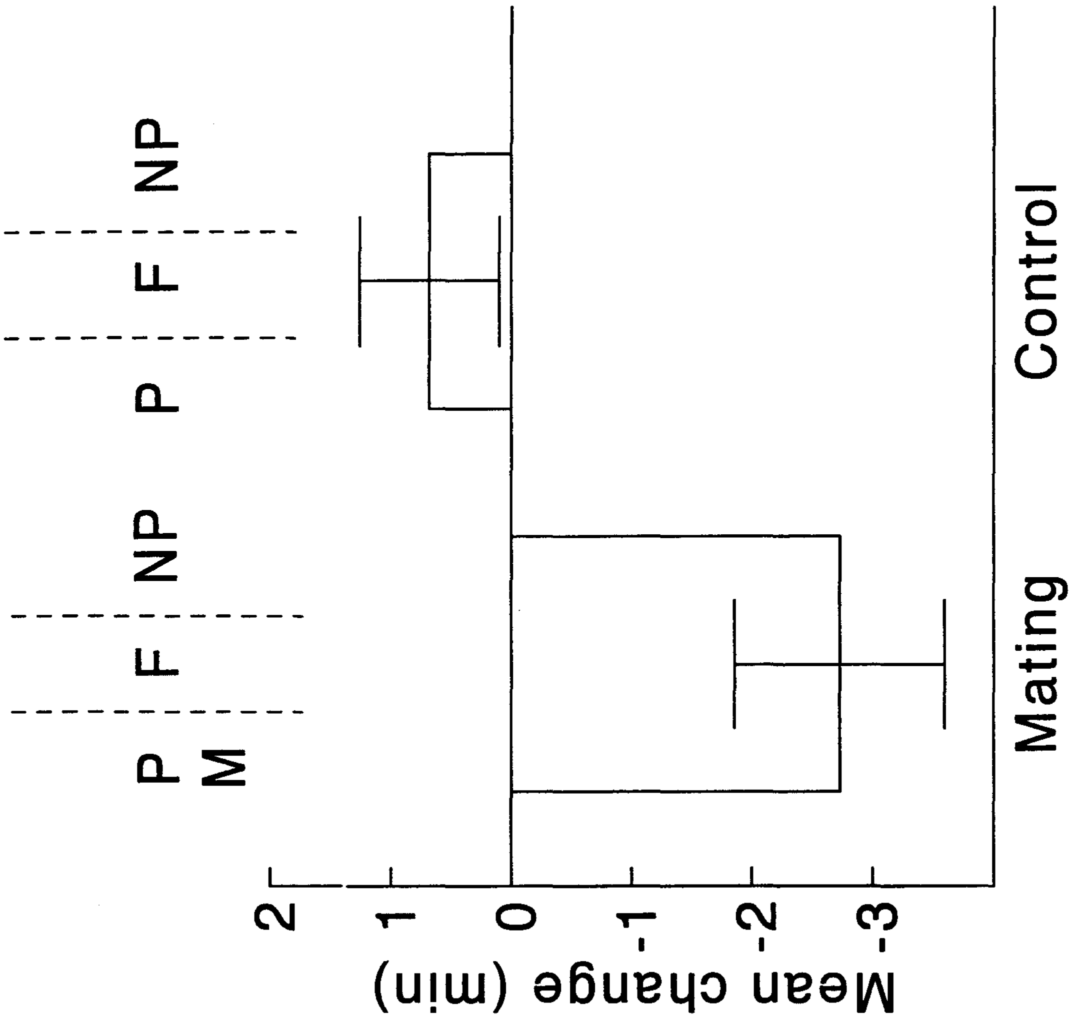
End Chamber
HC
Choice Arena
TV


Mean change (min)
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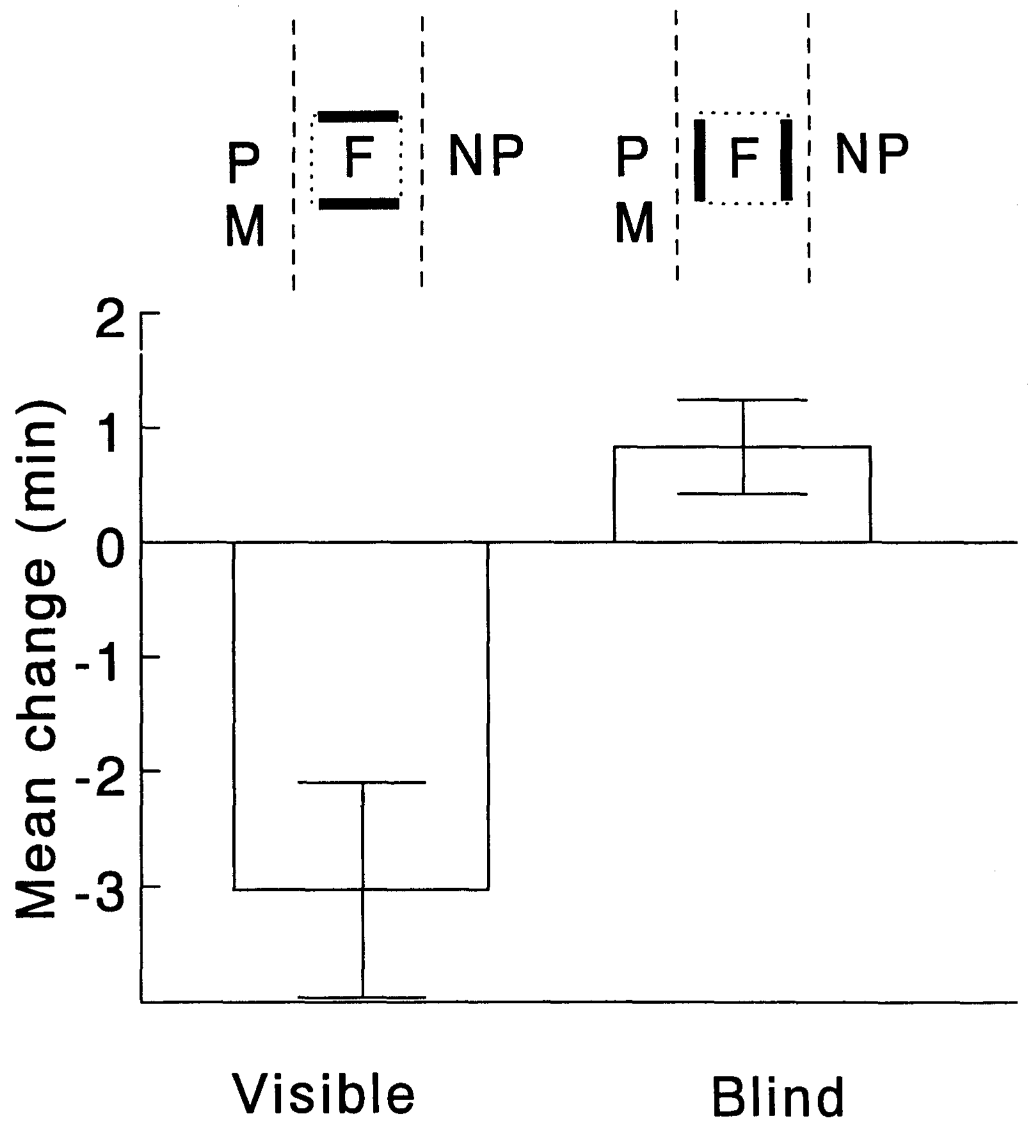
0
-1
-2
-3
P
M
F
NP
P
F
NP
Mating
Control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M
F
NP
P
M
F
NP
Mean change (min)
