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## Previous Experience Shapes Mate Preferences of Female Zebra Finches (*Taeniopygia guttata*)

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**Previous Experience Shapes Mate Preferences of Female Zebra Finches  
(*Taeniopygia guttata*)**

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**Bachelor of Science, University of Mary Washington, 2005**

**A Thesis presented to the Graduate Faculty  
of the College of William and Mary in Candidacy for the Degree of  
Master of Science**

**Department of Biology**

**The College of William and Mary  
January, 2009**

## COMPLIANCE PAGE

Research approved by

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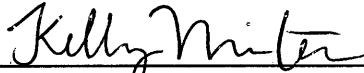
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## APPROVAL PAGE

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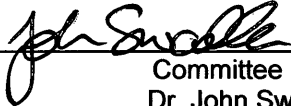
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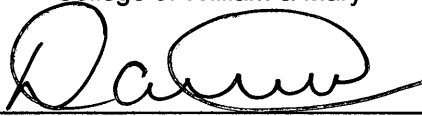
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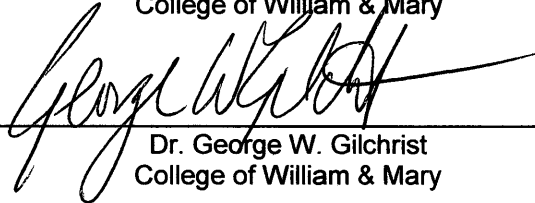
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## ABSTRACT PAGE

Adaptive decision-making can be beneficial to an individual selecting food, habitat, or a mate when better decisions lead to higher fitness. While decision-making is critical to processes that shape both individual fitness and population-level evolutionary trajectories, it is not well understood how information from multiple experiences influences decision-making. This study seeks to better understand the mate choice process in the female zebra finch (*Taeniopygia guttata*) by providing females with information about the quality of potential mates through social interaction and 'personal' breeding experience. Female preference for leg band color was assessed in mate preference trials after a two-week period of social interaction with males wearing colored leg bands, and again after females bred with assigned mates also wearing colored leg bands. Mates were assigned such that half of the females were paired with males wearing the leg band color they preferred in mate preference trials after social experience, and half were paired with males wearing the leg band color they avoided. Females were assigned to mates and nests were manipulated so that approximately a quarter of the females were successful with males wearing the leg band color they preferred, a quarter were successful with males wearing the color they avoided, a quarter were unsuccessful with males wearing the preferred color, and a quarter were unsuccessful with males wearing the avoided color. In this way, half the females received information that supported the preferences generated by social experience (attractive mate/successful breeding, unattractive mate/unsuccessful breeding) and half received information that contradicts their post-social experience preferences (attractive mate/unsuccessful breeding, unattractive mate/successful breeding). After social experience, females showed a preference for the unfamiliar leg band color over the leg band color they observed on males during the social experience trials. The attractiveness of a female's mate had the biggest influence on post-breeding preferences, though there was an interaction between mate attractiveness and nest success, which suggests that the four treatment groups did utilize information differently from each other. Because females appear to avoid unpaired males, this suggests that previous studies of mate choice copying may need to be revisited to allow for the importance of avoiding unpaired males in addition to the importance of preferring previously-chosen males. The results of the post-breeding experience mate preference trials suggest that, while social experience seems to play the biggest role in shaping the mate preferences of female zebra finches, information collected from other sources (like breeding experience) also shape mate preference formation. Mate preferences are dynamic, and mate choice is shaped by an individual's past experiences. In zebra finch populations, sexual selection appears to be shaped predominantly by social interaction, and future research should focus on determining the cues from social experience that have the biggest impact on mate preferences.

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## CHAPTER I: BACKGROUND

Phenotypic plasticity is the capacity of a single genotype to produce multiple phenotypic variants in response to different conditions, and, when adaptive, it has the potential to maximize an individual's fitness in variable environments (Dudley and Schmitt 1996; Scheiner 1993; Thompson 1991; Via 1993; Via et al. 1995). Phenotypic plasticity can also be maladaptive, though, for the sake of brevity and simplicity, only adaptive phenotypic plasticity will be discussed in detail here. Reaction norms indicate the extent of plasticity in a trait by correlating phenotypic expression of individuals sharing a genotype with an environmental gradient. An environmental gradient can result from variation in any abiotic or biotic factor that affects the population of interest. Variation in the social environment, for example, may influence traits just as much as variation in an abiotic factor such as climate or soil composition. If a trait is not plastic, mean phenotypic expression will remain constant across an environmental gradient, and the reaction norm will be a flat line, as shown in Figure 1a. If a trait is plastic, the extent and direction of phenotypic change across environments will be evident by how much the shape and slope of the reaction norm differ from a flat line, depicted in Figure 1b and 1c (Dudley and Schmitt 1996; Scheiner 1993; Via et al. 1995; Gavrillets and Scheiner 1993).

Understanding reaction norms and phenotypic plasticity is important because it provides a greater understanding of evolution. A static genotype may not be adaptive in every environment in which it is found, and individuals carrying this genotype may have reduced fitness in some environments. Plastic genotypes, on the other hand,



respond to environmental change, and individuals carrying these genotypes may have less variation in fitness across environments. Because of this, plastic genotypes can stay at higher frequencies in populations across environmental gradients, and phenotypic variation will be preserved in these populations even if genotypic variation is constrained (Dudley and Schmitt 1996; Scheiner 1993; Thompson 1991; Via et al. 1995).

Furthermore, reaction norms for the different genotypes present in a single population spread across an environmental gradient can be bundled to provide information about the variation in plasticity between different genotypes as well as the degree of trait variation in the population as a whole in a given environment (see Figure 2). Tightly bundled groups of reaction norms indicate that there is little variation in plasticity between genotypes, while loosely bundled reaction norms indicate greater variation in plasticity. A group of reaction norms may also indicate wide variation in trait value between genotypes in a specific environment if the reaction norms are widely spaced relative to the y-axis at a single point on the x-axis. Reaction norms that are close together relative to the y-axis indicate less variation in trait value, and reactions norms that converge to a single point indicate no variation in trait value between the genotypes in a single environment (Dudley and Schmitt 1996; Scheiner 1993; Via et al. 1995; Gavrilets and Scheiner 1993).

Phenotypic plasticity can give rise to phenotypic variation at various points during an organism's lifespan. Plasticity may occur during embryonic development, pre-reproductive life stages, reproductive life stages, or some combination thereof. In one of the simplest cases where plasticity is seen only during embryonic development,

phenotypic plasticity is analogous to a switch (Dodson 1989). Once this switch is thrown, phenotype remains static for the duration of the individual's lifespan. One such example is of species in the genus *Daphnia*. *Daphnia* embryos developing in waters populated with predators develop elaborate body armor for defense, but embryos in waters free of predators do not develop these costly armaments. Unprotected *Daphnia* transplanted to a predated environment do not suddenly grow body armor; though this trait is plastic, the phenotype is fixed during development (Dodson 1989).

While in the previous example, phenotype varied discretely with discrete changes in the environment, plastic traits can also vary continuously in response to continuous environmental variation. Continuous variation is particularly likely for morphological traits like body size and behavioral traits such as mate preference when a slight change in trait value is more adaptive than a large change. While it is fairly intuitive that behaviors would vary slightly across a changing environment, most work on phenotypic plasticity has focused on morphological rather than behavioral traits. This leaves a gap in evolutionary models dependent on the behavior of individuals, such as models of sexual selection that depend upon mate preferences, that is slowly starting to be filled by studies of the impact of experience and environment on adult behavior.

Experience during the early stages of development can have strong and lasting impacts on adult behavior (Clayton 1990; Engeszer 2007; Engeszer et al. 2004; Freeberg 2000; Ten Cate 1984). For example, zebrafish (*Danio rerio*) exhibit shoaling preferences later in life based on the conspecific phenotype experienced in their early

environment (Engeszer 2007; Engeszer et al. 2004). Wild-type fish typically prefer to shoal with other wild-type fish, but, when exposed to a mutant phenotype called *nacre*, wild-type fish will prefer to associate with *nacre* individuals (Engeszer 2007; Engeszer et al. 2004). This preference does not change later in life, even if the adult fish are exposed to individuals of the non-preferred phenotype for long periods of time (Engeszer 2007). Imprinting and early experience are important not only in forming social group preferences, but also in developing mate preferences. For example, female zebra finches sexually imprint on the male vocalizations present in their early social environment and prefer males with similar vocalizations as mates (Clayton 1990; Freeberg 2000).

Encountering different environments as an adult can also result in different behaviors in individuals with the same genotype. For example, in a species of soil predatory mite (*Hypoaspis aculeifer*), hybrids of two selected lines of mites may be either superior or inferior to pure-breeding individuals depending on the composition of the mites' diet (Lesna and Sabelis 1999). When the diet favors hybrids, females mate with males from the other line to produce hybrid offspring. When diet does not favor hybrids, females mate assortatively with males from their own line. Females of this species do have active mate choice, and individuals with genetic backgrounds like those used in the two laboratory-maintained lines would encounter each other in the wild. Furthermore, prey availability is stable in the wild, and is not likely to change appreciably in the amount of time it takes for a female to mate and produce offspring. Therefore, the environment in which a female chooses a mate is likely to be the same as the environment her offspring occupy, and thus plasticity in mate preference for

individuals of different genetic backgrounds has the potential to increase fitness (Lesna and Sabelis 1999).

Adaptive plasticity in mate preference, like in the previous example, may be linked to differences in reproductive effort (Qvarnstrom et al. 2000). Female collared flycatchers (*Ficedula albicollis*) previously have been thought to prefer males with large forehead patches, but more recent work suggests that this preference may be present or absent depending on the timing within the breeding season (Qvarnstrom et al. 2000). Only females breeding later in the season prefer males with large forehead patches, and only late-breeding females receive increased reproductive success from mating with males with larger forehead patches. Furthermore, females with large-patched mates put more investment into later clutches than do females with smaller-patched males. Decision-making during the breeding season may influence reproductive effort and overall reproductive success for the year. Decision-making can be a source of plasticity in behavioral traits like mate preferences when the actual decision made and its outcome vary with environmental conditions. Individuals that demonstrate adaptive plasticity may pass more of their genes to the next generation than those that do not (Qvarnstrom et al. 2000).

### **Learning occurs when behaviors are plastic**

In order to respond to varying environments in a way that best maximizes fitness, individuals must be able to accurately perceive the environment around them (Valone 2007). While the physiological mechanisms behind perception may be largely genetically determined, inherited knowledge about the environment may not be useful

if the environment changes from generation to generation. When this is the case, the ability to collect information and learn is advantageous (Danchin et al. 2004). An individual may have the machinery necessary to accurately assess its world, but the fitness gains resulting from this ability may be limited if the individual does not apply collected environmental information towards decision-making. If decision-making is influenced by environmental information and decision-making processes vary with environmental conditions, decision-making is one manifestation of phenotypic plasticity.

