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Repeatability of Mate Preferences and Mate-Choice Copying in Female Zebra Finches

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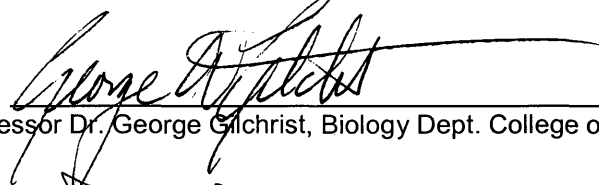
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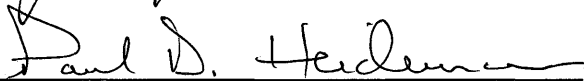Approved by the Committee, May 2007

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ABSTRACT PAGE

I investigated whether female zebra finches', mate preferences are repeatable within females using three female preference trials for random selections of males wearing colored leg bands (red versus green preferences). Repeatability in female mate choice is an underlying assumption of sexual selection models and demonstrating repeatability is important because it indicates that a female preference is a definable property of an individual that can evolve and is not simply a plastic response to environmental cues. If female preferences are repeatable then it is more likely that a preference trait can evolve to benefit or harm males and females, an assumption of all sexual selection models. In addition, I explored the role of mate choice copying, a non-genetic process, in the inheritance of female preferences. In some species, females can copy the mate choice exhibited by others in the population, creating a mechanism of social inheritance or "culture" of mate preferences. Such mate choice copying is a possible mechanism through which an individual can use public information to select a mate. Demonstrating this mechanism is important because social inheritance of preferences may cause changes in sexual selection pressures on male display traits. I found that female zebra finches had almost significant repeatability in their mate preferences and their initial mate preferences differ from those found in past research. Female zebra finches are also capable of mate choice copying particular traits through social information although sexual experience influenced their copying behavior. This study confirms that purely genetic models of sexual selection need to be modified to include social inheritance of mate preferences, especially since social information can affect monogamous species as well as polygamous and lekking species.

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DEDICATION

To my Mother, Father, and Jeff for their patience, support, and guidance

ACKNOWLEDGEMENTS

CHAPTER I

1.0 - What is sexual selection?

Sexual selection is a form of natural selection in which individuals differ in their mating success (Alcock 2001). As Darwin (1871) suggested, sexual selection selects for traits that are associated with mating success. Sexual selection is thought to increase fitness by favoring traits that allow an organism to have greater access to mates, thus producing more offspring, which ultimately gives the parent a greater net fitness (Andersson 1994; Dorak 2005).

Sexual selection is driven by two major processes: competition between members of the same sex and mate choice between members of the opposite sex (Andersson & Iwasa 1996). Competition between same sex individuals is usually over a mate, territory, or resources important in attracting a mate. Male-male competition is sometimes referred to as intrasexual selection. High contest rates in male quail, *Callipepla squamata*, are an example of intrasexual selection (Hagelin 2002). These male quail use calls and tidbitting as threat displays towards other males. Males that win contests usually display threats faster than males who display threats more slowly (Hagelin 2002). Mate choice, sometimes termed intersexual selection, involves one sex evaluating and choosing a member of the opposite sex with whom to mate. Mate choice has often been studied as females evaluating potential males as mates (Andersson & Iwasa 1996). For example, female quail, *Callipepla squamata*, prefer to mate with males that win male-male contests. Females are often considered the "choosy" sex because reproduction is very costly and females usually invest more heavily in their offspring than males through behaviors such as offspring production, feeding, and nurturing. Thus, females commonly

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experience greater costs than males in raising offspring (Trivers 1972). When females have a larger parental investment in their offspring than males, females will generally have a lower reproductive potential than males because males are able to fertilize more females at a lower cost (Andersson & Iwasa 1996).

Typically, competition has lead to the evolution of more dramatic male traits that may act as weapons against other males or signals to attract females (Moore & Moore 1999); whereas, mate choice has evolved to increase female preferences for males of supposed higher quality (Reynolds & Gross 1990; Andersson & Iwasa 1996). I will focus this introduction on mate choice, particularly mate choice copying, because not as much research has examined this area of sexual selection.

2.0 - Mate Choice

Choosing a mate is a costly endeavor for most animals because it can involve a large time commitment in searching for a mate, courtship activities, copulation, risk of injury or depredation, and loss of mate (Trivers 1972; Pomiankowski 1987; Reynolds & Gross 1990). A choosy female can maximize her reproductive success by using a trade-off system between the number of mates she obtains and the quality of the mate she chooses (Andersson & Iwasa 1996). In this way a female could gain direct and/or indirect benefits by choosing the mating strategy that would result in the highest number and quality of offspring produced.

Direct benefits are benefits that are passed on directly from a male to his mate to increase her fitness and fecundity. Examples of direct benefits are increased parental care (Forsgren et al 2004) and greater food resources (Saetre et al 1995; Bussière et al 2005).

Indirect benefits are actions or behaviors that increase the fitness and fecundity of a female's offspring (Nowicki et al 2000). Since offspring carry some of the female's genes, she indirectly receives benefits by producing offspring with a high quality male. Despite which type of benefit a female receives, evolution of mating preferences will favor a preference that increases the fitness of the female except if the preference evolved as a sensory bias and there is antagonistic selection between males and females.

2.1 - Evolution of mating preferences

There are several main models that explain the evolution of mating preferences. Five such examples are direct benefits of preferences, indirect benefits of preferences via a runaway process, indirect benefits of preferences via good genes processes, chase-away selection, and sensory biases (Kirkpatrick & Ryan 1991; Andersson & Simmons 2006). First, a female preference can be selected for if it provides a female with direct benefits, such as increased offspring production and longer lifespan, while also reducing the cost of finding a mate, such as preferring one type of male over another because of conspicuous coloration (Kodric-Brown 1989). Selection will favor female preferences that benefit the female directly if these benefits increase her average fitness (Kirkpatrick & Ryan 1991). Direct benefits can be very important to a female; however a recent review of the literature found that the benefits a female received from direct benefits were only slightly higher than the benefits a female received indirectly through her offspring (Møller & Jennions 2001). Thus, emphasis on direct benefits models for the evolution of female mate preferences must be made with caution.

Mate preferences can also evolve through indirect Fisherian runaway selection (Fisher 1958). Fisher's runaway process describes the genetic correlation between a

female preference and male display trait, and how this coupling ultimately leads to the exaggeration of both the preference and display trait. This process begins with an arbitrary female preference which arises for reasons outside of mating. The female preference will then spread among the population and a male trait will arise that coincidently cues in on this sensory bias. Females will then mate with males with that trait which forms a genetic correlation between the female preference and male trait. Males with the trait will also experience an increase in fitness because of higher mating success. The offspring produced by such matings will have both the female preference and male trait. A feedback process can then begin where daughters will have stronger preferences and sons will have a more exaggerated trait. The runaway process will continue in a population until there is no longer any genetic variation or natural selection stops the whole process. A female would gain indirectly through runaway selection by producing sons with these exaggerated traits because they will gain more matings in the future. Thus, the female passes on more of her genes than a female who produces average sons (sexy son hypothesis) (Weatherhead & Robertson 1979). This process is difficult to test but is considered in mate preference models due to its historical importance (Kirkpatrick & Ryan 1991).

Preferences may also evolve via a good genes model (Kirkpatrick & Ryan 1991). In good genes models, a female mated with a male of high genetic quality will receive fitness benefits because her offspring will inherit "good genes" and outcompete offspring produced by other females mated with lower quality males (Zahavi 1975; Kirkpatrick & Ryan 1991). The handicap hypothesis (Zahavi 1975) is an example of indirect benefits via a good genes model. The handicap hypothesis states that male display traits indicate

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male genetic quality because these traits carry a large cost. Therefore, only males that have the highest genetic quality will be able to carry the best display traits, such as increased ornamentation, because they are capable of dealing with the costs (Zahavi 1975). Males use these traits as honest signals to females because the trait represents the genetic quality of the male and how he can survive with a costly trait (Fisher 1915; Zahavi 1975). Hamilton and Zuk (1982) provided an example of good genes mechanisms in terms of the evolution of parasite resistance. They described the continuous coevolution between parasites and hosts and how this cycle might play a role in the evolution of preferences for extreme male traits. Parasite-host coevolution may occur because there is a correlation between resistance genes against parasites and the expression of male display traits. They hypothesized that males with better genes for resistance against parasites would also have higher genetic quality, hence a correlation between these two traits. However, only males that were in the best condition without parasites would be able to carry display traits due to their costliness. The parasite hypothesis is based on the idea that only the healthiest males would be able to produce elaborate display traits. Females with preferences for these exaggerated male traits would mate with these higher resistance males, forming and enforcing a correlation between preference and resistance genes (Hamilton & Zuk 1982; Kirkpatrick & Ryan 1991).