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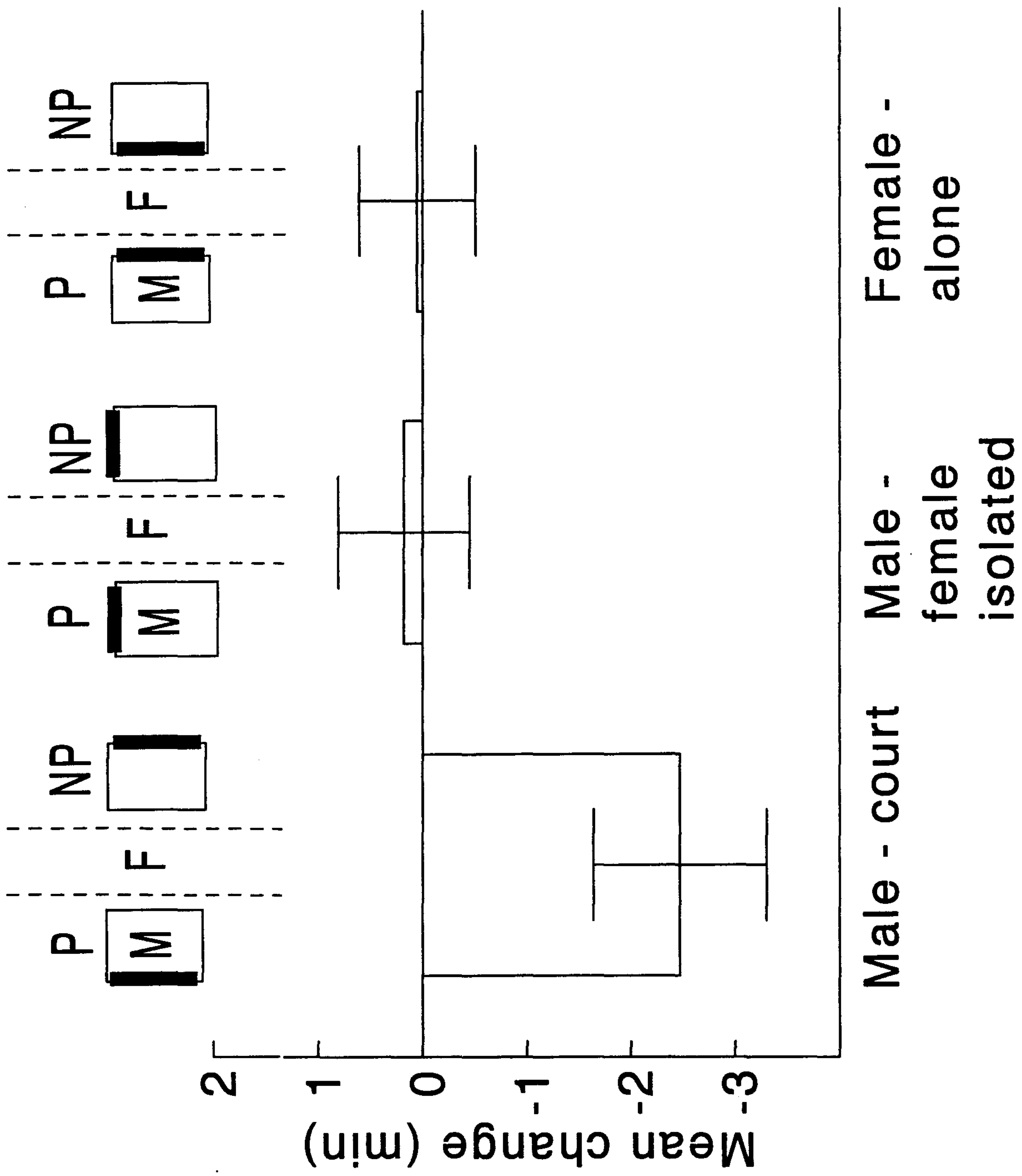
0
-1
-2
-3
Visible
Blind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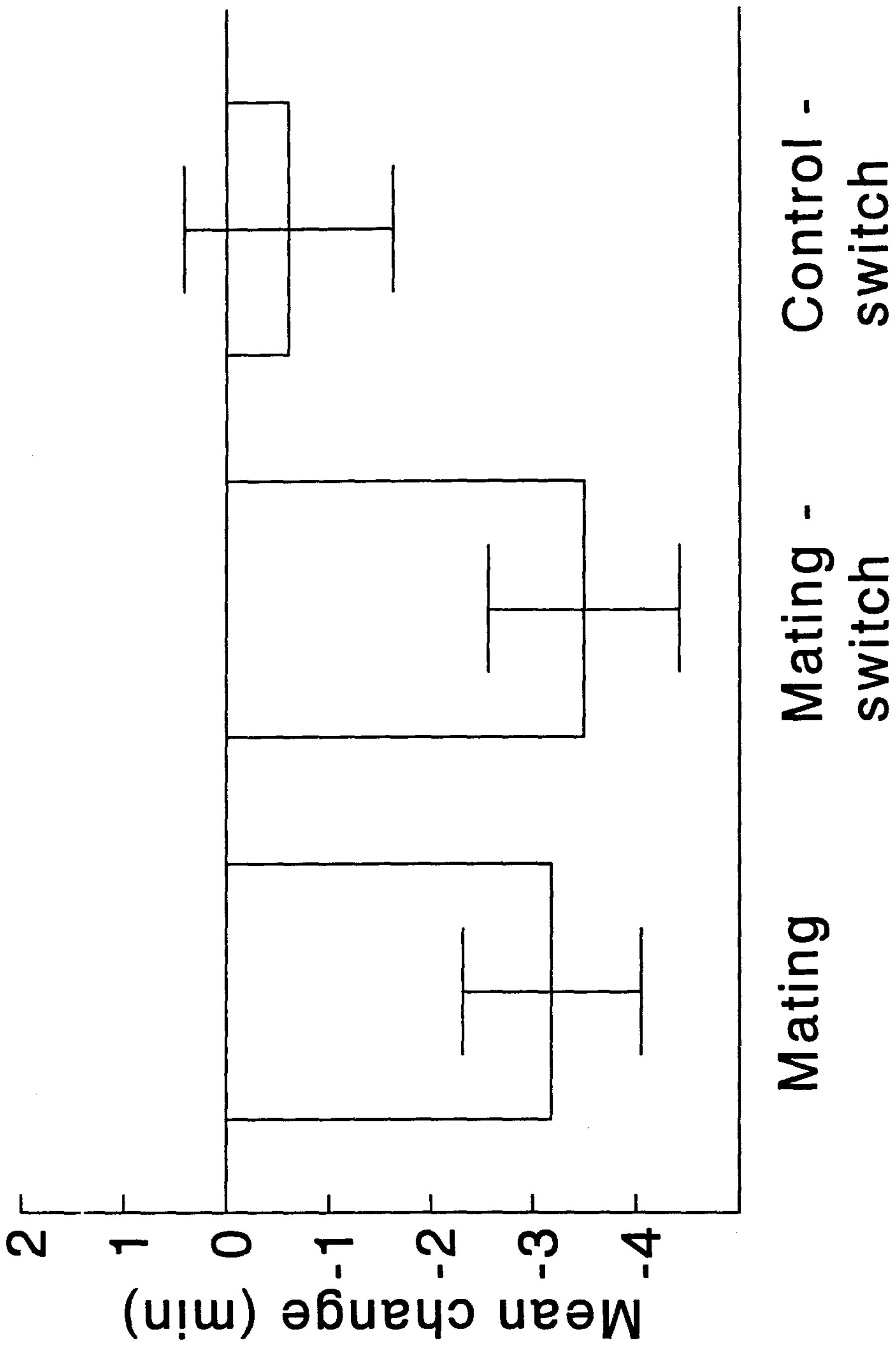
M
F
NP
P
M
F
NP
P
M
F
NP
Male - court
Male - female isolated
Female - alone
2
1
0
-1
-2
-3
Mean change (min)