Theoretical studies suggest that learning strategies will be most advantageous to individuals when the environment is predictable but not constant. Information becomes much less valuable when conditions are so unpredictable that collected pieces of information are never again relevant (Doligez et al. 2003). Learning can be either social or asocial (Danchin et al. 2004). Social learning occurs as the result of observation of, or interaction with, other individuals (Swaney et al. 2001; Galef and Giraldeau 2001), and can be based on evolved signals or can occur unbeknownst to the 'tutor' (i.e., eavesdropping) (Danchin et al. 2004). Inadvertent social information is reliable because it is not produced for the sake of information transfer. Producers of inadvertent social information make the best decisions possible for their own benefit; other individuals notice and use the behavior resulting from these decisions to make their own decisions (Danchin et al. 2004). Inadvertent social information is also known in the literature as public information, and will be referred to as such from here. Asocial learning is often trial-and-error learning, and is independent of the behavior of other individuals. Regardless of which type of learning is going on, the

individual receives information about the environment that can be applied towards decision-making (Heyes 1994). Again, if individuals show variation in behavioral traits as a result of environmental change, learning that informs decision-making and results in behavioral variation can generate phenotypic plasticity.

**Public information: information for foraging choice, habitat selection, and mate choice**

Using public information often makes it possible for an individual to assess the quality of a resource faster and more accurately (Valone 2007; Clark and Mangel 1986; Templeton and Giraldeau 1996; Valone 1989; Nordell and Valone 1998). Here I review the use of public information as applied to foraging choice, habitat selection, and mate choice, although public information is also used to modify numerous other life history strategies (Valone 2007).

Fringe-lipped bats (*Trachops cirrhosus*) have recently been shown to learn to associate calls from unpalatable species of frog, such as the cane toad (*Bufo marinus*), with a palatable food source (Page and Ryan 2006). Bats that observed tutor bats responding to the novel frog call and receiving a food reward learned to associate the call with reward much faster than either two naïve bats working together or one naïve bat. This ability is hypothesized to increase foraging success, and may be particularly important as a way to help these bats avoid ecological traps in the wild (Page and Ryan 2006; Ratcliffe and ter Hofstede 2005). Wild black bear cubs (*Ursus americanus*) also appear to learn foraging behavior from social cues (Mazur and Seher 2008). Cubs raised in areas where they saw their mother or other bears foraging from

trashcans, or other anthropogenic sources, were more likely to later forage from these sources than cubs who were raised in areas where they did not observe this behavior (Mazur and Seher 2008). Similarly, nine-spined sticklebacks (*Pungitius pungitius*) use public information about food richness in different patches from both conspecifics and heterospecifics to identify the best resources (Coolen et al. 2003; van Bergen et al. 2004)

When individuals need to select a habitat in which to settle for the breeding season, they may prospect to judge the quality of potential sites. Juveniles, nonbreeders, and failed breeders tend to prospect more often than successful breeders (Valone 2007; Doligez et al. 2003; Cadiou et al. 1994). These individuals would have the most to gain by acquiring such public information: juveniles have no personal prior information about breeding patch quality, and failed breeders have personal information that the patch in which they just bred is of low quality (Valone 2007). Prospecting behavior has been well studied in collared flycatchers (Doligez et al. 2003; Doligez et al. 2002; Doligez et al. 2004; Part and Doligez 2003). In the studied populations, prospecting was more common in breeding patches where the researchers had artificially increased reproductive success by adding nestlings from other populations to nests (Part and Doligez 2003). Local reproductive success of conspecifics is thought to be commonly used as a cue for habitat selection and is thought to be particularly informative because local reproductive success is influenced by all aspects of the environment (Doligez et al. 2003). While prospectors may not have time or opportunity to survey the number of nestlings in multiple nests within a patch, they may use parental activity as a surrogate for local reproductive success.

Higher parental activity indicates a larger numbers of nestlings (Part and Doligez 2003).

Public information can also be useful to individuals selecting mates (Valone 2007; Danchin et al. 2004). Empirical work suggests that females use public information when potential mates are of similar quality and when the females are otherwise unable to discriminate between the potential mates (Danchin et al. 2004; Valone and Templeton 2002). One of the ways a female can obtain public information about male quality is by observing male contests (Valone 2007). A female can either observe this contest herself, or, in the case of vocal contests such as song contests between male birds, she can eavesdrop on a competitive interaction. As a general rule, females prefer to mate with winners of aggressive interactions compared to losers (Doutrelant and McGregor 2000; Mennill et al. 2002; Otter et al. 1999; Ophir and Galef 2003).

Females may also be able to learn from the mate choices previously made by other females in their social environment. Mate choice copying occurs when females become more likely to mate with a male when they have seen this male mate previously with other females (Danchin et al. 2004; Brown and Fawcett 2005; Dugatkin 1992; Galef and White 1998; Hoglund et al. 1995; Swaddle et al. 2005; White and Galef 2000; Witte and Noltemeier 2002). In some species, such as the Japanese quail (*Coturnix coturnix japonica*) and black grouse (*Tetrao tetrix*), copying occurs only if the focal female sees an actual copulation occur (Galef and White 1998; Hoglund et al. 1995); for some species, like the guppy (*Poecilia reticulata*) and zebra finch (*Taeniopygia guttata*), observing a male associated with a female or females is



enough to influence preference (Dugatkin 1992; Swaddle et al. 2005). Some species are also able to generalize male traits. This means that females of these species form an association between the traits of a chosen or not chosen male and the status of being chosen or not chosen. In species that are unable to generalize traits, this association only forms for a specific male previously encountered and whether or not he was apparently chosen or not chosen at the time of that encounter. (Brown and Fawcett 2005; Swaddle et al. 2005; White and Galef 2000). The ability to generalize traits may be particularly important in monogamous species like the zebra finch in which a male observed in a pair is unlikely to be available as a social mate to choosing females (Zann 1996). In some cases, mate choice copying has a powerful enough effect to reverse an individual's previous preferences (Danchin et al. 2004). For example, a virgin female may express a preference for a male with specific traits and avoid males with different traits. If this female later observes other females preferring males with traits that the virgin female originally avoided, subsequent preference testing may show that the virgin female in question shows a preference for males with traits like those that other females prefer.

While use of public information in other contexts, like foraging choice or habitat selection, will influence lifetime fitness of individuals and is likely to have evolutionary repercussions, it is easiest to see the influence of public information on evolution when dealing with mate choice. Female mate choice copying has the potential to increase the variation in male reproductive success and can increase the intensity of sexual selection to act on a population (Dugatkin 1992; Agrawal 2001; Wade and Pruett-Jones 1990). If females select males with a wide variety of traits for

mates, variation in male traits will be carried to the next generation. If females copy these mate choices in the next breeding season, the variation in male traits will continue to be preserved. In this scenario, there is little variation in male reproductive success (everyone mates regardless of traits) and the intensity of sexual selection is low. However, if females only select males with a specific trait, such as a very dark red beak, and this choice is copied, variation in male reproductive success will increase (not all males mate), and the intensity of sexual selection will also increase, favoring the chosen trait. In this scenario, variation in male traits will decrease.

Copying behavior can spread through a population genetically. Theoretically, alleles for copying are predicted to become genetically associated with attractive male traits and could spread through a population if copiers are more successful than non-copiers (Agrawal 2001). Mate choice copying could lead to a cultural inheritance system, but mate choice copying is not a system of cultural inheritance in and of itself. A learned preference must stay consistent over time in order for it to be culturally transmitted (Brooks 1998). Through cultural transmission, mate choice copying could cause a novel male trait to sweep through a population even without a pre-existing genetic preference for the trait (Agrawal 2001). Because it can alter gene frequencies within a population as well as spread preferences via cultural processes, mate choice copying represents an interaction between genetic and cultural evolutionary processes within a population (Agrawal 2001).

Agrawal's model predicts that mate choice copying can cause positive or negative directional selection or positive or negative frequency-dependent selection on male traits, depending on the details of how females are influenced by the pairings

they observe (2001). In other words, mate choice copying could dampen or increase the strength and direction of sexual selection depending on how copying occurs within populations. To understand how exactly copying impacts sexual selection in a population, it is important to know if females always copy or sometimes copy, if all the females copy or only some, and if females copy others indiscriminately or only copy certain individuals.

### **'Personal' information: learning through experience**

Asocial learning occurs independently of other individuals in the environment and instead results from personal experience or trial-and-error learning (Heyes 1994).

Trial-and-error learning works quickly and can form strong associations not easily reversed. For example, taste-toxicity associations can be learned in as quickly as a single trial and are persistent (Ratcliffe and Fenton 2006; Ratcliffe et al. 2003).

Asocial learning, like social learning, may take place at any point during an individual's lifespan (Heyes 1994).

Like studies of public information, the influence of personal information on mate choice has been a topic of interest in recent years. Personal breeding success is influenced by phenotypic factors, environmental factors, and the interaction between phenotype and environment, and can be more accessible, informative, and reliable than public information (Doligez et al. 2003). For example, female fruit flies (*Drosophila melanogaster*) show mate preferences for large males, but, when given an opportunity to mate again, females with previous sexual experience with small males are more likely to mate again with a small male than females who have no such prior

experience (Dukas 2005). In a similar study, female collared flycatchers with previous experience with males with an artificial trait were more likely to mate again during the next breeding season with a male of the same artificial phenotype than were females with no prior experience with the novel trait (Qvarnstrom et al. 2004). In both cases, it is unclear as to whether this learned preference is the result of learning from a positive experience with a formerly non-preferred male phenotype or if the developed preference is the result of a process more along the lines of sexual conditioning (Domjan 1992). While it is important to understand the underlying mechanism, in either case the developed preference is the result of personal experience.

Personal experience can influence mate choice beyond increasing the attractiveness of previous mates, and may produce the opposite effect and cause females to avoid males like their former mates. For example, female Japanese quail prefer to mate with the winners of aggressive interactions. However, this effect is only seen in virgin female quail; experienced females prefer the losers of aggressive interactions (Ophir and Galef 2004). In a previous study, Ophir and Galef found that males that are more aggressive with other males (winners of fights) tend to also be more aggressive towards, and potentially harmful to, females while courting and mating (Ophir and Galef 2003, 2004). Female quail face a trade-off between mating with the most dominant male and avoiding injuries that may compromise future breeding attempts (Ophir and Galef 2004).

While all of the previous highlighted studies deal with information gained in the past and applied to future mate choices, females may also show variation in preference based on current conditions. Current personal status may influence mate

preferences in addition to past personal information. For example, female zebra finches that perceive themselves to be in low condition are less choosy than female zebra finches that perceive themselves to be in high condition (Burley and Foster 2006). This suggests that females may compensate for their own reduced attractiveness when choosing a mate (Burley and Foster 2006).

### **Public information and personal information interact in decision-making**

Less well understood than public information or personal information is how the two interact to influence decision-making. Studies of public information assume that individuals only copy when their discrimination ability is lacking, typically due to lack of experience and pre-existing personal information. Because of this, we expect copying behavior to be more common not only when personal information is limited or unreliable, but also as it becomes more difficult to discriminate among options (Valone 2007; Nordell and Valone 1998; Brooks 1998). For example, when presented with a colorful male and a drab male, young female guppies readily chose the more colorful male because they can readily discriminate between the two males based on traits only. However, with matched males, young female guppies often copy the mate choice of other females because they cannot otherwise discriminate between the two males (Dugatkin and Godin 1993).