Female mate preferences may have arisen via mechanisms that are not beneficial to both males and females, such as through chase-away selection. Chase-away selection is an antagonistic process between female preferences and male traits (Alcock 2001). In chase-away selection, a male trait may evolve that enables the male to exploit the sensory

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system of females. Males that can successfully exploit the sensory system of females are favored and gain more matings with females. However, the male trait will decrease the fitness of females. Females can evolve a trait that negates the effect of the male trait and females who succeed in developing a block against male exploitation are then favored by selection and will have higher fitness. The female trait will decrease the fitness of males, so males that are successful at evolving a new trait or can improve upon the initial trait are favored because they will increase their fitness at the expense of females. This process of conflict between females and males results in the overall antagonistic process of chase-away selection where both sexes are trying to maximize their fitness which results in a decrease of fitness in the opposite sex (Alcock 2001; Rice et al 2006).

Finally, female mate preferences may have initially arisen via natural selection for reasons not associated with mating, such as foraging or predation (Endler & Basolo 1998; Rodd et al 2002; Fuller et al 2005). Males can take advantage of this female sensory bias and mimic it in a mating context, producing a female preference from a pre-existing sensory bias (Rodd et al 2002). Males may use sensory biases in both runaway selection and chase-away selection because the initial male trait arises arbitrarily. An arbitrary male trait that could be successful and result in the evolution of female preferences would be a trait that can take advantage of the female sensory system (Alcock 2001). Males that are able to exploit pre-existing female preferences are favored by sexual selection in runaway selection and chase-away selection (Ryan 1998; Andersson & Simmons 2006).

2.2 - Variation in preferences and traits

The evolution of female preferences and male display traits cannot occur unless there is heritable variation present in the preference or trait (Fisher 1958). Female guppies,

Poecilia reticulata, display a large degree of variation in their mate preferences for brightly colored males where a few females only prefer drab colored males, most females prefer bright colored males, and some females only prefer bright colored males (Godin & Dugatkin 1995). The extent of variation in female preferences affects the strength of sexual selection acting on male display traits. For example, if there was little variation in female preferences, most females would prefer the same (or very similar) male phenotype(s), resulting in strong selection for the preferred male trait. However, if there was large variation in female preferences, mating success would be more evenly spread among males, hence, decreasing the strength of selection acting on male displays.

Variation in female mate preferences can also be influenced by the environment or reproductive effort, introducing plasticity to female preferences (Jennions & Petrie 1997; Qvarnström et al 2000). For example, females may exhibit different mate preferences depending on the costs of finding a mate during the mating season (Jennions & Petrie 1997). Also, if the genetic contribution to a female's preference is low, then environmental factors can strongly affect female preferences producing genotype by environment interactions (Rodríguez & Greenfield 2003). This has been shown in gray tree frogs, *Hyla versicolor*, where different male calls will be favored by females in different environments, making different genotypes successful in certain environments but not in others (Welch 2003). This ultimately favors plasticity in the male trait so that the male may be successful in more than one environment.

Females' preferences may also covary with individual state, for example body condition, size, or age. As the relative costs and benefits of following a particular mate preference strategy can vary with condition, size, or age, you may expect state-dependent

plasticity in mate preferences to evolve (Jennions & Petrie 1997). For example, a female in high condition may have stronger mate preferences which allow her to be choosier and prefer males with the most elaborate display traits (Höglund & Alatalo 1995). Therefore, mate preferences may vary among individuals not only for genetic and environmental reasons, but also vary within individuals as they change in condition, size, or age. Mate preferences are a lot more variable and plastic than traditionally thought.

Overall, mate choice offers females the opportunity to weigh the costs and benefits (direct and indirect) of choosing a mate so that a female may ultimately mate with an appropriate male. Who is an appropriate male varies among females but can also vary over time within a female because of state-dependent mate choice. In the following section, I discuss another reason why we might expect female preferences to vary within individuals over time.

3.0 - Mate choice copying

Finding and choosing a mate can be costly (Trivers 1972), therefore it would benefit females to gather information about potential mates in order to make the most appropriate mate choice decision (White 2004). One way in which a female could gather such information is through a process termed "mate choice copying" (Brooks 1996). Here a female can use publicly available information, by observing mate choice behaviors of other females in the population, to assess the suitability of potential mates (Dugatkin 1992). Typically in mate choice copying, a female will observe a model female exhibit a mate preference and then internalize this information. When the observer female is given the opportunity to choose a mate she will rely on the information learned by the model

female to make her own decision, skewing her preference toward the kind of male the female she observed preferred (Godin et al 2005). Hence, mate choice copying results in non-independent mate choice among the females in a population, as females will copy preferences from each other (Pruett-Jones 1992; White 2004).

I define mate choice copying as the act of a focal female observing the mate preferences of a model female and then, upon given the chance to choose a mate, the focal female will display a similar preference as the model female (*sensu* Pruett-Jones 1992). Therefore, mate choice copying can be viewed as a form of social learning, when social learning is defined as an act by an individual where information (e.g. a new behavior) is internalized through observation or interaction with other individuals (Brown & Laland 2003).

Most models explaining the acquisition of mate preferences assume genetic inheritance alone (Andersson & Simmons 2006). The possible social inheritance of mate preferences through mate choice copying indicates that female preferences not only can be passed down from mother to daughter but can also be spread to other relatives as well as non-relatives within the same generation (Dugatkin 1998; Swaddle et al 2005), substantially altering patterns and the speed of preference inheritance.

Models that examine the effects of social inheritance of mate preferences have concluded several different things. First, copying preferences when there are costs to mate choice will reduce these costs (Dugatkin & Höglund 1995; Stöhr 1998). For example, social acquisition of mate preferences can reduce time and energy expenditures in sampling mates, reduce risk of injury and predation, and also minimize the fitness consequences of mate loss by promoting rapid repairing (Dugatkin & Godin 1992; Pruett-

Jones 1992; Jennions & Petrie 1997). Second, copying should occur if there are differences in female discrimination ability of males, such that females could be divided into "copiers" and "choosers" (Losey et al 1986; Pruett-Jones 1992; Stöhr 1998). Mate assessment ability could be related to age or sexual experience differences in the females of a population (Pruett-Jones 1992; Stöhr 1998). Third, copying will affect males by increasing the variance in their mating success (Wade & Pruett-Jones 1990). This could occur because females preferentially mate with only males they have seen other females visit or copulate with (Sirot 2001). Finally, mate copying can cause different selection pressures on male traits depending on how females are influenced by the social information they see (Agrawal 2001). For example, females could cause positive or negative directional selection or positive or negative frequency-dependent selection of male traits depending on the number of females she observes with a common or rare type male in relation to the mean type male of the population (Agrawal 2001). However, most of these models assume mate copying in only lekking or polygamous species and therefore modeling of monogamous species that meet the requirements for mate copying should be examined (Losey et al 1986).