Mean change (min)
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1
0
-1
-2
-3
-4
Mating
Mating - switch
Control - switch

Chapter 5

Affiliative preferences are stable and predict mate choices in both sexes of Japanese quail, *Coturnix japonica*

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DAVID J. WHITE & BENNETT G. GALEF, JR.

Department of Psychology, McMaster University

Abstract

Most laboratory studies of mate choice use affiliative tendency as a surrogate measure for actual mate preference. In a series of recent studies using affiliation as a dependent variable, we have shown that the tendency of both male and female Japanese quail to affiliate with members of the opposite sex is profoundly affected by seeing them mate with others: female quail show an increased tendency to affiliate with males that they have seen mating; male quail show a decreased tendency to affiliate with females that they have seen mating. In the present experiments, we examined: (1) the consistency of affiliative preferences of male and female quail for individuals of both the same and opposite sex, and (2) the validity of affiliative preference as a predictor of choice of an individual with whom to mate. We found that: (1) both male and female quail exhibit consistency from trial to trial in their affiliative preferences for members of the opposite sex, but not for members of the same sex, and (2) affiliative preference is a powerful predictor of choice of a partner for copulation in both male and female quail. The results show that in at least one species affiliative behaviour of females predicts their mate choice.

The study of mate choice has been largely motivated by recognition of the potential importance of heritable female preferences in the evolution of male characteristics (Andersson 1994). In the laboratory, the most commonly used method to measure mate choice, what we will refer to here as the 'standard method', involves presenting a 'focal' female with two or more 'target' males confined some distance apart, and comparing the time that the focal female spends near each target male during a single test (fishes: Noonan 1983; Basolo 1990; Dugatkin 1996b; Schlupp, Marler & Ryan 1994; Houde 1997; Howard et al. 1998; Kraak & Bakker 1998. birds: Bateson 1982; Swaddle & Cutchill 1994; Fiske & Admunsen 1997; Tobias & Hill 1998; Hill et al. 1999. mammals: Gubernick & Addington 1994).

There are, however, potential problems with using a single test of affiliative preference as a dependent measure in studies of mate choice. First, as Boake (1989) has indicated, consistency in female preference sets an upper bound on the heritability of female preference for males (Falconer 1981). Consistency of choice can increase the rate of selection for a male trait or provide stabilizing selection. On the other hand, if female mate choices vary from one occasion to the next, they will have relatively little effect on the evolution of male traits (Janetos 1980; Wiegmann et al. 1996). A single test of preference, as used in the standard method does not permit determination of consistency of female mate choice (Boake 1989) and few researchers have attempted to measure consistency of female choice (e.g. Poramarcom & Boake 1991; Møller 1994; Godin & Dugatkin 1995; Jennions, Blackwell & Passmore 1995).

Second, and more obviously, the standard method uses affiliative tendency as a dependent variable, whereas affiliative preference is biologically important only if it is positively correlated with choice of an individual with which to mate (Wagner 1998). It is rarely determined whether affiliation actually predicts mate choice. In sum, reproductive advantage is conferred on those males that reliably get chosen by females as sex partners, not on those males that females prefer to stand near.

Recently, there has been interest in the possibility that individual experience, particularly individual social experience, can modify heritable female mate preferences. Dugatkin (1996a, 1996b) has shown that female Trinidadian guppies, *Poecilia reticulata*, that observe a normally non-preferred male mate with a female exhibit an increase in preference for that male. We have provided evidence of social influences on the affiliative preferences of both male and female Japanese quail, *Coturnix japonica*; focal female quail are more likely to affiliate with a previously non-preferred male after seeing him mate with another female (Galef & White 1998: chapter 2; White & Galef 1999a: chapter 3), whereas focal male quail are less likely to affiliate with a preferred female after seeing her mate with another male (White & Galef 1999b: chapter 4).

In the present series of experiments, we determined both for male and for female quail: (1) whether affiliative preferences are reliable across repeated tests (experiment 1), and (2) whether tests of affiliative preference predict subsequent choice of a partner for copulation (experiments 2 and 3).

EXPERIMENT 1: RELIABILITY OF AFFILIATIVE PREFERENCE

In experiment 1, we determined whether affiliative preferences of individual quail of both sexes are consistent across trials. Because we were interested not only in the reliability of affiliative preferences, but also in the relationship between affiliation and sexual preference, we gave focal subjects opportunity to affiliate with target individuals of both the same and opposite sex. Differences in the reliability of focal subjects' affiliative responses, as a function of the sex of target subjects, would be consistent with the view that affiliative preferences expressed in the standard method are directly related to sexual behaviour.

Methods

Subjects

We used as subjects 21 male and 24 female Japanese quail acquired from a local commercial breeder (Speck's Poultry Farm, Vineland, ON) at 48 days of age. After we transported subjects to our laboratory (Hamilton, Ontario), we placed birds in individual, stainless-steel cages, measuring 45.7 x 61.0 x 40.6 cm, housed in a colony room that was illuminated for 16-hr/day, with light onset at 0600 h.

We maintained all birds on ad libitum Mazuri Pheasant Starter 5637 (PMI Feeds, St. Louis, MO) and water, and for environmental enrichment, twice each week we gave each bird access to a handful of autoclaved hay.