Using a combination of public and personal information may be the best strategy for adaptive decision-making (van Bergen et al. 2004). Many previous models that have incorporated both public and personal information assume that the two types of information are weighted equally in decision-making, but this is likely an

oversimplification (Valone 2007; King and Cowlshaw 2007). It is likely that one type of information is more reliable than the other depending on the context, and individuals may gain the greatest benefit by preferentially using the most reliable information (van Bergen et al. 2004). One such possibility is that young, inexperienced individuals might benefit from weighting public information more heavily than their personal information if they have underdeveloped assessment abilities (Valone 2007). Another possibility is that, if accurate personal information is readily available at low cost, an individual may be better off using only personal information (Templeton and Giraldeau 1996; van Bergen et al. 2004).

Studies have begun to address these issues with regards to foraging choice, habitat selection, and, in a very limited sense, mate choice. When presented with contradictory public information provided by foraging conspecifics, guppies with personal information about the relative quality of two foraging locations ignore the conflicting public information unless acting on personal information alone inflicts a cost, such as breaking from the shoal (Templeton and Giraldeau 1996; van Bergen et al. 2004; Day et al. 2004). Nine-spined sticklebacks also weight public and private information differently, depending on circumstances, to make adaptive foraging decisions (van Bergen et al. 2004). Similarly to the guppies, they will ignore contradictory public information when they have personal information that is both reliable and recent. However, when personal information has not been updated for seven days, they will make foraging decisions based on recent-though-contradictory public information (van Bergen et al. 2004). This suggests that fish prefer to use personal information to make foraging decisions except when personal information

about patch quality is old or unreliable, which is consistent with the hypotheses about when individuals should use public versus personal information (Templeton and Giraldeau 1996; Nordell and Valone 1998; van Bergen et al. 2004). Putting an 'expiration date' on information may be adaptive for individuals living in environments that change frequently (van Bergen et al. 2004).

Empirical evidence suggests public information, in the form of the presence of conspecifics in a breeding patch, and personal information, in the form of individual reproductive success within a breeding patch, are used by individuals to make habitat settlement decisions (Galef and Giraldeau 2001; Templeton and Giraldeau 1996; Valone 1989; Doligez et al. 2004; Valone and Templeton 2002). Breeders typically use their own reproductive success as an indication of the quality of their current breeding patch, and decide whether to leave based on this information (Doligez et al. 2003; Switzer 1997). However, while the decision on whether or not to emigrate can be made solely using personal information, breeders are reliant on public information about the quality of other breeding patches to which they could immigrate (Doligez et al. 2003; Doligez et al. 2004; Danchin et al. 1998). In a nest manipulation study of collared flycatchers, individuals whose broods were reduced were more likely to disperse to patches where broods were increased than were un-manipulated individuals, and individuals whose broods were increased were less likely to disperse to increased patches than un-manipulated individuals (Doligez et al. 2002). While, in this case, emigration decisions are based on personal information and immigration decisions are based on public information, both types of information go into the overall habitat selection process. Furthermore, the meaning of public information cues

may vary with the individual's personal experience, making it very difficult to truly understand public information usage without also understanding the role of personal information (Doligez et al. 2002; Valone and Giraldeau 1993). Adding further complexity to the problem, different cues are used for different decisions, and individuals with different phenotypes may use these cues differently depending on their own skills and experience (Doligez et al. 2002; Parejo et al. 2007)

In a similar study of blue tits (*Cyanistes caeruleus*), failed breeders moved from patches with low to medium local reproductive success and from high to low density patches (Parejo et al. 2007). Successful breeders, however, moved from patches with high to medium local reproductive success and from low to high density patches; in other words, successful breeders settled in better quality patches than failed breeders (Parejo et al. 2007). These results may have been due to a difference in the competitive abilities of the failed versus successful breeders, or they may have been due to a difference in selectivity of the failed versus successful breeders (Doligez et al. 1999; Parejo et al. 2005). This study also suggests that juveniles may decide on a breeding patch in their first year based solely on patch density in their first breeding year, but adults are able to take into account both density and local reproductive success from the previous year (Parejo et al. 2007). Juveniles may be unable to gather information about local reproductive success in their birth year due to limited time. This further strengthens the argument that multiple cues go into habitat selection, and suggests that individuals may use different sources or amounts of information depending on their age (Doligez et al. 2003; Doligez et al. 2004; Parejo et al. 2007; Muller et al. 1997; Reed and Oring 1992).



To date, there has been little data collected on the interaction between public and personal information as applies to mate choice (Domjan 1992; Dubois 2007). It has been suggested that personal information from sexual experiences in adulthood can outweigh public information collected during social experiences as a juvenile (Domjan 1992). There is some evidence from male Japanese quail that support this claim (Domjan 1992), but, to my knowledge, this has not yet been tested in female quail or other taxa. It is also thought that females may use different types of information differently, depending on whether they are selecting a social mate or an extra-pair mate (Dubois 2007). There is some support for this from the female pied flycatcher (*Ficedula hypoleuca*), which seems to ignore personal information about male quality when choosing an extra-pair mate. It is suggested that they use personal information when choosing a social mate, but use another source of information to choose an extra-pair mate. More research is needed to support or refute this hypothesis (Dubois 2007; Slagsvold et al. 2001). Of course, an individual is likely to have multiple pieces of both public and personal information available, but how multiple cues of any sort factor into a single decision is not well understood.

While decision-making in any context is not thoroughly understood at this point, mate choice is particularly lacking. What is clear, however, is that decision-making of any sort is complex; public information and personal information are used in different ways at different times by different individuals (Doligez et al. 2002; Valone and Giraldeau 1993; Parejo et al. 2007). Studies are needed to further disentangle how public and personal information are used to select food, habitat, and mates. The literature is particularly weak in investigations of how multiple of pieces of

information, either public or personal, are used to make single decision. Flexible decision-making comes from plasticity in traits like food preference, habitat preference, and mate preference when different decisions are made in different environmental conditions. Phenotypic plasticity maintains variation in traits, which, in turn, increases the opportunity for natural or sexual selection to act, and can impact the strength and direction of selection. Understanding the decision-making process is one step in fully understanding how selection affects wild populations.

## CHAPTER II: EXPERIMENT

This study seeks to compare the influence of different types of information on mate preferences for leg band colors in female zebra finches. As stated in the previous chapter, little is known about how public and personal information specifically interact to form a mate choice, or how multiple pieces of information about a potential mate's quality boil down into a single mate choice. Filling in this gap is critical to the complete understanding of decision-making processes and the associated evolutionary implications.

There is already evidence of plasticity in the mate preferences of female zebra finches (Clayton 1990; Ten Cate 1984; Swaddle et al. 2005; Burley and Foster 2006; Collins 1995; Ten Cate 2006; Doucet et al. 2004), and it is known that they use both public information from mate choice copying (Swaddle et al. 2005) and personal information (Burley and Foster 2006) for mate choice. It is not known how female zebra finches use multiple cues, like mate choice copying or personal condition, to make a mate choice, or how different types of cues rank in terms of importance. The overall goal of this study is to assess the influence of information from social and breeding experience on mate preferences of female zebra finches, and compare the relative influence of information from these two contexts. Female zebra finches, as well as females of other social species, will have social experience with males of varying quality in both captive and wild populations throughout their lifetimes as well as information about male quality collected through breeding experience. I seek to

investigate these concepts by first providing virgin female zebra finches with an opportunity to interact socially with male finches, and then allowing these females to breed with assigned mates. The females may receive public information from their social interaction with males if they eavesdrop on male behavior, they may receive personal information from their interactions with individual males, or they may receive a combination of both. This study does not seek to determine exactly what cue or cues, if any, the females use from social interaction. It only seeks to determine the effect of social interaction on mate choice and its importance for mate choice relative to cues obtained from breeding experience. Breeding experience will provide the females with personal information exclusively.

I hypothesize that both social interaction and breeding experience will influence the mate preferences of female zebra finches due to the precedence in the literature for social interactions as well as personal status to impact mate preferences (Swaddle et al. 2005; Burley and Foster 2006). I predict that social interaction with males wearing a certain leg band color will increase female preference for that color. In other words, interacting with males wearing a certain color will make that color attractive to the females. Half of the females will receive information from breeding experience that corroborates with the preferences generated by social experience. Specifically, females paired to males wearing the leg band color they preferred post-social experience who successfully fledge offspring will maintain their preference for their mate's leg band color. Females paired to males wearing the color they avoided post-social experience who are unsuccessful with their mates will continue to avoid their mate's leg band color. The other half of the females will receive information

about their assigned mate's quality that contradicts the information received through social experience, and I predict that these females will act in accordance with the more recent information from breeding experience. Females unsuccessful with attractive mates will lessen their preference for their mate's leg band color, and females successful with unattractive mates will increase their preference for their mate's color. These predictions are summarized in Table 2.

## METHODS

I used 38 adult wild-type virgin female zebra finches and 11 sexually-experienced adult females in social experience and mate preference trials (described below) in order to assess how visual and auditory exposure to males influenced adult female mate preferences. I also used 38 adult males as stimuli in social experience and mate preference trials. These birds were selected from our larger outbred colony, maintained at approximately 20 °C on a 14:10 light:dark photoperiod with ad libitum access to nutritionally-complete seed mix. Females did not have prior experience with the individual males that they viewed as stimuli. Additionally, virgin females in our colony were visually, but not acoustically, separated from all males.

### **Social experience trials**

I placed 4 to 8 virgin females in each of 8 metal wire cages (4 females in 6 smaller cages approximately 50 x 30 x 40 cm, 8 in a larger cage, and 6 in another larger cage, both approximately 90 x 30 x 50 cm) where each of the female cages was placed adjacent to a similar cage of an identical number of randomly chosen males. In other words, each cage of females was paired to a cage of stimulus males where the females could see only that cage of males and were visually isolated from all other birds. All of the males in a social experience cage wore either one green or one red small plastic leg band, resulting in 3 smaller and 1 larger cage of green-banded stimulus males and 3 smaller and 1 larger cage of red-banded stimulus males. Band color treatments were randomly assigned to stimulus cages. Females viewed their cage of males for two

weeks, and I expected females to develop a preference for the band color worn by the males they interacted with. This response would develop due to a process such as sexual conditioning in which individuals prefer mates like those of whom they have previous experience (Domjan 1992). There was no physical contact between males and females in this social experience phase.

Following the two-week social experience period, I assessed each female's relative preference for different males wearing green versus red leg bands in a two-chamber choice apparatus (described below). I repeated this process with 11 sexually experienced females in 3 of the smaller metal wire cages (5 females in one cage, 4 females in one cage and 2 females in one cage) observing 11 males in 3 separate cages (matched for number of birds), all wearing one small green leg band. The process was identical to the protocol used for the virgin females.