A population of females must satisfy several conditions for mate choice copying to be beneficial. Mate choice copying may be generally advantageous when, first, a copying female is likely to select a higher quality mate through copying rather than through independent mate choice (Losey et al 1986). This may occur if females who mate earlier in the season pair or mate with the best quality males, leaving copying females with two strategies: to mate with the remaining low quality males or to copy the preference for higher quality males. When a population has variation in the ability for

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females to discriminate between males, females that can accurately sample males should use independent mate choice ("choosers") and females that are not successful at sampling males should use copied preferences ("copiers"), leading to two mate choice strategies within a population of females (Losey et al 1986). Also, when costs of mate choice are high, such as waiting until the end of the mating season to pair, females should copy mate preferences to reduce the sampling costs associated with mate choice (Pruett-Jones 1992; Stöhr 1998). Second, copying females must have the opportunity to observe the mate choices of other females in the population (Losey et al 1986). If females are never able to observe other females make mate preferences then it is impossible for "copiers" to copy mate preferences (Wade & Pruett-Jones 1990). As can be seen from these conditions, we would generally expect mate choice copying to be more prevalent in polygamous and lekking species than in more monogamous and solitary breeding species (Losey et al 1986). This general pattern appears to hold, as most evidence for mate choice copying comes from polygamous and lekking systems (Dugatkin 1992; Dugatkin & Godin 1992; Höglund et al 1995; White & Galef 1999; Witte & Noltemeier 2002; Witte & Ryan 2002; Ophir & Galef 2004; Godin et al 2005).

Mate choice copying may be a conditional evolutionary stable strategy with "choosers" and "copiers" in a mixed population (Losey et al 1986; Pruett-Jones 1992). This could occur if "copier" females were not able to assess male fitness traits and relied on "chooser" females' mate choices to determine their mate preference (Losey et al 1986). Interestingly, there does appear to be genetic variation for the tendency to copy, at least in guppy populations (Godin & Dugatkin 1995). Hence, it seems plausible that

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there could be mixed strategies of "choosers" and "copiers" in a population (Wade & Pruett-Jones 1990; Pruett-Jones 1992).

Factors such as age and sexual experience of the female may also play a role in determining if mate choice copying is used as a strategy for finding a mate (Losey et al 1986; Pruett-Jones 1992; Stöhr 1998). For example, virgin female Japanese quail, *Coturnix coturnix japonica*, tend to prefer aggressive males as mates but these males also exhibit aggressive behaviors towards females as well as males. As a result, sexually experienced females will avoid aggressive males as mates while virgins will prefer aggressive males as mates (Ophir & Galef 2004). The different preferences of females based on sexual experience could mean that virgin females will tend to make their own preference based on male aggression rather than copy the mate preference of an older female. However, if a virgin female quail did copy the preference for a less aggressive mate, then she may gain fitness benefits from that mate because she will not have to deal with aggressive attacks on herself from her mate. In guppies, young females copied the preferences of older model females, but not younger model females (Amlacher & Dugatkin 2005). In this case, it seems that virgin females do weigh the mate preferences of older females more strongly, which could give younger females fitness benefits if they copy the preference of an older female. This could occur if the older females mated with males who were more successful at providing nutrition, caring for young, or increased a female's fecundity.

The relative strength or persistence of a copied preference relative to innate preferences is important as we have little information on how effective copied preferences are in changing overall sexual selection pressures (Dugatkin 1998). For

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example, sailfin molly females, *Poecilia latipinna*, are able to copy mate preferences when choosing between two males of similar body sizes (Witte & Ryan 1998). However, sailfin molly females do not copy the mate choice of a model female when the copying female is presented with males of two different sizes. In this case, the female will consistently prefer a larger male to a smaller male, which is a pre-existing preference in this species (Witte & Ryan 1998). Thus, in this case, social learning does not override a seemingly strong pre-existing mate preference. This may be true in other organisms that have strong sensory biases or pre-existing preferences such as orange coloration in male Trinidadian guppies (Dugatkin 1996). Hence, I hypothesize that some pre-existing mate preferences are too strong to be altered by social learning. Pre-existing versus learned mate preference strengths could have been examined in Japanese quail (White & Galef 2000) if they had allowed females to choose between pseudomutant males and normal wild-type males in their experiment, however only mate choice copying of a novel trait was studied so we cannot say if quail also demonstrate stronger pre-existing mate preferences.

The duration and decay of copied mate preferences are also important for sexual selection models. If a copied preference lasts a short amount of time then it may be relevant for only one breeding attempt, exerting weak selection on display traits. However, if a copied preference has little or slow decay then a female would retain the copied preference over multiple breeding attempts, increasing selection for preferred traits in the population. There have been few studies on the decay of copied preferences however, female sailfin mollies have been shown to maintain copied preferences for nonpreferred (smaller) males for up to five weeks (Witte & Noltemeier 2002) and

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females can also remember males that were associated with a model female (copied preference) after 24 hours (Witte & Massmann 2003). This is evidence that fish have the ability to maintain copied preferences and have a good memory to do so, which is necessary if selection is to act on copied preferences.

3.1 - Evidence of mate choice copying

Research studying mate choice copying has increased over the past two decades. Females of some species prefer individual males seen courting or copulating with a female based on social information (Dugatkin 1992; White & Galef 1999; Swaddle et al 2005). This phenomenon is termed copying a preference for an individual male (Westneat et al 2000). For example, copying a preference for an individual male has been demonstrated in the Trinidadian guppy (Dugatkin 1992; Dugatkin & Godin 1992; Godin et al 2005), sailfin molly (Witte & Noltemeier 2002; Witte & Ryan 2002), Japanese quail (White & Galef 1999; Ophir & Galef 2004), and the zebra finch (*Taeniopygia guttata*) (Swaddle et al 2005). As can be seen from this review, copying a preference for an individual male has most often been associated with lekking and polygamous species, perhaps because these females can easily view other females making mate preferences and there is substantial reproductive skew toward particular individual males (Dugatkin 1992). The monogamous zebra finch is a notable exception to this pattern, which I will return to later.

It is important to note that mate choice copying can function to increase female preferences for a particular male or to increase preferences for a general trait that is common among a group of males (Westneat et al 2000). Copying a preference for a general male trait implies that mate choice copying can select for females who are

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currently unmated, as long as they possess trait(s) in common with chosen males, indicating a significant role for mate choice copying even in monogamous species (Swaddle et al 2005). So far, copying of preferences for general male traits has been demonstrated in zebra finches and Japanese quail only (White & Galef 2000; Swaddle et al 2005). It is important that females have the ability to generalize trait preferences so that socially learned information can influence evolution of mate choice at the population level (Brooks 1998).

Female Japanese quail spent significantly more time with males that had color patterns similar to males they observed with a model female than males that were alone, which indicates that females were able to copy a color pattern preference and then generalize that copied preference when given different males to choose from (White & Galef 2000). Female zebra finches copied preferences for individual males associated with a model female after two weeks of social information. Female zebra finches were also able to generalize leg band colors to prefer the color band that was associated with a mixed-sex stimulus paired male after social information (Swaddle et al 2005). Zebra finches are monogamous and have low rates of extra pair copulation, therefore it is somewhat surprising that females exhibit mate choice copying, increasing the probability that unmated females would observe mate choices of others in the population (Zann 1996; Swaddle et al. 2005). Also, zebra finches are known to show sexual imprinting (Witte & Sawka 2003), which can be viewed as another way in which social information affects the acquisition of mate preferences. Therefore, although the zebra finch is socially and genetically monogamous, there are other features of its life history that make it a reasonable candidate to show mate choice copying.

3.2 - Significance and results of mate choice copying

Mate choice copying can have several affects on sexual selection processes. First, mate choice copying can increase the variance of male mating success as females that copy mate preferences of model females will favor similar males, skewing mating success toward a particular set of similar males in the population. As mating skew increases, the strength of sexual selection will also increase (Wade & Pruett-Jones 1990). If copied mate preferences persist from generation to generation, male alleles for the preferred trait would quickly increase over time resulting in more rapid evolution than if mate choice copying did not occur (Agrawal 2001).