To allow birds to come into breeding condition, we waited for 30 days before we started experimental work. We considered a female to be ready to breed when she started to lay eggs once every 2 days. To determine whether males would mate when given access to females, we placed each male with a succession of females in breeding condition in one of the end chambers of the apparatus (Fig. 1) that we subsequently used for experiments. We gave each male access to a randomly selected female each day until he either mounted females on 2 successive days or 2 weeks passed without his mounting a female.

After a male had mated with two females in succession, we left him in isolation for 7 to 10 days, then started the experiment. We first assigned males and females to 32 trios, each consisting of either a single focal female and two target males (8 trios), a single focal male and two target females (8 trios), a focal male and two target males (8 trios), or a focal female and two target females (8 trios). No bird served both in a trio containing a focal male and in a trio containing a focal female.

Although it would have been preferable if each animal participated only once in the experiment, practical constraints made it impossible for us to maintain the number of quail needed to achieve that goal. We did, however, ensure that: (1) no focal subject saw any target subject twice, (2) no two focal subjects ever chose between the same pair of target subjects, and (3) no target animal served together as members of more than one trio.

Each focal female and each focal male served as a member of two trios, one containing target subjects of the same sex and one containing target subjects of the opposite sex. We counterbalanced across focal subjects the order in which they served in same-sex and opposite-sex trios.

Apparatus

We conducted all experiments in an enclosure, measuring 121.9 x 61.0 x 30.5 cm, constructed predominantly of painted plywood (Fig. 1). The enclosure had a transparent Plexiglas roof and front wall, and rested on an aluminium tray covered with disposable, absorbent paper pads (Tray Liners, Lilo Products, Hamilton, Ontario, Canada). Hardware-cloth partitions, placed 30.5 cm from opposite ends of the enclosure, divided it into three compartments.

We also drew a line from top to bottom of the front wall of the enclosure in the middle of the choice arena to enable us to determine, at any time, the end of the enclosure to which a focal subject was closer.

We cut a 25.4 x 25.4 cm opening in the centre of the roof of the choice arena so that we could raise or lower a transparent Plexiglas holding cage, measuring 25.2 x 25.2 x 40.6 cm (Fig. 1), using a pulley system that we operated from a room adjacent to that housing the enclosure.

A colour CCTV video camera (Panasonic WV-CP412) attached to a video-cassette recorder (Panasonic AG-1240) and colour video monitor (CT

1331y) faced the transparent Plexiglas front wall of the enclosure and permitted us to observe all behaviour occurring within the enclosure and to record that behaviour on videotape for later scoring.

Procedure

Each test consisted of three 10-min phases: a pre-test, a delay, and a post-test:

Pre-test

To begin the experiment, we placed a focal subject in the holding cage in the centre of the choice arena and a target subject in each end compartment of the apparatus, and then waited for 1 min to let all subjects settle down. We then started the video-tape recorder and raised the holding cage to release the focal subject. In the 10 min after the focal subject took its first step, we recorded the time he or she spent on each side of the choice arena. We refer below to the target subject held on the side of the enclosure where a focal subject spent more than half the 10-min pre-test as that focal subject's 'preferred' target subject and the other target subject as that focal subject's 'non-preferred' target subject.

Delay

At the end of the 10-min pre-test, we returned the focal subject to the holding cage and left it there undisturbed for 10-min.

Post-test

We conducted the post-test exactly as we had conducted the pre-test, first raising the holding cage, then waiting for the focal subject to take its first step, and afterwards recording, for 10 min, the time that the focal subject spent in each half of the choice arena.

We used as focal subjects, 20 female and 20 male quail, and half the focal subjects of each sex chose between two male target subjects and half between two female target subjects.

Results and Discussion

Pre-test

During the pre-test focal subjects assigned to the four kinds of trio spent an average (± SE) of from 6.47 ± 0.30 min to 9.03 ± 0.57 min nearer their respective preferred target subjects. There was a significant effect of trio assignment on the time that focal subjects in trios of the four types spent near their respective preferred target subjects (Repeated-measures ANOVA, between subjects $F_{1,13} = 21.18$, $P < 0.001$). This difference was due to differences between male and female focal subjects in the time that they spent near preferred target subjects. There was no within subjects effect of trio assignment ($F_{1,13} = 0.26$, NS) on the time that focal subjects spent near their preferred male and female target subjects.

Post-test

Both male and female focal subjects showed no change between pre- and post-test in the time that they spent with preferred subjects of the opposite sex (matched-t tests, both $ts_7 < 1.03$, NS; Fig. 2), whereas both male and female focal subjects showed a significant change between pre- and post-test in the time that they spent with preferred subjects of the same sex (both matched $ts_7 > 3.13$, both $Ps < 0.05$; Fig. 2).

EXPERIMENT 2: CORRELATIONS BETWEEN AFFILIATIVE PREFERENCE AND MATE CHOICE (FEMALES)

In experiment 2, we observed each focal female on two occasions while she chose between a pair of males. In the first of these preference tests, we used the same apparatus and procedures that we had used in the pre-test of experiment 1 to measure focal females' affiliative preferences between pairs of target males. In the second, we tethered the males a female had chosen between in the first preference test at opposite ends of an enclosure, then allowed that focal female to move about the entire enclosure and mate with the tethered males as she would.

We had to tether males because males not only fought when free to do so, but also actively pursued females throughout the enclosure, making it impossible to determine whether females were choosing a male or cornered by him.

We hoped to determine whether the measure of affiliative preference that we had used both in experiment 1, and in our previous studies of 'mate choice' in female Japanese quail (Galef & White 1998: chapter 2; White & Galef 1999a: chapter 3), reliably predicted which male a female would actually choose as a mate.

Methods

Subjects

Fifteen female and 10 male Japanese quail served as subjects. All mated readily when placed in the apparatus (see Methods of Experiment 1). We listed all 45 possible combinations of pairs of males, then randomly selected 15 of those pairs and assigned one focal female to each.

Apparatus

We used the same apparatus that we had used in experiment 1 during the pre-test except that, during both preference tests in the present experiment, target males wore cloth harnesses and were tethered to opposite ends of the enclosure. Each harness, made of cotton cloth weighing 2.5 g, fit over a male's head and around his wings, and could be closed across his chest with a Velcro fastener. To prevent target males from fighting with one another and from pursuing focal females about the enclosure during the second preference test, we attached a 30-cm piece of twine to the back of each harness and tethered the two males to opposite end walls of the enclosure. Males wore their harnesses and were tethered during both preference tests to minimize disturbance of subjects during the experiment.

Procedure

Each day for 10 min/day, for 14 days before the start of testing, we placed each male in a harness and allowed him to move about the enclosure. At the end of this 2-week period of habituation, we determined whether each male would mate while wearing a harness. For 10 min/day for 5 consecutive days, we placed a different, randomly selected female in one end chamber of the apparatus together with a male in harness. We removed from the experiment those 8 males that did not copulate with females by the fifth day of testing.

Preference test 1 (affiliation)

The procedure for the first preference test was the same as that of both tests 1 and 2 in experiment 1 except that the two males were wearing their harnesses and were tethered.