### **Post-social experience mate preference trials**

I assessed individual female mate preferences for leg band color immediately following the two-week social experience period for both virgin and sexually-experienced females. Each of the 49 (38 virgin and 11 sexually experienced) females completed one 3-hour mate preference trial. For each trial, I placed a female randomly selected from those ready for mate preference trials in the mate preference chamber (see Figure 3) in a room empty of other birds, and I randomly selected a red-banded male and a green-banded male from the pool of banded males used for social experience, excluding those previously encountered by each female. I decided which male would start the trial on which side (left or right) of the preference chamber by a

coin toss. Females in the mate preference chamber were visually isolated from the stimulus males until the start of the trial, at which point I removed cardboard barriers separating the female cage from the two male cages. I recorded all trials using a Sony Handycam HDR-SR1 to minimize the distraction to the birds, and then burned all recordings to DVDs for later analysis. The trials ran undisturbed except for a brief interruption midway through the trial (i.e., after 90 min), at which point I switched the male cages to correct for a possible female side bias in the chamber.

I calculated preference as the proportion of time a female showed active courtship behaviors (watching the visible male, hopping from perch to perch, vocalizing, etc.) in the areas of the preference chamber closest to each of the stimulus males (red or green banded) relative to the total time the female spent interacting with either male. I ignored any time the female spent sleeping, preening, or sitting with her back to the male as I wanted to generate a conservative estimate of band color preference. To reduce the influence my presence and handling had on female behavior, I did not analyze the first ten minutes or the ten minutes immediately following the midway period when I switched the stimulus cages around in each of the trials. Of the original 38 virgin females and 11 experienced females, 30 virgin trials and 5 experienced trials were used in post-social experience data analysis. In cases where birds were excluded, either the video of the trial was unusable, the female did not move in the preference chamber for the duration of the trial, or the female died or became injured or sick during social experience.



## **Breeding**

Following leg band color preference trials, 22 of the 38 virgin females were paired in a breeding cage with randomly determined unfamiliar males. Females not included in the breeding portion of this study had either died or were in poor condition at the end of post-social experience testing. Half of the females were paired with a male wearing the leg band color that they preferred in their post-social experience preference trial, and the other half were paired with males wearing the leg band color they did not prefer. Hence, females were paired with seemingly attractive or unattractive mates. Within each of these two mate attractiveness groups, I assigned half of the females to a successful nest treatment group, and half to an unsuccessful group. Females designated as successful nesters were allowed to breed undisturbed. Unsuccessful nesters experienced experimentally-induced nest failure, where I dipped all eggs produced by these females in vegetable oil for approximately 5 minutes on the day after the female finished laying. I then wiped the eggs off with paper towels and returned them to the nest box. Hence, these manipulations gave rise to a set of four factorial treatment groups: attractive/successful, attractive/unsuccessful, unattractive/successful, and unattractive/unsuccessful (Figure 4).

Each breeding pair was housed in either a metal ( $N = 24$ , dimensions approximately 50 x 30 x 40 cm) or a wooden cage ( $N = 4$ , dimensions approximately 60 x 30 x 40 cm) containing two wooden perches, a nest box, and ad libitum access to nutritionally-complete seed, drinking water, cuttlebone, and nesting material. I provided all breeding pairs with Timothy hay on a regular basis, and added cotton nesting material once the pair had begun building a nest with the hay. Breeding pairs

also began receiving a vitamin supplement (Vita-Sol UltraVite) in their food daily midway through the breeding portion of the study.

Pairs were given three months to initiate a first nest. Not all pairs were successful in producing eggs, and some of the pairs assigned to successful nest treatments groups were unable to produce viable eggs. Because the results of the breeding attempt in terms of fitness was the same for these pairs as for the pairs whose clutches were manipulated to be unsuccessful, naturally unsuccessful pairs were included in the unsuccessful treatment groups. The number of females in each treatment group used for analysis was as follows: 2 females in the attractive/successful group, 5 females in the attractive/unsuccessful group, 4 females in the unattractive/successful group, and 5 females in the unattractive/unsuccessful group.

### **Post-breeding mate preference testing**

After completion of the breeding trials, I assessed post-breeding mate preference employing the same procedures as in post-social experience preference trials on a per-female basis. The exact time at which I ran post-breeding mate preference testing varied depending on treatment group and the outcome of the breeding attempt. Sixteen of the 28 females that entered the breeding stage of the experiment were assessed for post-breeding leg band color preference. The sample size was reduced due to death or to females being in poor condition following breeding. I tested post-breeding color band preference to examine changes in band preference following experimentally-induced mate death or desertion. Specifically, I removed each female's mate for 48 to 72 hours prior to running a post-breeding preference trial. I tested successful females

after their fledglings became fully independent in the case of successful pairs, within the fourth week post-hatching, and manipulated unsuccessful females within the third week after completion of the failed clutch, when the eggs would have hatched if not manipulated. I tested naturally unsuccessful females after the pair had had three months to initiate a clutch and failed to do so.

### **Statistical analyses**

All post-social experience data were analyzed first using a paired samples Students' *t*-test comparing preference for the familiar color (the color worn by the males observed during social experience trials) to preference for the unfamiliar color. Virgin females were analyzed in a separate test from experienced females. Significance was based on the *t* statistic and taken at a level of  $p = 0.05$ . All preference scores were arcsine square-root transformed prior to running this and all other analyses. The post-social experience data were further analyzed using a repeated-measures ANOVA in which preference for the familiar color and unfamiliar color were taken as the repeated measures, and the leg band color observed during social experience and status of each female as virgin or experienced were between-subjects factors. Significance was based on the *F* statistic and taken at a level of  $p = 0.05$ . Breeding data were analyzed using a repeated-measures ANOVA. Preference for each female's mate's leg band color in post-social experience and post-breeding trials were the repeated measures. The attractiveness of each female's mate (attractive or unattractive) and the success of each female's breeding attempt (successful or unsuccessful) were between-subjects factors.

Significance was again based on the  $F$  statistic and taken at a level of  $p = 0.05$ . All analyses were run using SPSS v14 (Chicago, Illinois, U.S.A.).

## RESULTS

### Post-social experience preference trials

Virgin females showed a near-significant trend towards preference for the unfamiliar color (paired samples t-test,  $n = 30$ ,  $t = -1.831$ , d.f. = 29,  $p = 0.077$ ). I took significance at the  $p < 0.05$  level; any p-value below 0.05 indicates a result unlikely to be seen by chance alone. I consider a p-value of 0.077 to indicate a near-significant result, which suggests that social experience may have a significant effect. However, this result should be treated with some caution as the effect seen is slightly more likely to have been generated by chance than a result with a lower p-value. Experienced females showed a significant preference for the unfamiliar color (paired samples t-test,  $n = 5$ ,  $t = -4.189$ , d.f. = 4,  $p = 0.014$ ). For the range and skew of post-social experience preference for the unfamiliar color see Figure 5. Because a t-test does not look at mean preference specifically and it does not give information about the potential differential effects of interacting with males wearing green versus red leg bands, I also analyzed the post-social experience data using a repeated measures ANOVA. Mean preference for the familiar color was also significantly different from mean preference for the other color in both virgin and experienced females (repeated-measures ANOVA,  $n = 35$ ,  $F = 7.429$ , d.f. = 1,  $p = 0.010$ ). The within-female relative band color preference brought about by social experience was not affected by the color the females saw during social experience ( $F = 0.246$ , d.f. = 1,  $p = 0.624$ ), but the female's status as virgin or experienced did significantly influence preference ( $F = 5.797$ , d.f. =

1,  $p = 0.022$ ). Experienced females showed a larger preference for the unfamiliar overall than did virgin females, as shown in Figure 6.

### **Post-breeding preference trials**

Whether a female was paired to a male whose leg band color she finds attractive (based on a preference demonstrated during post-social experience preference trials) or unattractive (based on an avoidance) accounted for a significant amount of the variation in preference for the mate's leg band color from the repeated-measures ANOVA ( $n = 16$ ,  $F = 9.218$ , d.f. = 1,  $p = 0.010$ ). Females' preferences after breeding were largely dependent on their initial assessment of their mate's attractiveness, based on their social experience. There was also a significant interaction between this manipulation, referred to from here as attractiveness, and nest success ( $F = 4.842$ , d.f. = 1,  $p = 0.048$ ). While attractiveness has a larger effect on preference, breeding experience and resultant nest success does influence mate preferences within the context of attractiveness. In other words, the four treatment groups showed different responses. Nest success did not significantly impact change in female preference ( $F = 0.618$ , d.f. = 1,  $p = 0.447$ ). Females who mated unsuccessfully with attractive mates originally had preferences for their mate's leg band color of  $0.906 \pm 0.141$  (mean  $\pm$  SD) that reduced to  $0.490 \pm 0.189$  after breeding. An average preference near 0.5 indicates that the females prefer neither their mate's color nor the other color, and is essentially no different from random mate choice. Females in the attractive/successful treatment group still preferred their mate's color after breeding, with average preferences before breeding of  $0.640 \pm 0.008$  and preferences of  $0.684 \pm 0.055$  after.

Both unattractive groups still show strong avoidance of their mate's color after breeding (unattractive/successful:  $0.224 \pm 0.114$ , unattractive/unsuccessful:  $0.322 \pm 0.259$ ) which changed little from the preference scores seen before breeding (unattractive/successful:  $0.197 \pm 0.234$ , unattractive/unsuccessful:  $0.168 \pm 0.180$ ). While the unattractive/unsuccessful average preference for the mate's leg band color did nearly double after breeding, this is likely an artifact of small sample size.

## DISCUSSION

Whereas I originally hypothesized that social experience would create a preference for the leg band color worn by stimulus males, the opposite effect seems to take place. The social experience trials appear to provide females with negative information about the stimulus males they observed, which translates to a generalized negative association with the leg band color the stimulus males wore. Females appear to selectively avoid males that wore the same band colors as males in the social experience trials. One possibility for why this occurs is that females avoid unpaired males, or males with traits like those of unpaired males (all males in social experience trials were unpaired and in the presence of other males). This interpretation is consistent with our current understanding of mate choice copying in zebra finches. Mate choice copying studies indicate that female zebra finches show preference for male phenotypes that they have seen paired previously, but these studies can also be interpreted as females avoiding the phenotypes of unpaired males (Danchin et al. 2004; Brown and Fawcett 2005; Dugatkin 1992; Galef and White 1998; Hoglund et al. 1995; Swaddle et al. 2005; White and Galef 2000; Dugatkin and Godin 1993). It may be just as important for females to avoid unpaired males as it is to choose males shown to be attractive to other females. While there is certainly much more work needed on the subject of how social experience shapes mate preferences, this suggests that previous interpretations of mate choice copying may need to be revisited to incorporate the importance of avoiding unpaired males.



To help distinguish between the two possible interpretations of mate choice copying studies, future work could use a “no choice” preference assay where females can choose to associate with a seemingly preferred phenotype or avoid it. Then, in a subsequent trial, assess the females’ willingness to associate with a non-preferred phenotype or to avoid it. Comparing patterns of association with the two phenotypes will render relative preference and avoidance metrics without preference for one phenotype being confounded with avoidance of the other.

But why would females avoid unpaired males? One reason could be that they avoid aggressive males, as female in our social experience trials most likely observed aggressive behavior among males in the social experience cages. While in many species females seem to prefer the winners of aggressive encounters and, therefore, prefer more aggressive males, this strategy may not be profitable if a male who is more aggressive with other males is also more aggressive with his mate (Doutrelant and McGregor 2000; Mennill et al. 2002; Otter et al. 1999; Ophir and Galef 2003). While this is anecdotal evidence, one female had to be excluded from the breeding trials after suffering injuries resulting from an attack by her assigned mate. Other females showed some signs of aggression from their mates (i.e. feathers missing from the back of the neck), though none as severe as the excluded female (Zann 1996). Like the female Japanese quail mentioned in the first chapter (Ophir and Galef 2003, 2004), female zebra finches may avoid potentially aggressive mates as a way to avoid injuries that might limit future reproduction.