Second, the evolution of mate choice copying can reduce mate searching and sampling costs, which would allow females to spend less energy and time on finding a quality mate and more time involved in mating and raising offspring (Stöhr 1998). The reduction in the cost of mate choice would be significant because it would allow females to identify high quality males with less effort and consequence, making sexual selection stronger on preferred male traits and preferences for these traits (Kokko et al 2002). Females that are unable to distinguish high quality males from lower quality males, young, sexually inexperienced females, and females who have no mate near the end of the breeding season would especially benefit from mate choice copying (Stöhr 1998; Ophir & Galef 2004). If females can use mate choice copying to avoid the direct costs of mate choice (e.g. reduced female fecundity) and environmental costs of mate choice, then mate choice copying would be very beneficial to decrease the costs of mate choice and increase sexual selection pressures on copied preferences and traits, leading to the evolution and spread of these preferences and traits in a population (Kokko et al 2002).

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Third, mate choice copying can increase the fitness of a female's male offspring if they inherit the preferred (copied) traits and preference for this trait is maintained over the generations (Sirot 2001). In other words, females can receive indirect benefits by producing sexy sons, as in Fisherian runaway selection. These indirect benefits will accumulate more quickly for females in the presence of mate choice copying as the preference for sexy sons will spread more rapidly through social rather than solely genetic mechanisms. Hence, if copied preferences are stable, mate choice copying can speed up a Fisherian runaway process. In general, as preferences are spread through social mechanisms, the intensity of selection on preferred traits can increase as horizontal transmission of preferences allows for rapid changes in selection pressures (Agrawal 2001). This argument only holds if copied preferences are stable over time and last for several generations. Currently, we know very little about the stability of copied preferences over time.

4.0 - Conclusion

As an increasing number of species appear to make use of social information in acquiring mate preferences, there is a need to update sexual selection models to further incorporate non-genetic inheritance mechanisms. The most widely used models of sexual selection and mate preference evolution restrict inheritance to genetic mechanisms (Eshel et al 2002). However, we have seen that social mechanisms of inheritance can alter evolutionary outcomes (Agrawal 2001; Sirot 2001). Although there is limited theory that has incorporated mate choice copying, these cases have focused on polygamous and lekking mating systems, when there is now the need to thoroughly explore the

consequences of mate choice copying in other mating systems, such as the monogamous zebra finch.

There are also substantial gaps in our empirical knowledge that we need to fill. For example, we need to understand how copied preferences persist in populations. If females retain copied preferences over long time periods then display traits could experience intense sexual selection. However, if copied mate preferences are temporary and short-lived, mate choice copying may purely add noise to genetic processes and outcomes of sexual selection. Importantly, there is also relatively little information about how copied preferences interact with strong, pre-existing mate preferences. Therefore, currently it is difficult to interpret much of the experimental data on mate choice copying in an ecologically and evolutionarily meaningful context. In chapter two, I report an investigation of how pre-existing mate preferences are affected by social information in female zebra finches.

Overall, mate choice copying may affect sexual selection processes, perhaps by increasing the variance of male mating success, reducing the costs of mate searching and choice in females, and spreading preferences more quickly through a population which could increase the speed and intensity of Fisherian runaway selection. However, our understanding of the evolutionary consequences, in both an empirical and theoretical sense, is under-developed for monogamous mating systems.

CHAPTER II

Introduction

Finding and choosing a mate can be costly. For example, females may need to search for a mate, assess those mates against each other or some internalized standard, engage in courtship activities, copulate and expose themselves to predation risk, and often invest in substantial parental care (Trivers 1972). Often, females pay greater costs of reproduction than males (Trivers 1972); therefore, females are often choosy about who they mate with. The processes by which a female chooses a mate can be influenced by intrinsic sensory biases (Basolo 1990; Ryan 1998; Rodd et al 2002) or learning (Andersson 1994; Witte & Sawka 2003).

Females could benefit by gathering information about potential mates so they can make the optimal mate choice decision (White 2004). Mate choice copying offers one such mechanism. As described in Chapter 1, mate choice copying is the act of a focal female observing the mate preferences of a model female and then, when given the chance to choose a mate, the focal female will display a similar preference as the model female (Pruett-Jones 1992).

For mate choice copying to occur, the copying female must observe either unpaired females displaying a mate preference, or paired females associating with their chosen mates. The copier internalizes information about these preferred males such that when the copier is given the opportunity to choose a mate her preferences will be biased toward males that are similar to the previously preferred males (Godin et al 2005). Hence, mate preferences acquired through mate choice copying are non-independent from other mating decisions in the population (Pruett-Jones 1992; Westneat et al 2000;

White 2004). As discussed in Chapter 1, we would expect to observe mate choice

copying in situations where it is highly beneficial to establish a mate preference quickly

(e.g. on a lek), or where the costs of developing a mate preference are particularly high

(e.g. when it is difficult to sample multiple males) (Dugatkin & Godin 1992; Pruett-Jones

1992; Jennions & Petrie 1997).

There is evidence for mate choice copying in a broad taxonomic range of

vertebrates. For example, mate choice copying has been studied as an individual-based

preference in the Trinidadian guppy (Dugatkin 1992; Dugatkin & Godin 1992; Godin et

al 2005), sailfin molly (Witte & Noltemeier 2002; Witte & Ryan 2002), Japanese quail

(White & Galef 1999; Ophir & Galef 2004), and the zebra finch (Swaddle et al 2005).

Females can also copy preferences for generalized traits of males, skewing mating

towards males with similar traits as the copied male. This had been demonstrated in

Japanese quail (White & Galef 1999; Ophir & Galef 2004) and the zebra finch (Swaddle

et al 2005).

Although mate choice copying has most often been demonstrated in lekking and

polygamous species (Dugatkin 1992; Dugatkin & Godin 1992; White & Galef 1999;

Witte & Noltemeier 2002; Witte & Ryan 2002; Ophir & Galef 2004; Godin et al 2005),

there is recent evidence for this process in a monogamous species, the zebra finch

(Swaddle et al 2005). Demonstrating that monogamous species also exhibit mate choice

copying is important because it implies that social inheritance of mate preferences could

be much more widespread than currently thought. This means that female preferences

are generally plastic and that sexual selection could be much stronger than once

described, as I discussed in Chapter 1 (Swaddle et al 2005). Mate choice copying is

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important because it may have evolved to minimize mate searching and sampling costs (Pruett-Jones 1992; Stöhr 1998). Ultimately, mate choice copying could lead to the rapid evolution of male display traits (Brooks 1996), which could result in the spread of a male display trait preference in females, meaning that females observing social information from successfully paired females would exhibit this preference over other pre-existing preferences (Dugatkin & Godin, 1992; Dugatkin, 1996; Westneat, 2000; Agrawal, 2001; Shuster and Wade, 2003; Godin et al., 2005). Male alleles for that particular trait would quickly increase over time if enough females copied the same trait preference, skewing the mating patterns of a given population as described in Chapter 1 (Agrawal 2001; Swaddle et al 2005).

I explored the role of mate choice copying in the inheritance of female preferences in zebra finches. Recently, Swaddle et al (2005) provided evidence of mate choice copying by female zebra finches. They found that female zebra finches are able to use social information to influence mate preferences for individual males as well as generalized traits after observing model females with a male for two weeks. I further explored mate choice copying in female zebra finches by examining whether pre-existing mate preferences (for color bands of known attractiveness worn by males) can be altered by social information. This is important because most research focuses on lekking or polygamous species but there are some monogamous species that meet the requirements for copying and these species need to be investigated. It is broadly accepted that female zebra finches have a preference for males wearing particular colors of small plastic leg bands (Burley et al. 1982; Burley 1986; Burley 1988). In particular, females prefer males wearing red leg bands and dislike males wearing light green bands (Burley et al. 1982;

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Burley 1986; Burley 1988; Hunt et al 1997). I explored whether females in our laboratory population of zebra finches exhibit the predicted color band preferences (i.e. whether females prefer males wearing red versus green leg bands) and if these initial preferences can be changed through a mate choice copying process. I hypothesized that females, on average, would exhibit an initial preference for males with red bands and that mate choice copying would change this initial preference.