Delay

At the end of the first 10-min preference test, we returned the focal female to the Plexiglas holding cage for 5 min.

Preference test 2 (mating)

At the end of the 5-min delay, we first removed the partitions separating the end compartments from the choice arena, then released the focal female from the holding cage. During the following 10 min, we recorded all cloacal contacts between each male and the focal female.

Results and Discussion

Preference Test 1 (affiliation)

During the first preference test, when focal females could affiliate but not mate with males, focal females spent a mean (± SE) of 8.06 ± 0.43 min closer to their respective preferred males.

Preference test 2 (mating)

During the second preference test each focal female mated one or more times with a male (mean ± SE = 3.4 ± 0.51 mounts/female during the 10-min test) and 84.4 percent of copulations were with males preferred during preference test 1. Both the first and the last copulation of each focal female were significantly more likely to involve the male that female had preferred during preference test 1 (Binomial tests: first copulation, $x_{15} = 2$, $P < 0.01$, Fig. 3a; last copulation, $x_{15} = 2$, $P < 0.01$, Fig. 3b), and during preference test 2, females copulated significantly more frequently with the males they had preferred than with the males they had not preferred during preference test 1 ($x_{15} = 1$, $P = 0.005$, Fig. 3c). First mating (e.g. Sullivan 1994; Blackwell & Passmore 1996), last mating (Birkhead & Møller 1992), and number of matings (Birkhead & Møller 1992) may all be important determinants of fertilization of birds.

Correlation between Preference Tests 1 and 2

The correlation between the time focal females spent near their preferred males during Preference Test 1 and the proportion of copulations that the preferred male obtained during Preference Test 2 was positive, but not significant (Spearman's rank-order correlation, $r = 0.34$, $P > 0.21$). The non-significant result seems to reflect a severe restriction of range (10 of the 15 focal females copulated exclusively with their respective preferred males).

The results of the present experiment suggest that, whatever the parameters of copulation determining reproductive success in Japanese quail, a male with whom a female tends to affiliate is also a male with whom she prefers to mate.

EXPERIMENT 3: CORRELATIONS BETWEEN AFFILIATIVE PREFERENCE AND MATE CHOICE (MALES)

In experiment 1, we found that male Japanese quail, like females of their species, show consistent affiliative preferences when choosing between members of the opposite sex. In the present experiment, we determined whether in male quail, as in females, the affiliative preference of a male predicts his choice of a female with whom to mate. In the present experiment we did not harness females during the test of male mate preference because female quail, unlike males, do not interact aggressively during brief periods of contact, and males are far more active in their pursuit of females than are females in their choice of males.

Methods

Subjects

Fifteen female and 17 male Japanese quail served as subjects. All mated readily when placed in the apparatus (see Methods of Experiment 1). We listed all 105 possible combinations of pairs of females, then randomly selected 17 of those pairs and assigned one focal male to each.

Procedure

Preference Test 1 (affiliation)

The procedure was identical to that of experiment 2 except that, in the present experiment, a focal male chose between two females in the end enclosures during the 10-min preference test and target females were not wearing harnesses, so there was no need to habituate females to them.

Delay

As in experiment 2, at the end of preference test 1, for 5 min, we restrained the focal male in the holding cage in the centre of the choice arena.

Preference Test 2 (mating)

At the end of the 5-min period of restraint, we removed the partitions separating the choice arena and end compartments, released the focal male from the holding cage, and recorded all cloacal contacts between the focal male and the two target females for 10 min.

Results and Discussion

Preference Test 1 (affiliation)

Focal males spent an average (±SE) of 7.78 ± 0.37 min nearer their preferred than non-preferred female.

Preference Test 2 (mating)

On average, each male mated 3.76 ± 0.47 times during the 10-min preference test. Eighty percent of copulations were with females preferred during preference test 1, significantly more males directed both their first and last matings toward the female they had preferred during preference test 1 (both $x\mathrm{s}_{17} = 3$, $P < .02$; Fig. 4a, 4b), and significantly more focal males mated more frequently with their preferred than with their non-preferred female $x_{14} = 0$, $P < 0.001$; Fig. 4c).

Correlation between Preference Tests 1 and 2

The correlation between the time focal males spent near their preferred females during Preference Test 1 and the proportion of copulations that the preferred female obtained during Preference Test 2 was significant (Spearman's rank-order correlation, $r = 0.49$, $P < 0.05$).

For male Japanese quail as for females of their species, measures of affiliation predict choice of a mating partner with considerable success.

GENERAL DISCUSSION

The results of experiment 1 indicate that both male and female Japanese quail show consistent tendencies to affiliate with particular members of the opposite, but not of the same, sex. Experiments 2 and 3 show that, for both male and female Japanese quail, affiliative preferences measured using the standard procedure are consistent with the preferences expressed in a situation where mating takes place. Taken together, the results of all three experiments indicate that the measure of affiliative preference used in previous studies of 'mate choice' in quail (Galef & White 1998: chapter 2; White & Galef, 1999a: chapter 3, 1999b: chapter 4) are not only reliable, but also predictive of actual mating behaviour. It would be useful to know whether the similar relationships exist in other species in which affiliative behaviour has been used as a surrogate measure of mate choice.