While it seems plausible that aggression may affect female mate preference during social experience, another, non-mutually exclusive, explanation for the

avoidance of the familiar color is that the females respond strongly to the introduction of a novel leg band color. The virgin females were naïve to leg bands of any color prior to social experience, so they may show preference for the unfamiliar color simply because they have not seen this leg band color before. Female zebra finches have been previously shown to prefer males with novel, artificial crests; this sets a precedent for an attraction to novelty (Burley and Symanski 1998). If this is the case, we would not expect the experienced females to show the same trend as the virgins because they had already interacted with males wearing both red or green leg bands. and it would be surprising to see such a strong preference for a familiar color among experienced females. Because the sample size of experienced females was very low, it is possible that this perceived effect is due only to random chance, and, if this is the case, a larger sample would show different results. Response to novelty is an avenue worth investigating further as previous research suggests that female zebra finches pay attention to and may show preference for novel male traits (Burley and Symanski 1998). The possibilities proposed here are not necessarily mutually exclusive. For example, virgin females may respond more strongly to novelty than do experienced females, and experienced females may place more importance on avoiding aggressive males. Furthermore, avoiding unpaired males might trump responding to novelty or avoiding aggression in some or all age classes of females.

Though it seems plausible that observing male aggression or responding to novelty may play a role in shaping female mate preferences, other cues from the stimulus males' behavior may form a negative association between the social cue and leg band color. It is also possible that the lack of females in the same space as the

stimulus males is a strong enough stimulus to shape female preferences without any other social cues. In the zebra finch, females tend to mate for life, so, at any point in time, there are more virgins than experienced females making mate choices (Zann 1996). For this species, understanding how virgin females choose mates will explain most of the mate choices made in a population. However, a species that frequently chooses new mates may have a different ratio of virgin to experienced females making mate choices at the start of each breeding season. If the majority of choosing females are experienced, it may make more sense to focus study on those females to understand how the majority choose their mates. The best age class for investigating optimal decision-making depends on the life history of the species, and it cannot be assumed that all age classes will behave the same way. This study suggests that experienced females form an even stronger avoidance of males wearing the familiar leg band color than do virgin females. Habitat selection studies suggest that individuals of different ages use information differently (Parejo et al. 2007), and, if cue use varies with age when making decisions in one context, it follows that cue use may vary with age in other contexts like mate choice.

If female preference is a composite of information collected through social experience and breeding experience, we would expect a significant interaction between perceived male attractiveness prior to breeding (influenced by information from social experience) and the success of a breeding attempt (information from personal experience). If information from social experience is weighted more heavily in mate choice, preference should change relatively little after breeding and attractiveness should account for a large portion of the variation in preference.

However, if information from breeding experience is weighted more heavily, preference should change greatly after breeding and nest success should account for a large portion of the variation. There was a significant effect of the interaction between attractiveness and nest success, which suggests that both sources of information are important in mate choice when both types of information are available. I originally expected to see no change in preference in the attractive/successful and unattractive/unsuccessful treatment groups, an increased preference for the mate's color in the attractive/successful group, and a decreased preference in the attractive/successful group. Instead, there was little change in either successful group, and, while the attractive/unsuccessful group did show a decrease in preference as predicted, the unattractive/unsuccessful group showed an unexpected small increase in preference for the mate's color. Because the attractive/unsuccessful group showed the largest change in preference for the mate's color (a decrease, see Table 2 for summary), it is possible that this may be driving the significance of the interaction between attractiveness and nest success. Future work should attempt to replicate these results to clarify whether or not there is a significant interaction and whether or not information from both social and breeding experience influence mate preferences.

The unexpected increase in preference for the former mate's leg band color seen in the unattractive/unsuccessful group is small enough that it may be the result of a small sample size, but it could also be explained by a complication in the experimental design. The only difference between the attractive/unsuccessful group and the unattractive/unsuccessful group should be mate attractiveness. However, there is another difference that may explain the behavior of the two groups. The

attractive/unsuccessful group contains some females whose clutches were manipulated to simulate a nest failure; the unattractive/unsuccessful group is made up entirely of females whose clutches failed naturally. Burley and Foster (2006) have previously suggested that a female's condition may influence her mate preferences, and females in poor condition are less choosy and will show preferences for males not preferred by females in good condition. It is possible that the females in the unattractive/unsuccessful group showed an small increase in preference for their mate's color because they are in poorer condition overall than the females in the attractive/unsuccessful group. Future work should clarify if this increase only exists when females in this treatment group are in poor condition. I suggest that females who are in good condition may attribute a nest failure to their mate's quality, and females in poor condition may perceive a nest failure as evidence of their own poor condition rather than that of their mate. Surprisingly there was essentially no change in preference for either successful group. An increase in fitness may not have as large of an effect on mate preferences as a decrease in fitness. A successful breeding attempt may validate a female's previous preferences regardless of whether she actually mated with the type of male she prefers or not.

There was a significant effect of attractiveness on the change in preference, which suggests that, while both social and breeding experience appear to influence mate choice, public information may be weighted more heavily and be more important when choosing a new mate. This may be because, in this case, females who were successful with their mates showed little change in their preferences from before breeding to after. Half of the study population appears to ignore information from

breeding experience. However, the attractive/unsuccessful and unattractive/unsuccessful groups did show change in preference after breeding, and do seem to be incorporating information from breeding experience into mate choice. The two groups applied breeding experience information differently based on whether the females were mated to attractive or unattractive males, which suggests that, while information from breeding experience was used, it was used in the context of mate attractiveness. Breeding information may be most useful to females choosing a new mate when they form an association between a loss in fitness and a particular male trait. The direction in which breeding information shifts a pre-existing mate preference will be dictated in part by whether the female perceives her mate to be attractive or unattractive, which appears to be influenced most strongly by social experience.

Because of this, the social environment may play the greatest role in determining the traits that make a male zebra finch attractive. This makes sense in the context of zebra finch life history, as most of the females choosing mates will be virgin females lacking personal breeding experience (Zann 1996). If this is the case, isolated subpopulations will show differences in female preference when the social environment between two subpopulations differ, and, in populations with dynamic social environments, female preferences will change continuously. In either case, variation in female preference and male traits is preserved in the population.

It is important to note that, in the middle of this study, the health of the aviary population declined and then, after making some husbandry changes, improved again. Unfortunately this health situation arose at a point in the study at which I was running breeding trials and post-breeding trials, and I was unable to simply stop progress on

the project until the situation was resolved. I did take precautions to lessen the effect of this problem on my data. I did not run trials with birds (focal females or stimulus males) obviously in poor health, and I excluded females from analysis who became ill soon after I completed a trial with that female. It was very obvious both physically and behaviorally when a bird was in poor health, so I believe that I excluded all affected birds, and my results as reported here reflect the behavior of healthy birds. This complication should have very little, if any, effect on this study.

Another potential confounding factor is the timing of post-breeding trials. While all post-social experience trials were conducted within a week of the end of the social experience period, there was considerable variation in exactly when post-breeding trials were completed relative to when each breeding trial was initiated. While some pairs quickly initiated clutches, others took months to even begin building a nest. Some pairs 'timed out' of the breeding trial, and post-breeding trials were run after months of inactivity. While it was important to ensure that all pairs had plenty of time to initiate a clutch, the resulting variation is quite large, and some females were exposed to their mate's leg band color for much longer than were others. Particularly because of the health issues that arose in the aviary during the breeding phase of my study, minimizing variation in exposure to the mate's leg band color would have resulted in dramatically reducing the number of successful nests and increasing the number of naturally failed nests. This variation may influence the results of the post-breeding preference trials, but, under these conditions, it would have been very difficult to control and adequately preserve sample size for each treatment group.

Future work should focus on replicating the results seen here and expanding upon this study to investigate the influence of social and breeding experience on mate choice in different contexts and in different species. To better understand the specific cues females pick up and incorporate into mate preferences during social experience, future studies should analyze male behavior and look for aggressive behaviors such as displacement from a prime perch position close to the female cage, aggressive, directed singing towards other males, or mounting of other males. This could be accomplished by recording male behavior at several points during the social experience period and then correlating the average number of aggressive behaviors observed in the duration of one recording within one male cage to the average preference of the females in the corresponding cage for the familiar color. Another option would be to manipulate male aggression and to standardize the levels of aggression that different groups of females observe during social experience. Future researchers could create continuous loops of video footage of male zebra finches engaging in low, medium, and high levels of aggressive behavior. Rather than having the females interact with a cage of actual males, females would be exposed to one of the video loops for the duration of the social experience period. Female zebra finches will respond to video of male finches, but pilot work would be necessary to make sure that they are responding in the same way to the video as they would to live males of the same aggression level (Swaddle et al. 2006). This would divide the female study population into discrete treatment groups rather than relying on correlation.

Regardless of experimental design, if females are avoiding unpaired males because they observe aggression during social experience, females that witness the



most aggressive interactions should avoid the familiar color most strongly or show the highest preference for the unfamiliar color in post-social experience preference testing. Females would ideally choose an attractive mate who will vigorously defend the nest, but, in practice, females may be faced with a trade-off between choosing less attractive, less aggressive males and choosing overly aggressive males who may cause them harm. Because a male with the optimal balance of attractiveness and aggression is not likely to be present in the pool of potential mates, females will have to choose mates on either side of the optimal, thus preserving variation in male aggression.

Future studies should also investigate the potential role of novelty in the response to social experience seen in this study. The simplest way to assess this could be to introduce a new leg band color into post-social experience preference testing using experienced females. In this study, experienced females were exposed to both red and green leg bands at some point. To expand upon this framework, each female would have a choice between three different males, one wearing the familiar leg band color, one wearing the other color of leg band that the female has previously seen, and one male wearing a new leg band color not yet introduced. If the virgin females in this study showed a preference for the unfamiliar color out of a positive response to novelty, we would expect to see the females in this three-way mate preference test showing a preference for the novel color, and avoiding both previously-seen colors regardless of which one was seen during the social experience trials. This does not rule out a negative association with the familiar color, but it does suggest a strong influence of novelty upon mate preferences. If novelty is not a driving force in mate preference formation, we would expect to still see an avoidance of the familiar color,

but we would not expect to see a strong overall preference for the novel color. Instead, we would expect to see females spending most of their time in the mate preference chamber interacting with either the male wearing the familiar color not seen during the most recent social experience trial or the novel color. The resulting preference scores may indicate a preference for the familiar color not seen during the most recent social experience or a lack of clear preference for either color not seen during social experience.