I also investigated the within-female repeatability of color band preferences. Repeatability in female mate choice is an underlying assumption of sexual selection models because repeatability estimates are needed to aid in determining if mate preferences can evolve (Jennions & Petrie 1997; Widemo & Saether 1999). Empirically demonstrating repeatability of mate preferences is important because it indicates that a female preference is a definable property of an individual that can presumably be targeted for selection and is not simply a plastic response to environmental cues. Importantly, an empirical measure of the repeatability of mate preferences places an upper limit on the heritability estimate of the preference, indicating how preferences can evolve in response to sexual selection pressures (Godin & Dugatkin, 1995). If female preferences are repeatable then it is more likely that a preference trait can evolve, which is an assumption of all sexual selection models. If mate preferences are not repeatable, this indicates that preferences will not respond genetically to selection pressures. Surprisingly little is known about the repeatability of female mate preferences for any species. To my knowledge, significant repeatability of mate preferences has been demonstrated in only a few select systems, for example, in the Trinidad guppy (Godin & Dugatkin, 1995; Brooks, 1996; Godin et al., 2005) and somewhat anecdotally in zebra finches (Forstmeier

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& Birkhead, 2004). Mate preferences have been shown to possess significant additive genetic variation, but only in a small number of cases (Majerus et al 1982; Moore 1989; Bakker 1993; Houde 1994; Godin & Dugatkin 1995; Brooks 1996), including the zebra finch (Forstmeier & Birkhead 2004).

I examined the repeatability of female zebra finch mate preferences for males wearing colored leg bands (red versus green bands). From previous work, I predicted that most females would be consistent in preferring red-banded males but that there would be among female variation in the strength of this preference (Burley et al. 1982; Burley 1986; Burley 1988, Hunt et al 1997). I studied color band preferences because band manipulation offered me a way of standardizing the male display trait across trials (and females), therefore increasing the probability of detecting real among female variation in preferences. Prior research into the repeatability of female zebra finch mate preferences is limited to one study which compiled data from several different studies to calculate repeatability estimates (Forstmeier and Birkhead 2004). I gathered data using a single experimental design and calculated repeatability estimates for preferences for a single trait (red versus green band color). Hence, I performed the first concerted effort to estimate the repeatability of a broadly recognized female preference trait in female zebra finches. Given previous estimates of significant moderate repeatability of female zebra finch preferences for individual males ($R = 0.29$, Forstmeier and Birkhead 2004), I predicted that females would show significant but low repeatability in their leg band preferences.

Methods

All experiments were performed using our outbred colony of zebra finches, *Taeniopygia guttata*, that were founded from wild-caught individuals two generations ago. Females and males did not have previous experience with each other and were housed in same-sex groups of eight birds per cage (approximately 90 x 40 x 40 cm) when not undergoing experimental trials. Both sexes were visually but not acoustically isolated from the other. The birds were provided nutritionally-complete food and water *ad libitum* and housed at approximately 20°C with a photoperiod of 14:10 (light: dark) hours to prime the females for courtship. Full spectrum lighting was used to ensure that females were seeing naturalistic coloration.

Initial leg band preferences

I investigated female (*n* = 56; 39 virgins and 17 sexually experienced) preferences for males wearing red or green leg bands in a two-chamber apparatus (Figure 1). Stimulus males (*n* = 35) were randomly assigned to preference trials and leg band color. Each female was singly removed from her housing cage, weighed with an electronic balance (to 0.1g precision), and put into the mate preference apparatus (approximately 60 x 30 x 45 cm). Two randomly chosen males were added to the stimulus chambers of the mate choice apparatus (approximately 20 x 30 x 40 cm, see Figure 1). One male wore a small red plastic leg band on each leg (L & M Bands, California); the other male wore light green bands. Visual barriers prevented the female from initially seeing the males. After a 30 minute acclimation period, I removed the visual barriers and began collecting female preference behaviors for a 60 minute trial, recorded on a Sony digital camcorder. After 30 minutes I switched the two male stimulus cages to minimize the effects of any female

side bias on preference data. After switching males to the opposite end of the chamber, I

allowed for a further ten minute settling down period. Therefore, I collected actual

preference data for 40 minutes of each 60 minute exposure trial. Following a trial, leg

bands were removed and all birds were returned to their respective housing cages.

This procedure was repeated three times per female, but each female experienced

only one preference trial per day. I determined female preferences by recording the

proportion of time a female spent courting each male with ritual courtship hops (Swaddle

& Cuthill 1994; Swaddle 1996). Ritual courtship hops were defined as a movement by a

female where she jumped from the end perch to the closest perch and back again or as

rapid jumps on the same perch while she rotates her body 180° each turn.
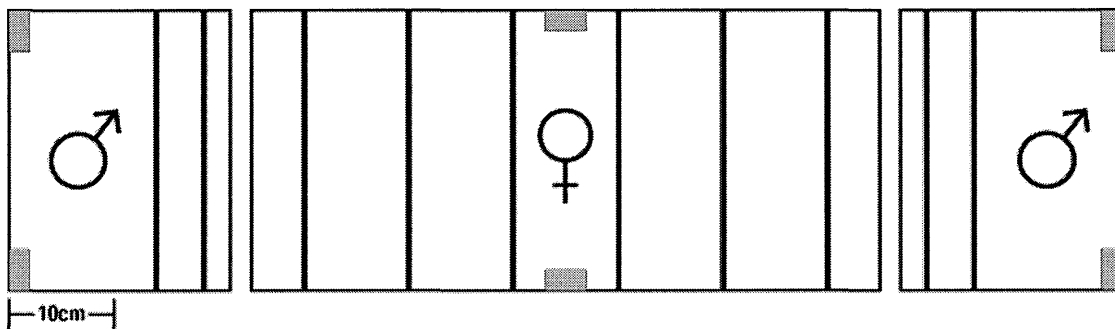
$\vdash$ 10cm $\dashv$

Figure 1. Representation of the mate preference apparatus used to test female preferences for males
wearing red versus green leg bands. Thick black bars represent perches and gray boxes represent food and
water dishes.

Mate choice copying

Within a week of the initial leg band preference trials, I placed females in a situation

where they could copy a leg band preference from another female (*sensu* Swaddle et al

2005). In the "copying" apparatus, each focal female was housed in a small central cage

(approximately 20 x 30 x 40 cm) where she could observe a stimulus female paired with

a stimulus male (defined as the mixed-sex male) in one cage (approximately 20 x 30 x 40

cm) and a stimulus male paired with another male in the other cage (defined as the same-sex male) for two weeks (Swaddle et al 2005). This period of time has been shown to induce mate choice copying for orange and white leg bands in female zebra finches (Swaddle et al. 2005). We assumed that the mixed-sex male appeared as an apparently chosen male and the same-sex male as an unchosen male. Half of mixed-sex (apparently chosen) males were assigned red leg bands (randomly determined), the other half wore green. Same-sex (apparently unchosen) males always wore the opposite band color. Therefore, we reinforced a preference for red bands in half of the females and for green bands in the remainder. Stimulus males were randomly assigned to each side of the copying apparatus to reduce side bias. Birds were provided food and water *ad libitum* at all times and kept under the general environmental conditions described earlier.
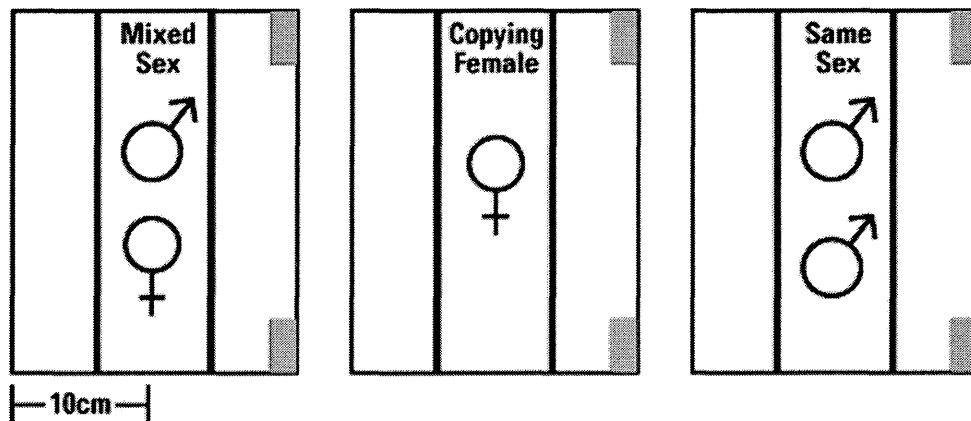

Figure 2. Diagram of the copying apparatus where focal females observed a mixed-sex stimulus pair male (on the left in this example) and a same-sex stimulus pair male (on the right) for two weeks. Thick black bars represent perches and gray boxes represent food and water dishes.