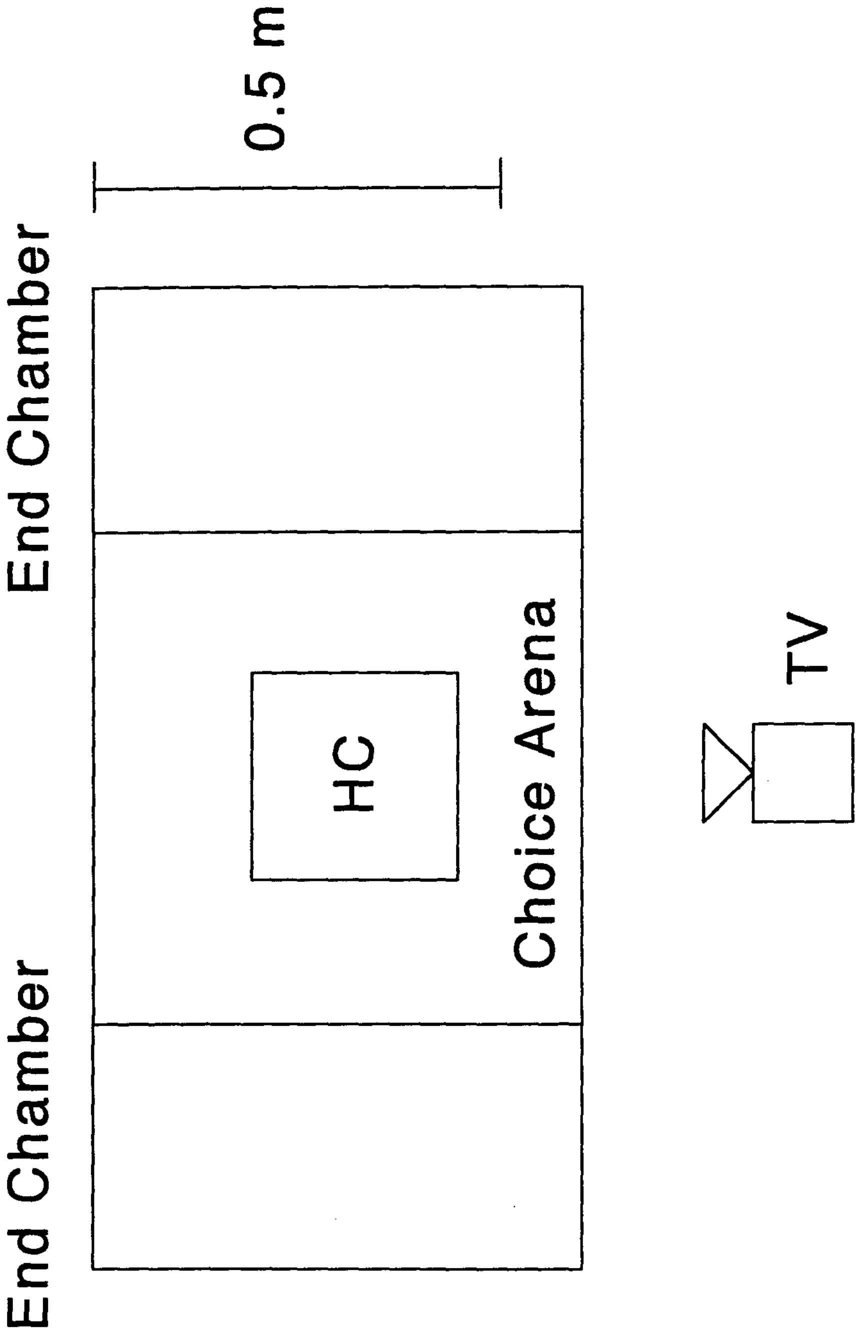
Figure Captions

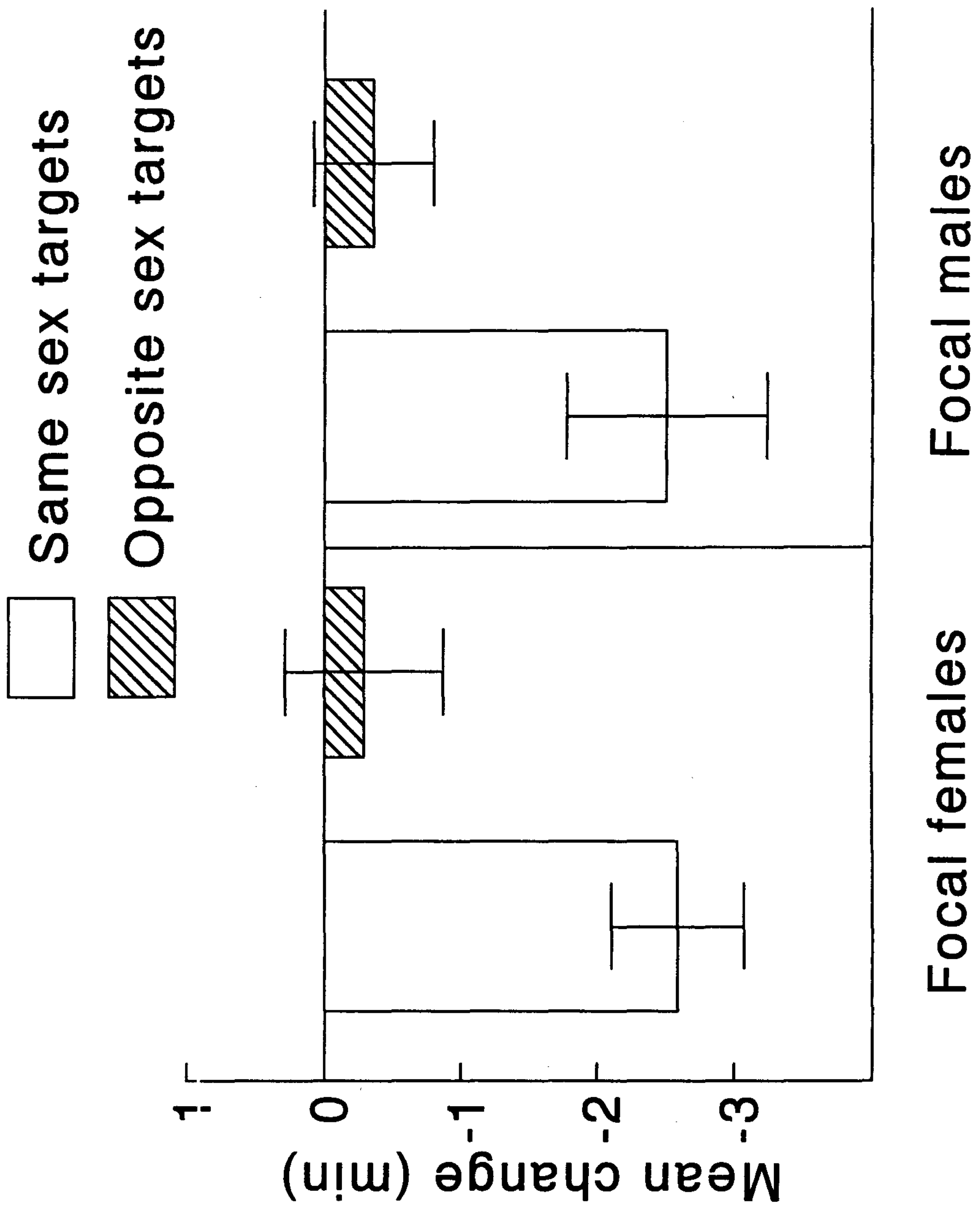
Figure 1. Overhead schematic of the apparatus. H.C. = holding cage, TV = television camera.