It is also important to better understand the role that age class plays in how information from social experience is utilized. In this study, it appears that experienced females avoided the familiar color from the most recent social experience trial more strongly than virgin females. First it is necessary to determine whether or not this result will stand up to a larger sample size. If the trend seen here remains the same, future work should next seek to determine if females with multiple breeding experiences continue to be responsive to social experience and continue to avoid the familiar color. Future studies could follow essentially the same framework as this one of running a pre-breeding mate preference trial, pairing females with males based upon the results of their trial and allowing them to breed, and then reassessing mate preference in a mate preference trial. The only change necessary would be to switch out the virgin females used in this study for females of a different age class or experience level. Answering these questions will increase the understanding of how mate preferences change across lifespan and will help to explain variation in mate preference. This will also increase the understanding of how sexual selection works in

natural populations and will give information about the applicability of the findings of mate choice studies using virgin versus experienced females.

Future work should also revisit the breeding portion of this study with a larger sample size and balanced treatment groups. Currently it appears that successful breeding experience does not alter pre-existing mate preferences, but a larger sample size might be able to pick up any small changes in preference after breeding. It is possible that with more birds we would have seen a small change in preference in either of the successful groups. Even a small change in preference would suggest that both social and breeding experience are important to successful breeders making new mate choices, as opposed to the current interpretation that successful breeders ignore personal information. Once we are able to clarify the way that virgin females use information from personal experience, similar studies should apply these questions to experienced females for comparison to virgin females. While it appears that both virgin and experienced females place importance on social experience and apply associated information to mate choice, there may be a point at which a female has collected enough information from breeding experience that this swamps the decision-making process and social experience matters less.

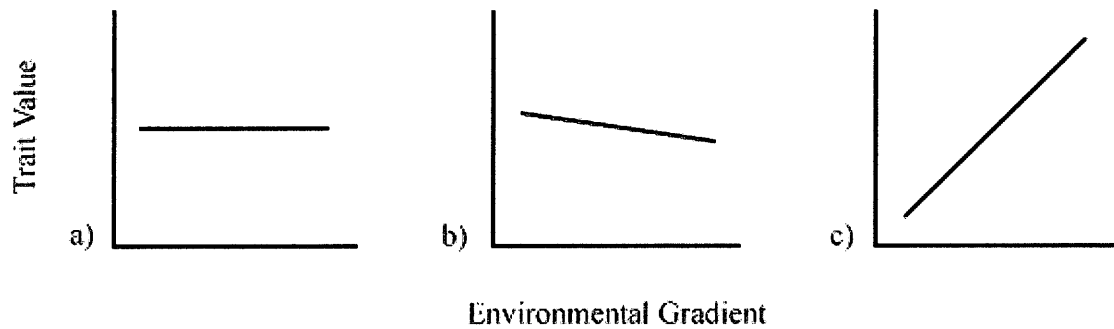
There are many other species with rich social environments that also need to balance multiple sources of public information and personal information to make mate choices. It is important to understand whether the trends seen here are applicable to other social species, or if there is much variation in information use from species to species. It may be particularly interesting to compare species, such as the zebra finch, that typically do not make a new mate choice before each breeding attempt (Zann

1996), to species who do frequently choose new mates. These questions can also be applied to extra-pair copulations to compare information use in two different contexts. There is some evidence that females may not be looking for the same qualities in a social mate as they look for in an extra-pair mate (Dubois 2007), so they may be using public and personal information differently depending on the type of mate choice being made. This also suggests that the process of selecting an extra-pair mate may be fundamentally different from the process of choosing a social mate and should be treating as separate processes.

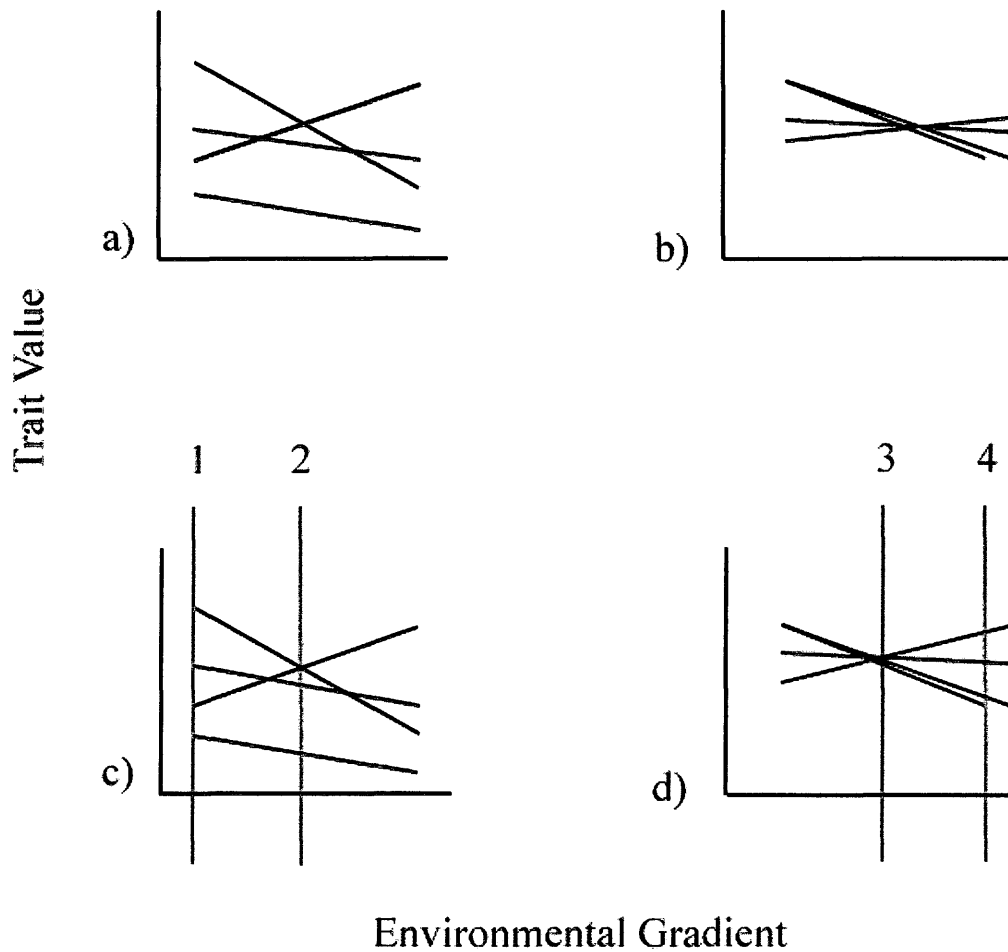
This study suggests that female zebra finches information from social experience alone to make mate choices when they have previously bred successfully, and use information from both social and breeding experience when they have bred unsuccessfully. The type of information used depends on the individual's past experiences, making decision-making a complex process unique to each individual and mate preferences very plastic. All females appear to avoid males like those they have previously seen unpaired, and, while future work should focus on finding the exact cues that make up this negative association, this suggests that morphological trait values such as leg band color or beak color may not be as meaningful to female zebra finches on their own as they are within a social context. In other words, a trait that has previously been demonstrated to be attractive may become unattractive if females observe unpaired males with this trait. Social interactions will have particularly large impacts on the overall shape of female mate preferences in zebra finch populations because most of the females making a mate choice are virgin females lacking any personal information (Zann 1996). Because of this strong social

component in the formation of mate preferences, what makes a male attractive may vary with the social environment, and this will maintain variation in both female mate preferences and male traits within and between populations. Plasticity in mate preferences, as influenced by social experience, will increase the opportunity for sexual selection to act in zebra finch populations, and, depending on the direction of these mate preferences, will dictate the direction and strength of sexual selection.

## APPENDIX: FIGURES



**Figure 1.** Schematic of possible reaction norms. All figures have the same independent variable of an environmental gradient, and all have the same dependent variable of trait value. In figure a, a reaction norm indicates that the trait value remains the same regardless of environment. In figure b, there is some variation in trait value across the gradient and a reaction norm does occur. In figure c, there is considerable variation in trait value. The extent of variation can be judged by looking at the slope of the line produced and compared for different traits or for different environmental gradients. While all of the examples here are straight lines, a reaction norm may also produce a curved line.

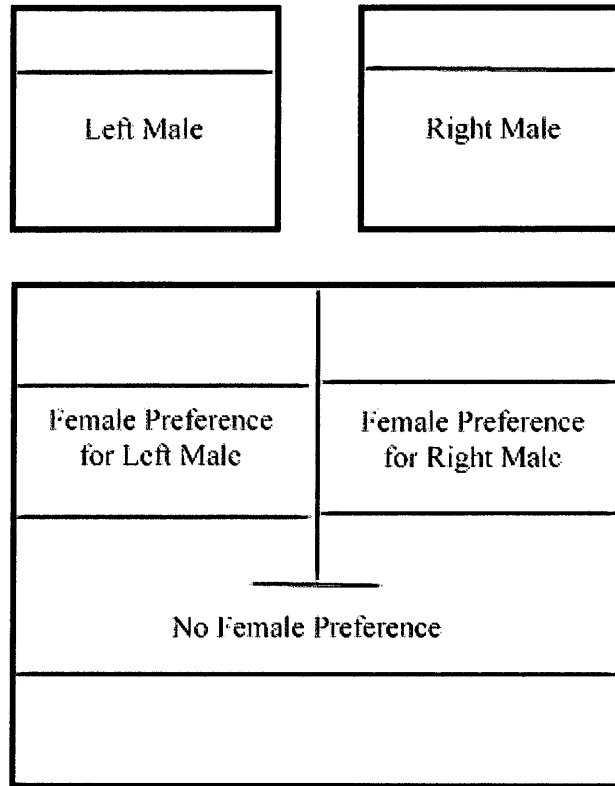


**Figure 2.** Schematic of possible reaction norm bundles. Like Figure 1, all figures have the same independent variable of an environmental gradient, and all have the same dependent variable of trait value. Figure a shows four reaction norms corresponding to four genotypes bundled more loosely than the four reaction norms shown in Figure b. This indicates greater variation in trait value across the environmental gradient as well as greater variation in plasticity itself. The numbered vertical lines in Figures c and d indicate specific environments along the overall environmental gradient. There is greater variation in trait value in Environment 1 than in 2, and greater variation in Environment 4 than in 3. Because all four reaction norms converge at the same point in Environment 3, there is no variation in trait value in this environment despite variation at the genotypic level.