After two weeks of observing a mate choice copying situation, I re-assessed band preference for each female, as described earlier. The post-copying preference trials were performed within a week of the end of the "copying" period for each female. Females

were unfamiliar to males throughout all stages of the experiment. The whole experiment was performed in seven blocks of eight focal females at a time.

Preference data were arcsin square root transformed to increase normality. I investigated within-female changes in band preferences from pre- to post-mate choice copying using a repeated measures ANOVA model in SPSS 13.0. I used the color females were assigned to copy, their sexual experience (i.e. virgin or previously mated), and block in the experiment as factors in the model along with body mass as a covariate. I tested whether initial (i.e. pre-copying) females' preferences for red versus green bands were significantly different from a random preference using a one-sample t-test against a prediction of no preference for red over green bands. Finally, I used a one-way ANOVA to calculate the repeatability of mate preferences before and after mate choice copying, in two separate tests. I used the mean square among and the mean square within from the one-way ANOVA in the following formula: $MS_A /(MS_W + MS_A)$ where $MS_A = [(MS_A - MS_W)/n_o]$.

Results

Contrary to our prediction, female zebra finches did not show strong band color preferences before "copying", as these preferences did not deviate significantly from a random preference of 0.5 ($t_{55} = -1.060$, $p = 0.294$, Figure 3). Females showed weak but almost significant repeatability of initial color band preferences ($R = 0.109$, $F_{55,167} = 1.37$, $p = 0.08$).
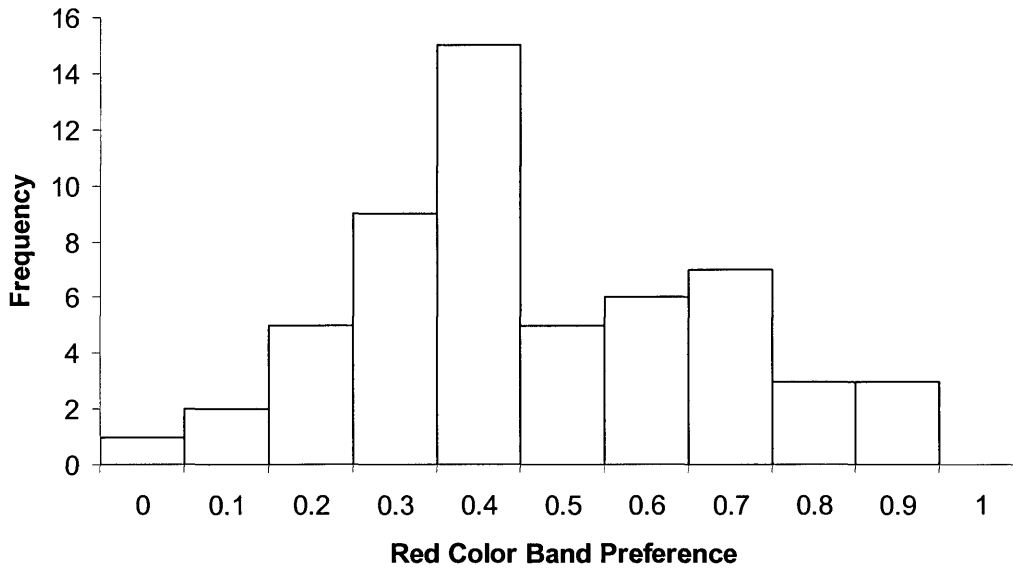
Figure 3. Relative female preference for red bands before presentation with social information. A zero preference represents a strong preference for green and a value of one represents a strong preference for red; a value of 0.5 indicates no preference between the two color bands. Each female (n = 56) is represented by one data point, which is the mean of three preference trials.

After observing a mate choice copying situation, repeatability of female color band preferences increased slightly but was still weak and slightly significant ($R = 0.148$, $F_{55,167} = 1.52$, $p = 0.03$). Importantly, our repeated-measures ANOVA indicated that females significantly altered their initial color band preferences after exposure to a mate choice copying situation ($F_{1,46} = 6.317$, $p = 0.016$; Figure 4). Surprisingly, this effect was opposite to what was predicted because females significantly reduced their preference for the band color worn by the mixed-sex male (Figure 4). There was also a significant interaction between female sexual experience and the change in color band preference over the experiment ($F_{1,46} = 6.582$, $p = 0.014$; Figure 5). Virgin females reduced their preference for the band color worn by the mixed-sex (i.e. apparently chosen) male, whereas previously mated females increased their preference for the color band worn by

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the apparently chosen mixed-sex male. There was a significant interaction between

female body mass and the change in band preferences through the experiment ($F_{1,46}=$

6.861, $p = 0.012$). Interestingly, female body mass was not significantly related to sexual

experience of females ($t_{55} = 1.098$, $p = 0.277$). A post-hoc correlation analysis indicated

a weakly positive relationship between female body mass and within-female change in

band preference ($r = 0.088$, p $= 0.52$, Figure 6). This means that the significant

interaction between female body mass and change in female preference could explained

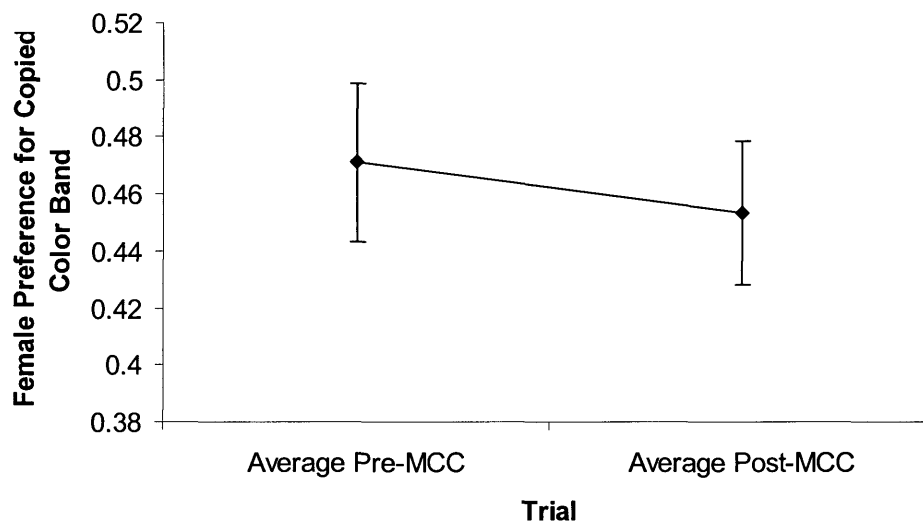by heavier females, who were more likely to alter their band color preference through the

experiment.

Figure 4. Mean (± SE) female band preference for the color band worn by the mixed-sex (apparently chosen) male between pre- and post-mate choice copying (MCC) trials.

Figure 5. Mean (± SE) female band preference for the color worn by the mixed-sex (apparently chosen) male between pre- and post-mate choice copying (MCC) trials. Solid line and circles represent mated females (n = 17), whereas the dashed line and squares represent the preference of virgin females (n = 39).