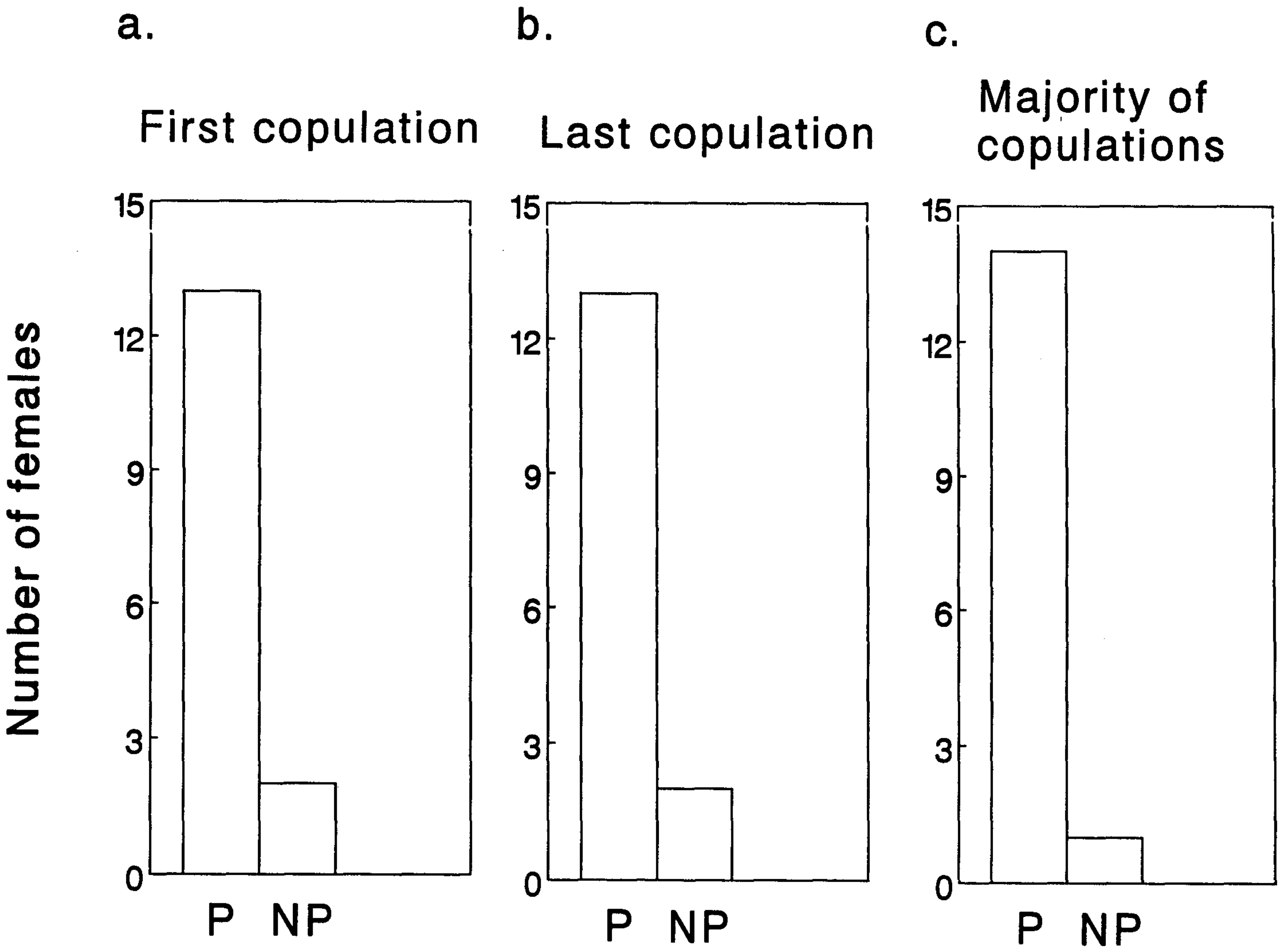
Figure 2. Mean (± SE) change between pre-test and post-test in minutes that focal male and female subjects spent nearer male and female target subjects that they had preferred during the pre-test.

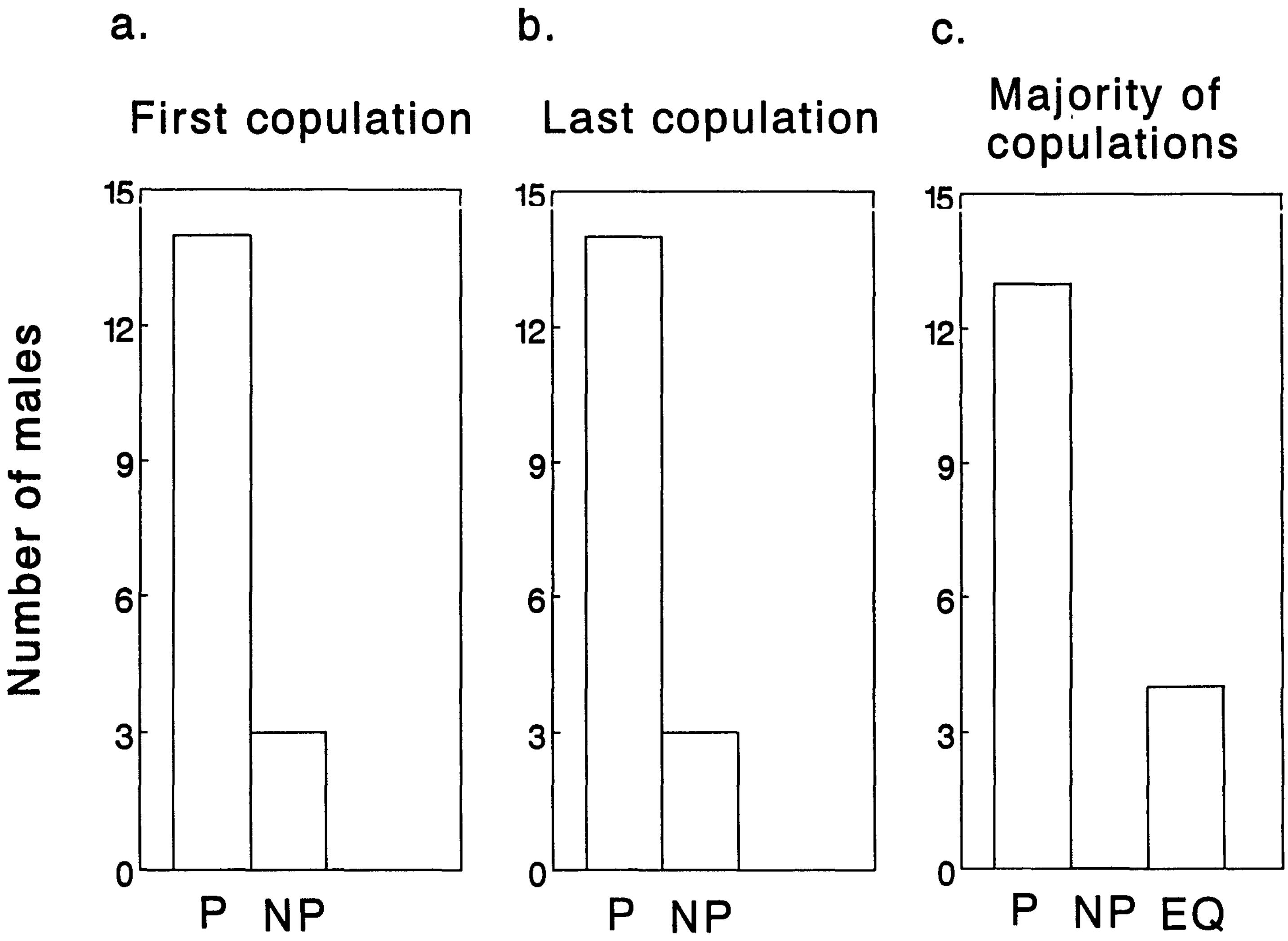
Figure 3. Number of focal females that, during preference test 2, (a) copulated first, (b) copulated last, and (c) copulated most frequently with the target male that they preferred and did not prefer during preference test 1. P: preferred; NP: not preferred

Figure 4. Number of focal males that, during preference test 2, (a) copulated first, (b) copulated last, and (c) copulated more frequently with the target female that they preferred and did not prefer during preference test 1. P: preferred; NP: not preferred; EQ equal number of copulations with preferred and non-preferred female.