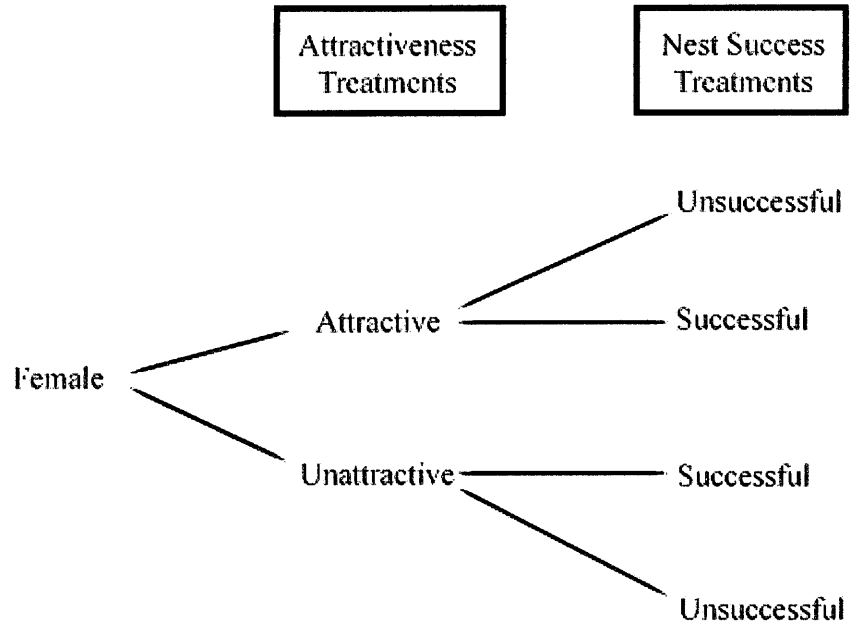
| <b>Treatment Group</b>    | <b>Predicted Effect on Preference for Mate's Color</b> |
|---------------------------|--|
| Attractive/Successful     | Preference increases or stays the same                 |
| Attractive/Unsuccessful   | Preference decreases                                   |
| Unattractive/Successful   | Preference increases                                   |
| Unattractive/Unsuccessful | Preference decreases or stays the same                 |

**Table 1.** Predictions for each of the four treatment groups. Females in the "Attractive" groups were paired to males wearing the leg band color that they previously demonstrated a preference for during post-social experience trials. Females in the "Unattractive" groups were paired to males wearing the leg band color that they previously avoided. The "Successful" and "Unsuccessful" groups refer to the nest success of the assigned pairs; successful pairs produced fledglings, whereas unsuccessful pairs did not. Because females in the Attractive/Successful and Unattractive/Unsuccessful groups receive corroborating information about their mate's quality from their breeding trials, I expect the new information to reinforce existing preferences. The females in the Attractive/Unsuccessful and Unattractive/Successful groups receive contradictory information about their mates from breeding trials, and I expect females in these groups to show preferences in line with the more recent information from breeding experience.

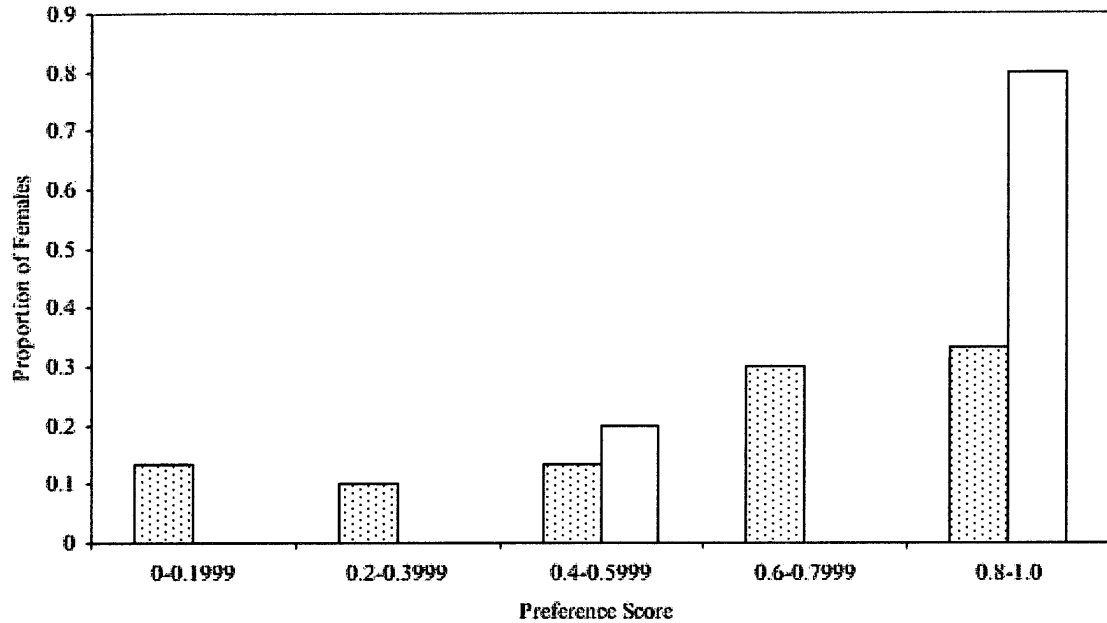




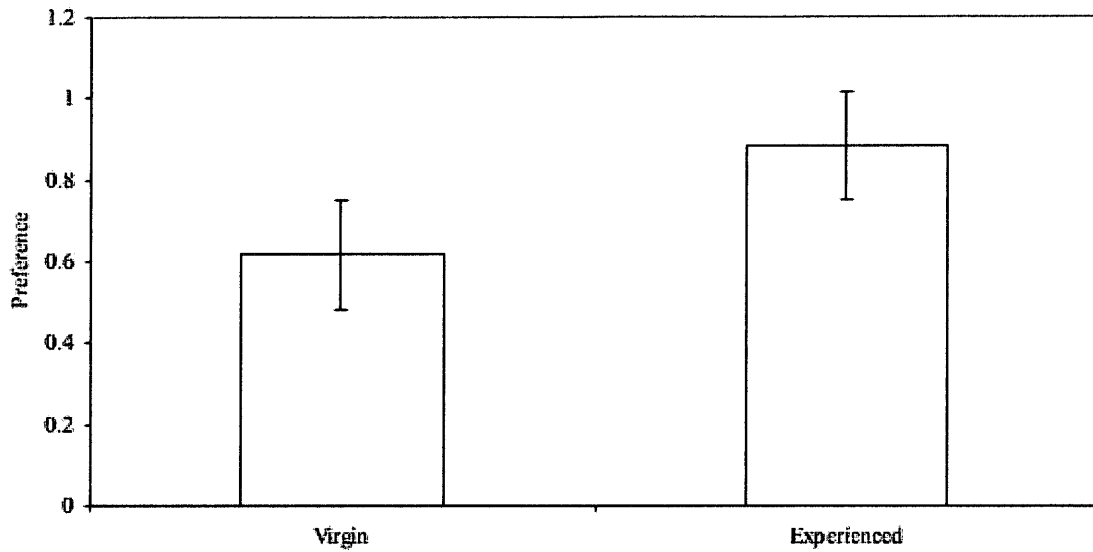
**Figure 3.** Plan view of mate preference chamber. Each box represents a cage. Each horizontal line represents a perch. Male cages measure approximately 30 x 20 x 40 cm, and the large, subdivided female cages measures approximately 80 x 80 x 40 cm.



**Figure 4.** Schematic for the mate attractiveness treatments and nest success treatments randomly assigned to each female.



**Figure 5.** Proportion of females with preference scores for the male wearing the unfamiliar leg band color during post-social experience preference testing in five 20-point categories. Preference was measured as the proportion of time that the female spent interacting with the stimulus male wearing the color of interest out of the total time that the female spent interacting with either stimulus male during a preference trial. A preference score of 0 means that the female spent no time with the male wearing the unfamiliar color during post-social experience preference testing, and indicates a complete avoidance of the unfamiliar color. A preference score of 1 means that she spent all of her interaction time with the male wearing the unfamiliar color, and indicates a complete preference for this color. A score of 0.5 means that she split her time evenly between the two males and indicates no preference. Dotted bars indicate virgin females ( $n = 30$ ), and open bars indicate experienced females ( $n = 5$ ).



**Figure 6.** Mean preference for the unfamiliar leg band color of virgin versus experienced females. There were 30 virgin females in this sample and 5 experienced females. Preference was measured as the proportion of time that the female spent interacting with the stimulus male wearing the color of interest out of the total time that the female spent interacting with either stimulus male during a preference trial. A preference score of 1 indicates that a female spent all of her interaction time with the male wearing the unfamiliar color and is a complete preference for the unfamiliar color. A score of 0.5 represents an even split of time between the two stimulus males and indicates no preference. Error bars represent standard error.

| <b>Treatment Group</b>    | <b>Prediction</b>     | <b>Result</b>  |
|---------------------------|-----------------------|----------------|
| Attractive/Successful     | Increase or no change | No change      |
| Attractive/Unsuccessful   | Decrease              | Decrease       |
| Unattractive/Successful   | Increase              | No change      |
| Unattractive/Unsuccessful | Decrease or no change | Small increase |

**Table 2.** Prediction and result for each of four treatment groups. The predictions from Table 1 are paired with the result from data analysis using a repeated-measures ANOVA. The results for the Attractive groups match the initial predictions whereas the results for the Unattractive groups do not. The small increase seen in the Unattractive/Unsuccessful is likely to be the result of either having a small sample size, working with birds of varying condition, or both. Similarly, a small increase in the preference of females in the Unattractive/Successful group may have been observable with a larger sample size. While the results are not in complete agreement with the original predictions, they are not so far off to necessitate fully dismissing the predictions.

## REFERENCES

- Dudley, S. & Schmitt, J.** 1996. Testing the adaptive plasticity hypothesis: density-dependent selection on manipulated stem length in *Impatiens capensis*. *American Naturalist*, 147, 445-465.
- Scheiner, S.** 1993. Genetics and evolution of phenotypic plasticity. *Annual Review of Ecology and Systematics*, 24, 35-68.
- Thompson, J.** 1991. Phenotypic plasticity as a component of evolutionary change. *Trends in Ecology & Evolution*, 6, 246-249.
- Via, S.** 1993. Adaptive phenotypic plasticity - target or by-product of selection in a variable environment. *American Naturalist*, 142, 352-365.
- Via, S., Gomulkiewicz, R., Dejong, G., Scheiner, S., Schlichting, C. & Vantienderen, P.** 1995. Adaptive phenotypic plasticity - consensus and controversy. *Trends in Ecology & Evolution*, 10, 212-217.
- Gavrilets, S. & Scheiner, S.** 1993. The genetics of phenotypic plasticity .5. evolution of reaction norm shape. *Journal of Evolutionary Biology*, 6, 31-48.
- Dodson, S.** 1989. Predator-induced reaction norms - cyclic changes in shape and size can be protective. *Bioscience*, 39, 447.
- Clayton, N.** 1990. Assortative mating in zebra finch subspecies, *Taeniopygia guttata guttata* and *T. g. castanotis*. *Proceedings of the Royal Society B-Biological Sciences*, 330, 351-370.
- Engeszer, R. E., Laura Alberici Da Barbiano, Michael J. Ryan, and David M. Parichy.** 2007. Timing and plasticity of shoaling behavior in the zebrafish, *Danio rerio*. *Animal Behaviour*, 74, 1269-1275.
- Engeszer, R. E., Ryan, M. J. & Parichy, D. M.** 2004. Learned social preference in zebrafish. *Current Biology*, 14, 881-884.
- Freeberg, T. M.** 2000. Culture and courtship in vertebrates: a review of social learning and transmission of courtship systems and mating patterns. *Behavioural Processes*, 51, 177-192.
- Ten Cate, C.** 1984. The influence of social relations on the development of species recognition in zebra finch males. *Behaviour*, 91, 263-285.
- Lesna, I. & Sabelis, M. W.** 1999. Diet-dependent female choice for males with 'good genes' in a soil predatory mite. *Nature*, 401, 581-584.
- Qvarnstrom, A., Part, T. & Sheldon, B. C.** 2000. Adaptive plasticity in mate preference linked to differences in reproductive effort. *Nature*, 405, 344-347.
- Valone, T. J.** 2007. From eavesdropping on performance to copying the behavior of others: a review of public information use. *Behavioral Ecology and Sociobiology*, 62, 1-14.
- Danchin, E., Giraldeau, L. A., Valone, T. J. & Wagner, R. H.** 2004. Public information: From nosy neighbors to cultural evolution. *Science*, 305, 487-491.
- Doligez, B., Cadet, C., Danchin, E. & Boulinier, T.** 2003. When to use public information for breeding habitat selection? The role of environmental predictability and density dependence. *Animal Behaviour*, 66, 973-988.