Figure 6. Correlation between the change in female band preference for the color worn by the mixed-sex (apparently chosen) male between pre- and post-mate choice copying (MCC) trials and female body mass.
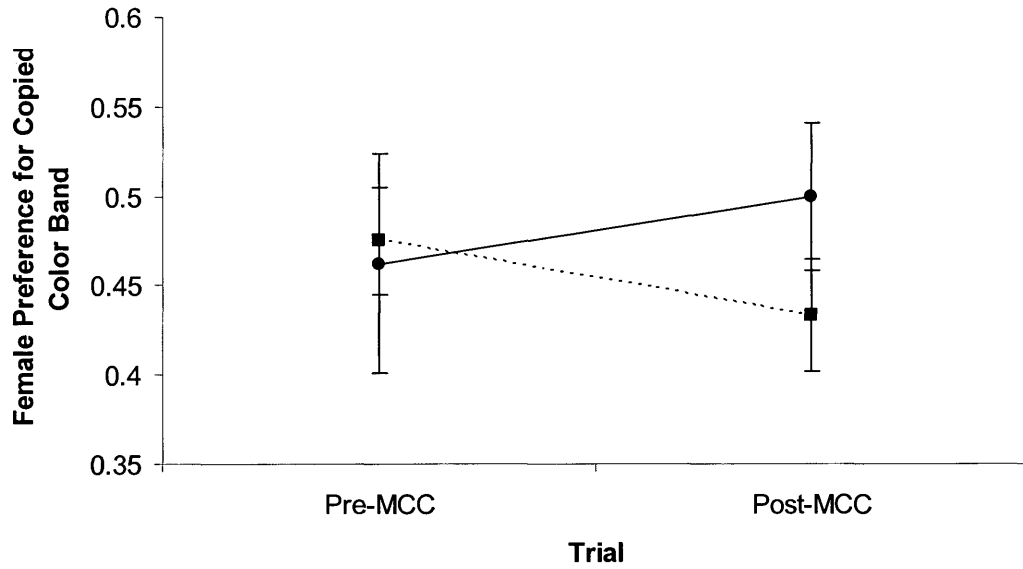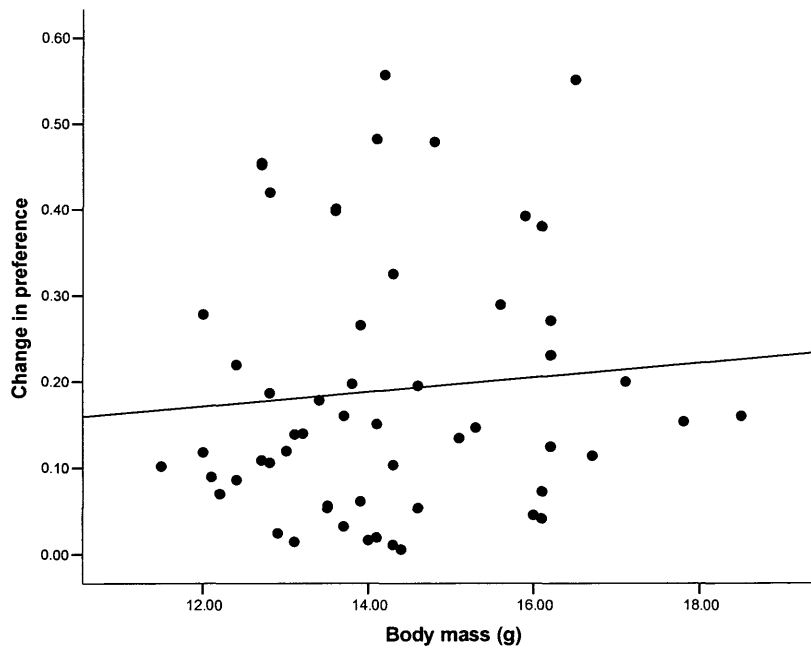
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Discussion

There was low within female repeatability in colored leg band preferences. In one case the preference was not quite significant (i.e. before social exposure) but did become weakly significantly repeatable after exposure to social information. In general our estimates of band preference repeatability are consistent with the only previous investigation of the repeatability of mate preferences in zebra finches (Forstmeier & Birkhead 2004). Our results are similar, however Forstmeier & Birkhead used a sample size approximately double my sample size (104 males) therefore increasing the chance of capturing among female variance and increasing the within female repeatability estimate. Due to the similarity in results, it seems clear that female zebra finches have low but noticeable repeatability in their mate preferences. Therefore, although female zebra finch mate preference is a definable individual trait, there is also substantial plasticity in this trait. This is consistent with our understanding of how female zebra finches acquire their mate preferences. Zebra finches display sexual imprinting (Immelmann 1972; ten Cate 1985; Vos 1995; Witte & Sawka 2003) and are known to exhibit some forms of mate choice copying (Swaddle et al 2005). Therefore, our results indicate that information from the environment can affect genetically inherited mate preferences in female zebra finches.

Repeatability of mate preferences is not only useful in determining how consistent females are within their own choices or how variable a population is in their preferences, but repeatability can provide the upper bound to heritability estimates (Falconer & Mackay 1996). Our zebra finches exhibit low repeatability in mate preferences, thus the heritability of mate preferences should also be low. If heritability of a trait is low that

means that the genetic component of inheritance is low, thus the environment can play a large role in influencing the expression of a trait. This argument justifies why monogamous zebra finches may be a good species to examine the influence of social information (i.e. environmental information).

It is also interesting that social information slightly increased the repeatability of female band color preferences. This is a little counter-intuitive as you may expect females to converge on the same preference, reducing estimates of within female repeatability. However, half of our females were reinforced to prefer red bands and the other half to prefer green bands, which could actually increase among female variance in preferences. In natural conditions, females may all copy the same preference which would reduce the available additive genetic variance for female mate preferences and thus lower the repeatability of mate preferences. If females are copying a range of preferences, within female repeatability of preference would increase but would be decoupled from additive genetic variance as the consistent preference is inherited through social mechanisms. Overall, our data suggest that mate choice copying types of processes will erode the additive genetic variance for mate preferences, requiring the formulation of alternative (i.e. social) mechanisms of inheritance in models of the evolution of mate preferences.

Repeatability of female zebra finch preferences is significant because preferences are a definable trait in which sexual selection may act. Environmental effects, such as social information, can also influence preference inheritance in monogamous zebra finches. However, repeatability of preferences may vary if populations are specific in their preferences but there is immigration from other populations which can bring in

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preferences that are different from the population of interest. This would create a more

heterogeneous population with varied preferences, increasing among female variation in

preferences over a population without immigration of different preferences.

The initial female color band preferences I found were not consistent with past

research (Figure 3). A series of previous experiments concluded that females preferred

males wearing red color bands and disliked males wearing light green color bands

(Burley et al. 1982; Burley 1986; Burley 1988; Hunt et al 1997). At the population level,

I did not find a significant initial preference for either red or green color bands. It seems

that just as many females consistently prefer red bands as others prefer green banded

males. Color preferences may differ in laboratory populations based on genetic

relatedness, lighting conditions, or the conditions under which and the number of years

birds are bred and housed in captivity. Differences in pre-existing color band preferences

indicate that females may exhibit a wider range of color preferences than previously

thought and/or are more plastic than many authors have stated (Burley et al. 1982; Burley

1986; Burley 1988). As our birds were two generations derived from the wild, outbred,

and housed with full spectrum lighting, I suspect that the variation in preferences I

documented here are a better reflection of wild zebra finch preferences than that reported

by Burley. However, other authors have noted "red" preferences in wild populations and

in wild birds in aviary conditions (Burley 1988; Hunt et al 1997). Wild zebra finch

populations may have strong color preferences, meaning that a single population will

strongly prefer one color over another. Our population of zebra finches was collected

from several different populations, therefore we could have collected females from

populations that varied in their color preferences and thus our population shows no strong

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preference for red or green bands because of this mixing. Ultimately, our population would then exhibit more variation in color preferences than perhaps a single color-specific population without immigration from other populations. Overall, mate preferences can be variable among females, with some females strongly preferring one color over another. Variation in these among female preferences can allow selection to act, however, if populations have long-standing preferences for single colors, then among female variation in preferences will decrease, repeatability of preferences should increase, but selection would have little to no variation to act on.

Earlier information indicated that some forms of mate choice copying, via social information, occur in female zebra finches (Swaddle et al 2005). Virgin female zebra finches copied preferences for neutral colored leg bands using the same general procedure I reported here (Swaddle et al 2005). Unexpectedly, my results show that females decreased their preference for the predicted band color (i.e. the one they were reinforced to "copy") after the period of social exposure (Figure 4).