0.5 m
End Chamber
HC
Choice Arena
End Chamber
TV


Same sex targets
Opposite sex targets
Mean change (min)
1
0
-1
-2
-3
Focal females
Focal males


a.
First copulation
b.
Last copulation
c.
Majority of copulations
Number of females
15
12
9
6
3
0
P
NP


a.
First copulation
b.
Last copulation
c.
Majority of copulations
Number of males
0
3
6
9
12
15
P
NP
EQ

Chapter 6

Conclusion

Taken together, the results of the series of experiments described in chapters 2 through 5 provide evidence consistent with the hypothesis that when making mate choices, Japanese quail of both sexes attend to and use information acquired socially. Males and females do, however, differ in how they respond to such social information. Females that viewed an initially non-preferred male mating with another female subsequently found that male more attractive, whereas males that viewed an initially attractive female mating with another male subsequently found her less attractive. This sexually dimorphic response suggests that differences in learning socially about potential mates may be a product of sexual selection.

In addition to reacting to social information differently, males and females also differed in what types of stimuli affected their affiliative preferences. Females increased their preference for any male seen near a female, whereas for males to reduce their preference for a female, they had to observe her mating with or being near a courting male. This difference in sensitivity toward sexual behaviour of conspecifics suggests that the functions of social information in modifying mate choice may differ for males and females, with males being more attentive than females to information about the immediate reproductive status of potential mates. Future investigation of the costs and benefits associated with mate choice for male and female quail is needed to interpret these results.

Female Choice: Mate-Choice Copying and Conspecific Cueing

Females gained information from observing the behaviour of other females, which is consistent with Pruett-Jones's (1992) definition of non-independent mate choice. The finding that focal females gained information from model females whether or not they displayed any sexual behaviour (chapter 3, expt. 2 & 3) is consistent with the notion that conspecific cueing plays a role in the behaviour of females; females moved to areas where other females were seen. Females did, however, show enhanced preference for males seen with other females, not just for areas where females were observed (chapter 2, expt. 4 & chapter 3, expt. 5). This enhanced preference for a male associated with another female requires mate-choice copying as an explanation.

Male Choice: Social Reversal of Preference due to Sperm Competition?

Focal males avoided females seen mating with other males. This result suggests that male behaviour is influenced by sperm competition. In birds in general, a male copulating with a female that has recently mated with another male has lower likelihood of fertilizing that female's egg than if he had mated with a female that had not recently mated (Birkhead & Møller 1992). The results of experiments in chapter 4 provide evidence consistent with the hypothesis that male quail used social cues to predict the fertilizability of females so as to avoid engaging in useless matings.

Other explanations do, however, exist for the observed behaviour of males. One possibility is that males avoided females that had been associating with a sexually active male in order to avoid aggressive responses from that male. This explanation in terms of avoidance of mate guarding males is, however, unlikely because males did not avoid areas where they had seen other males (chapter 4 expt. 3).

Alternatively, males may have avoided females that had recently mated in order to reduce the possibility of contracting a sexually transmitted disease (STD). Although the literature on STD in birds is small, what literature there is suggests: (a) the probability of female birds contracting STD increases with number of inseminations received, and (b) while testosterone stimulates development of secondary sexual characteristics, it depresses immune system response (Sheldon 1993). Thus, males may be more susceptible to contracting STD than females. This difference in susceptibility to STD might select for behavioural mechanisms in males that decrease the likelihood of contracting STD; unfortunately, prevalence of STD in wild or domesticated stocks of Japanese quail has never been studied.

Both avoidance of mate-guarding males and avoidance of STD can be differentiated experimentally from sperm competition as explanations of the males' behaviour toward females seen mating by investigating whether there is a change over time in males' behaviour towards a female seen mating with another male. Because of passive sperm loss, fertilization advantage of a first male is overcome by a second male as time progresses (Birkhead 1996). That is, with increases in the interval between two males mating with a female, the chances of the second male fertilizing the female's clutch improves. Thus, it would be predicted on the sperm competition hypothesis that as the interval increased between when a male saw a female mating and his opportunity to mate with her, the decrease in his preference for her resulting form seeing her mating would disappear. This hypothesis remains to be tested.

Measuring mate choice

Results from experiments described in chapter 5 indicate that, for quail of both sexes, affiliation time is a valid indicator of preference for mating with a target quail. The utility of indirect measures of mate preference used in other laboratory studies of mate choice has rarely been examined, but surely should be before evolutionary implications are drawn (Slagsvold & Viljugrein 1999; Wagner 1998).

Future Investigation of Social Influences on Mate Choice

Sexual selection. Most theoretical work on non-independent mate choice has been focused on the impacts of mate-choice copying on sexual selection. More work needs to be conducted on other ways in which social information may modify mate choice. For any given species, a variety of populational, environmental, stochastic, and social factors can interact to influence mate choice (Emlen & Oring 1977). Thus, each species may experience unique costs and benefits associated with mating and may deal with social information differently, leading to variability in how particular mechanisms are exhibited across species. Social influences on mate choice other than mate-choice copying may also have influences on sexual selection. For example, stickleback eggs in a nest increase the attractiveness to females of the nest, thus increasing the opportunity for sexual selection on the male guarding the nest (Ridley & Rechten 1981; Wade & Pruett-Jones 1990). Similarly, conspecific cueing in fallow deer can provide selection pressure on males' ability to hold a harem (Clutton-Brock et al. 1989).

Furthermore, theoretical work on social influences on mate choice has outdistanced empirical support for particular mechanisms. For example, mate-choice copying has been assumed to be an important agent of sexual selection due to females' acquisition of 'cultural' preferences for male traits (Brooks 1998). Currently, however, no empirical evidence exists that mate-choice copying can lead to preferences for traits of high quality males, or to generalized preferences for particular male characteristics.

Finally, more work needs to be done studying mate choice in free-living animals in order to understand how an animal's sensitivity to social factors can lead to production of adaptive behavioural repertoires in natural environmental circumstances (Crews & Moore 1986).

Mutual mate choice. Historically, the study of mate choice has dealt with the behaviour of each sex independently. Recent theoretical models of mutual mate choice, in which the sexes exhibit differing levels of choosiness, have shown that investigating the choice behaviour of both sexes simultaneously results in patterns of mate choice that could not be predicted by investigating each sex's choice strategies in isolation (Johnstone, Reynolds & Deutsch 1996; Johnstone & Marzluff 1990). The present thesis has provided evidence demonstrating that, at least in the laboratory, both sexes of Japanese quail will engage in mate choice when given opportunity to do so. Modeling how differences in social learning and mutual mate choice can impact assortative mating may be of importance to understanding trends in mating behaviour at the population level.

Chapter 7

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