- Swaney, W., Kendal, J., Capon, H., Brown, C. & Laland, K. N.** 2001. Familiarity facilitates social learning of foraging behaviour in the guppy. *Animal Behaviour*, 62, 591-598.
- Galef, B. G. & Giraldeau, L. A.** 2001. Social influences on foraging in vertebrates: causal mechanisms and adaptive functions. *Animal Behaviour*, 61, 3-15.
- Heyes, C.** 1994. Social learning in animals: categories and mechanisms. *Biological reviews of the Cambridge Philosophical Society*, 69, 207-231.
- Clark, C. W. & Mangel, M.** 1986. The evolutionary advantages of group feeding. *Theoretical Population Biology*, 30, 45-75.
- Templeton, J. J. & Giraldeau, L. A.** 1996. Vicarious sampling: the use of personal and public information by starlings foraging in a simple patchy environment. *Behavioral Ecology and Sociobiology*, 38, 105-114.
- Valone, T. J.** 1989. Group foraging, public information, and patch estimation. *Oikos*, 56, 893-903.
- Nordell, S. E. & Valone, T. J.** 1998. Mate choice copying as public information. *Ecology Letters*, 1, 74-76.
- Page, R. A. & Ryan, M. J.** 2006. Social transmission of novel foraging behavior in bats: Frog calls and their referents. *Current Biology*, 16, 1201-1205.
- Ratcliffe, J. M. & ter Hofstede, H. M.** 2005. Roosts as information centres: social learning of food preferences in bats. *Biology Letters*, 1, 72-74.
- Mazur, R. & Seher, V.** 2008. Socially learned foraging behaviour in wild black bears, *Ursus americanus*. *Animal Behaviour*, 75, 1503-1508.
- Coolen, I., van Bergen, Y., Day, R. L. & Laland, K. N.** 2003. Species difference in adaptive use of public information in sticklebacks. *Proceedings of the Royal Society of London Series B-Biological Sciences*, 270, 2413-2419.
- van Bergen, Y., Coolen, I. & Laland, K. N.** 2004. Nine-spined sticklebacks exploit the most reliable source when public and private information conflict. *Proceedings of the Royal Society of London Series B-Biological Sciences*, 271, 957-962.
- Cadiou, B., Monnat, J. Y. & Danchin, E.** 1994. Prospecting in the kittiwake, *Rissa tridactyla*: different behavioural patterns and the role of squatting in recruitment. *Animal Behaviour*, 47, 847-856.
- Doligez, B., Danchin, E. & Clobert, J.** 2002. Public information and breeding habitat selection in a wild bird population. *Science*, 297, 1168-1170.
- Doligez, B., Part, T., Danchin, E., Clobert, J. & Gustafsson, L.** 2004. Availability and use of public information and conspecific density for settlement decisions in the collared flycatcher. *Journal of Animal Ecology*, 73, 75-87.
- Part, T. & Doligez, B.** 2003. Gathering public information for habitat selection: prospecting birds cue on parental activity. *Proceedings of the Royal Society of London Series B-Biological Sciences*, 270, 1809-1813.
- Valone, T. J. & Templeton, J. J.** 2002. Public information for the assessment of quality: a widespread social phenomenon. *Proceedings of the Royal Society B-Biological Sciences*, 357, 1549-1557.
- Doutrelant, C. & McGregor, P. K.** 2000. Eavesdropping and mate choice in female fighting fish. *Behaviour*, 137, 1655-1669.

- Mennill, D. J., Ratcliffe, L. M. & Boag, P. T.** 2002. Female eavesdropping on male song contests in songbirds. *Science*, 296, 873.
- Otter, K., McGregor, P. K., Terry, A. M. R., Burford, F. R. L., Peake, T. M. & Dabelsteen, T.** 1999. Do female great tits (*Parus major*) assess males by eavesdropping? Field study using interactive song playback. *Proceedings of the Royal Society B-Biological Sciences*, 266, 1305-1309.
- Ophir, A. G. & Galef, B. G.** 2003. Female Japanese quail that eavesdrop on fighting males prefer losers to winners. *Animal Behaviour*, 66, 399-407.
- Brown, G. R. & Fawcett, T. W.** 2005. Sexual selection: Copycat mating in birds. *Current Biology*, 15, R626-R628.
- Dugatkin, L. A.** 1992. Sexual Selection and Imitation - Females Copy the Mate Choice of Others. *American Naturalist*, 139, 1384-1389.
- Galef, B. G. & White, D. J.** 1998. Mate-choice copying in Japanese quail, *Coturnix coturnix japonica*. *Animal Behaviour*, 55, 545-552.
- Hoglund, J., Alatalo, R. V., Gibson, R. M. & Lundberg, A.** 1995. Mate-Choice Copying in Black Grouse. *Animal Behaviour*, 49, 1627-1633.
- Swaddle, J. P., Cathey, M. G., Correll, M. & Hodkinson, B. P.** 2005. Socially transmitted mate preferences in a monogamous bird: a non-genetic mechanism of sexual selection. *Proceedings of the Royal Society B-Biological Sciences*, 272, 1053-1058.
- White, D. J. & Galef, B. G.** 2000. 'Culture' in quail: social influences on mate choices of female *Coturnix japonica*. *Animal Behaviour*, 59, 975-979.
- Witte, K. & Nolte, B.** 2002. The role of information in mate-choice copying in female sailfin mollies (*Poecilia latipinna*). *Behavioral Ecology and Sociobiology*, 52, 194-202.
- Zann, R. A.** 1996. *The zebra finch: a synthesis of field and laboratory studies*. Oxford: Oxford University Press.
- Agrawal, A. F.** 2001. The evolutionary consequences of mate copying on male traits. *Behavioral Ecology and Sociobiology*, 51, 33-40.
- Wade, M. J. & Pruett-Jones, S. G.** 1990. Female copying increases the variance in male mating success. *Proceedings of the National Academy of Sciences USA*, 87, 5749-5753.
- Brooks, R.** 1998. The importance of mate copying and cultural inheritance of mating preferences. *Trends in Ecology & Evolution*, 13, 45-46.
- Ratcliffe, J. M. & Fenton, M. B.** 2006. Animal behavior: Who will croak next? *Current Biology*, 16, R455-R456.
- Ratcliffe, J. M., Fenton, M. B. & Galef, B. G.** 2003. An exception to the rule: common vampire bats do not learn taste aversions. *Animal Behaviour*, 65, 385-389.
- Dukas, R.** 2005. Learning affects mate choice in female fruit flies. *Behavioral Ecology*, 16, 800-804.
- Qvarnstrom, A., Blomgren, V., Wiley, C. & Svedin, N.** 2004. Female collared flycatchers learn to prefer males with an artificial novel ornament. *Behavioral Ecology*, 15, 543-548.
- Domjan, M.** 1992. Adult Learning and Mate Choice - Possibilities and Experimental-Evidence. *American Zoologist*, 32, 48-61.



- Ophir, A. G. & Galef, B. G.** 2004. Sexual experience can affect use of public information in mate choice. *Animal Behaviour*, 68, 1221-1227.
- Burley, N. T. & Foster, V. S.** 2006. Variation in female choice of mates: condition influences selectivity. *Animal Behaviour*, 72, 713-719.
- Dugatkin, L. A. & Godin, J. G. J.** 1993. Female mate copying in the guppy (*Poecilia-reticulata*) - age-dependent effects. *Behavioral Ecology*, 4, 289-292.
- King, A. J. & Cowlshaw, G.** 2007. When to use social information: the advantage of large group size in individual decision making. *Biology Letters*, 3, 137-139.
- Day, R. L., Coolen, I. & Laland, K. N.** 2004. The role of conformity in guppy foraging when personal and social information conflict. *Behavioral Ecology*, 15, in press.
- Switzer, P. V.** 1997. Past reproductive success affects future habitat selection. *Behavioral Ecology and Sociobiology*, 40, 307-312.
- Danchin, E., Boulinier, T. & Massot, M.** 1998. Conspecific reproductive success and breeding habitat selection: implications for the study of coloniality. *Ecology*, 79, 2415-2428.
- Valone, T. J. & Giraldeau, L. A.** 1993. Patch estimation by group foragers - what information is used. *Animal Behaviour*, 45, 721-728.
- Parejo, D., White, J. & Danchin, E.** 2007. Settlement decisions in blue tits: difference in the use of social information according to age and individual success. *Naturwissenschaften*, 94, 749-757.
- Doligez, B., Danchin, E., Clobert, J. & Gustafsson, L.** 1999. The use of conspecific reproductive success for breeding habitat selection in a non-colonial, hole-nesting species, the collared flycatcher. *Journal of Animal Ecology*, 68, 1193-1206.
- Parejo, D., Danchin, E. & Aviles, J. M.** 2005. The heterospecific habitat copying hypothesis: can competitors indicate habitat quality? *Behavioral Ecology*, 16, 96-105.
- Muller, K. L., Stamps, J. A., Krishnan, V. V. & Willits, N. H.** 1997. The effects of conspecific attraction and habitat quality on habitat selection in territorial birds (*Troglodytes aedon*). *American Naturalist*, 150, 650-661.
- Reed, J. M. & Oring, L. W.** 1992. Reconnaissance for future breeding sites by spotted sandpipers. *Behavioral Ecology*, 3, 310-317.
- Dubois, F.** 2007. Mate choice copying in monogamous species: should females use public information to choose extrapair mates? *Animal Behaviour*, 74, 1785-1793.
- Slagsvold, T., Johnsen, A., Lampe, H. M. & Lifjeld, J. T.** 2001. Do female pied flycatchers seek extrapair copulations with familiar males? A test of the incomplete knowledge hypothesis. *Behavioral Ecology*, 12, 412-418.
- Collins, S. A.** 1995. The Effect of Recent Experience on Female Choice in Zebra Finches. *Animal Behaviour*, 49, 479-486.
- Ten Cate, C., Machteld N. Verzijden, and Eric Etman.** 2006. Sexual imprinting can induce sexual preferences for exaggerated parental traits. *Current Biology*, 16, 1128-1132.
- Doucet, S. M., Yezerinac, S. M. & Montgomerie, R.** 2004. Do female zebra finches (*Taeniopygia guttata*) copy each other's mate preferences? *Canadian Journal of Zoology-Revue Canadienne De Zoologie*, 82, 1-7.

- Burley, N. T. & Symanski, R.** 1998. "A taste for the beautiful": Latent aesthetic mate preferences for white crests in two species of Australian grassfinches. *American Naturalist*, 152, 792-802.
- Swaddle, J. P., McBride, L. & Malhotra, S.** 2006. Female zebra finches prefer unfamiliar males but not when watching noninteractive video. *Animal Behaviour*, 72, 161-167.