This decrease in band preference may, in part be explained, by my biased sample size of virgin females; I collected data from 39 virgin and 17 previously mated females. Virgin females tended to decrease their preferences for the predicted band color, whereas previously mated females tended to increase their preference for the color worn by mixed-sex males (Figure 5). Therefore, the larger sample of virgins skews my overall comparison of preferences towards the trend that virgins expressed. This still leaves unexplained why virgin and previously mated females responded so differently to the social information about band preferences.

Most models of mate choice copying predict that virgin females would be more likely to "copy" as a mate choice strategy, as inexperienced virgins may have a more difficult time (i.e. experience higher costs) in assessing male quality (Losey et al 1986; Stöhr 1998). Mate choice copying is sometimes described as an alternative method of determining mate choice where virgin females can observe experienced females choose a mate, giving virgin females more information about which males are higher in quality and would make good mates (Losey et al 1986; Stöhr 1998). Therefore, it is quite surprising that virgin females actively prefer the same-sex and/or actively avoid the mixed-sex male band color.

I believe that this pattern may occur for several reasons. First, virgin females may associate a male courting a female (i.e. the mixed-sex male) as a "taken" male. Since zebra finches have low rates of extra-pair copulation (Zann 1996) the observing virgin female may interpret the mixed-sex paired male information as a male who is unavailable or alternatively, a male displaying a similar trait may already be paired with a female because he has a similar high quality trait. However, this explanation is in direct opposition to the observations of Swaddle et al (2005), who noted that virgin females preferred band colors of mixed-sex males. Therefore, it seems that there may be something fundamentally different between the apparent attractiveness of mixed-sex males in the Swaddle et al (2005) experiment (where they wore neutral band colors) versus my experiment (where males wore colors that were meant to affect attractiveness).

Color bands have known effects on dominance in males (Zann 1996; Cuthill et al 1997), which could have caused a difference in perceived attractiveness of a male to a female. Virgin females may have exhibited a decrease in color band preference for the

color associated with the mixed-sex male because those females may not have been influenced by information from the mixed-sex male, but perhaps used information observed from the same-sex male. Male zebra finches banded with red leg bands displace light green banded males at a feeder, thus red-banded males display dominance over light green banded males (Cuthill et al 1997). If the focal female saw dominance interactions occurring during the social information stage, this could have influenced her "copying" behavior. Perhaps virgin females who decreased their preference for the color band associated with the mixed-sex male were actually more strongly influenced by the dominance interactions she observed occurring between the same-sex males. Thus, she used this information to influence her color preference after social information. However, mated females increased their preference for the color band associated with the mixed-sex male, therefore mated females may be more strongly influenced by the mating success of a male whereas an inexperienced virgin female is more strongly influenced by dominance interactions between males, which would be supported by these results. This would mean that females have a priority set of behaviors or traits they seek in mates and sexual experience can affect the order of a female's priorities, such as if virgin females seek different benefits from their mates or perceive genetic quality differently than mated females.

Another explanation for the change in preferences we found could be that mated females weigh more than virgin females and that color band preferences are condition-dependent. A post-hoc correlation analysis between the change in color preference (from pre- to post-female color band preference) and female body mass resulted in no significant correlation. Thus, there does not appear to be any correlation between the

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change in female color preferences and female body mass. However, the ANOVA model found a significant interaction between female body mass and color band preference. In this experiment, heavier females may have been more likely to alter their band color preference (Figure 6). Therefore, condition may effect how a female will be influenced by social information in the formation of mate preferences, leading to more variation and plasticity in female mate preferences.

Finally, past research in guppies has found that inexperienced females are more likely to copy the mate preferences of older females (Amlacher & Dugatkin 2005). I predicted that if a female was shown a model female with a male that the focal female would interpret that information as a successfully mated female. Thus I believed that virgin females would tend to copy the mate choice of the model female. However, I did not consider the age of the model female in my experiment. If female zebra finches do prefer to copy mate preferences from an older model then this may have affected my results. I did randomly assign females to a model situation so that would have decreased the chance of a large skew in age of the model and age of the copier but this can not be ruled out. A future experiment specifically examining whether female zebra finches prefer older females as models for copying is needed to determine if age influences the chances of copying preferences.

These results may be interpreted as demonstrating that female zebra finches have the ability to learn and acquire mate preferences via social information, a non-genetic mechanism for inheritance of preferences. This is important for models of sexual selection because they traditionally have only modeled genetic inheritance of preferences and now models should incorporate social information. Social inheritance of preferences

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can lead to faster spread and evolution of traits and preferences, which can ultimately lead to increased sexual selection in a population.

Traditionally, only lekking or polygamous species were though to acquire information through mate choice copying and other non-genetic processes but our results as well as the recent results from others, shows that monogamous species may also use social information in preference inheritance. This is significant because monogamous zebra finches meet the criteria for mate choice copying in that they have the opportunity to observe other females make mate preference decisions and they have slightly repeatable within individual yet variable among female preferences, which means that selection can still act on female preferences.

Future research in the field of mate choice copying, especially in monogamous species such as zebra finches, should examine the duration of copied preferences. To date only one study has examined the decay of a copied preference (Witte & Noltemeier 2002). They found that sailfin molly females copied a preference for smaller males and maintained this preference for up to five weeks (Witte & Noltemeier 2002). The duration of a copied preference would further indicate how much influence it could have on sexual selection processes. A copied preference that decays very quickly should have very little effect on sexual selection because information is not being retained long enough to pass on to many individuals or offspring. However, if social information, in the form of copied preferences, can be maintained over several generations preserving a consistent sexual selection pressure on the evolution of male display traits, then female preferences can spread quickly through the population. Therefore, the initial strength of selection on male traits would be increased in a situation with copying.

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As the zebra finch shows elements of mutual mate choice (Zann 1996), it seems relevant to explore whether male preferences for females is affected by social information. If female zebra finches can use copied information to form mate preferences then males should have the same ability. Past research using colored leg bands on males reveals that males have color preferences for leg bands on females (Burley 1986; Burley 1988). This experiment could follow the same methodology as this experiment and previous experiments but focus on male mate preferences and male mate choice copying. I predict that males would have the ability to socially acquire mate preferences because of the mutual mate choice involved in this species. This experiment would be significant because this would emphasize that both sexes of a monogamous species can use social information to influence their preferences, as well as many polygamous or lekking females. Male copying behaviors have been limited and are found mainly in sex-role reversed species (Widemo 2005), thus this would contribute significant information in terms of male mate choice and social acquisition of preferences.

In conclusion, my population of female zebra finches did not show strong preferences for males wearing red versus light green color bands, as previously described. Variation in preferences among females is necessary to investigate repeatability of preferences. Somewhat consistent with a previous report (Forstmeier & Birkhead 2004), female mate preferences showed low but sometimes significant repeatability. Repeatability of female mate preferences implies that mate preferences are traits which sexual selection may act upon. Variation and repeatability of preferences indicates that preferences are plastic and able to be influenced by non-genetic mechanisms, such as

social information. Transfer of social information about mate preferences led to a slight increase in the repeatability of mate preference, which is somewhat surprising as you may expect most females to converge on the same preference through social inheritance. However, substantial among female variation was maintained, possibly because females were exposed to two social learning situations which maintained variation in preferences whereas social learning of one preference would have decreased variation in preferences and decreased repeatability. Social information changed female mate preferences in my population of zebra finches, but not in the expected direction due to differences possibly explained by sexual experience. Overall, social information plays a role in mate preference inheritance in monogamous species, as well as polygamous and lekking species, which can influence sexual selection to change pressures on favored traits causing rapid evolution of these traits and preferences.

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Amanda Houck entered the College of William and Mary as a Master's student in the Department of Biology in August 2005. She worked with Dr. John P. Swaddle studying mate preferences in zebra finches. Amanda also worked part-time as a research assistant for Dr. Patty Zwollo studying B-cell immunology in trout. Upon graduation from the College of William and Mary, Amanda will be entering into the field of cancer biology and immunology.