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ENERGETICALLY COSTLY MATE SAMPLING AND FEMALE ZEBRA FINCH CHOICE

A Thesis

Presented to

The Faculty of the Department of Biology

The College of William and Mary in Virginia

In Partial Fulfillment

Of the Requirements for the Degree of

Master of Arts

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by

Timothy Ryan Crabtree

2004

APPROVAL SHEET

This thesis is submitted in partial fulfillment of

the requirements for the degree of

Master of Arts

Timothy Ryan Crabtree

Timothy Ryan Crabtree

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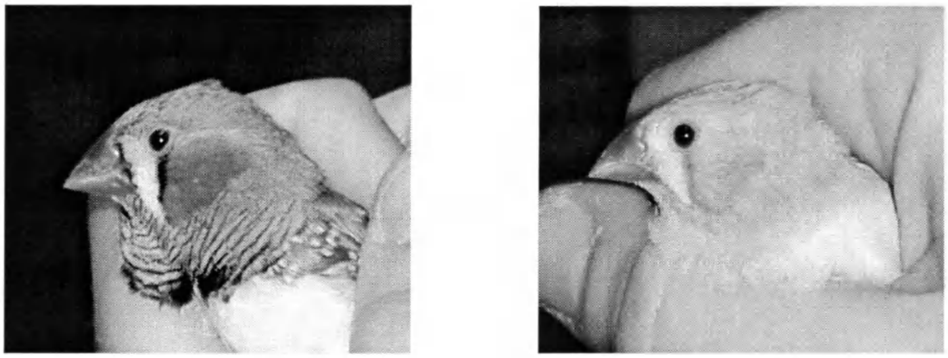
ABSTRACT

This thesis research involves female mate choice of zebra finches (*Taeniopygia guttata*) under simulated energetic costs of mate choice. Mate choice costs have been predicted to affect how sexual selection operates and how ornamental traits and sexual preferences evolve (Andersson & Iwasa 1996; Kokko *et al.* 2002). One of the goals of this thesis is to better understand how costs of mate choice can affect mate preferences and the evolution of sexually selected traits.

Male zebra finches have evolved several sexual ornaments (figure 1) that may signal individual quality to females. There have been a multitude of studies on the mating preferences of these birds (Burley & Coopersmith 1987; Swaddle & Cuthill 1994a; Collins & Ten Cate 1996; Blount *et al.* 2003; McGraw *et al.* 2003), but not much effort has been devoted to studying the dynamic of multiple female preferences and ornaments. A second goal of this thesis is to better understand the signaling content of the males' ornamentation and thereby determine which of features are attractive to the females. This goal will be met through an extensive literature review and analysis of extended mate choice experiments.

FIGURE 1



Male zebra finch

Female zebra finch

In the first chapter of this thesis I review the mechanisms of sexual selection and a number of mate choice studies relevant to my study system. I will also discuss theories about the evolution of multiple sexual ornaments and preferences. In the second chapter of this thesis I review previous studies about mate choice costs and their implications for evolution by sexual selection. I also frame the costs of mate choice within my thesis research and discuss their potential effects (proximate and ultimate) on zebra finch mating systems.

ENERGETICALLY COSTLY MATE SAMPLING AND FEMALE ZEBRA FINCH CHOICE

CHAPTER 1

SEXUAL SELECTION

1.1 – What is sexual selection?

While forming his theory of evolution by natural selection, Darwin observed that males of many species possessed conspicuous traits that seemed disadvantageous to survival (Darwin 1859; Darwin 1871). To address this peculiar observation Darwin formulated the theory of sexual selection – selection that occurs due to competition over mates or matings (Andersson 1994). He reasoned that if viable mates are limited, individuals will compete to gain access to this limited resource (Darwin 1859; Darwin 1871). Sexual selection is generally regarded to have two primary mechanisms – intrasexual contests and intersexual mate choice. Traits associated with contests and mate choice, though sometimes detrimental to survival, may be favored when they increase lifetime reproductive success by improving the ability of an individual to attract and fertilize mates (Andersson & Iwasa 1996; Stearns & Hoekstra 2000). There are several mechanisms by which these traits evolve with regard to intrasexual competition and intersexual mate choice.

Competition for mates, often through violent contests, is the most straight-forward mechanism of sexual selection (Andersson & Iwasa 1996). In most species, males have greater reproductive potential and therefore, are the sex that usually competes. Females commonly have the most invested in a sexual relationship and are usually the choosers (Andersson 1994; Andersson & Iwasa 1996). Large individuals or those possessing weaponry are more successful in competitions for mates. These individuals, therefore, produce more offspring that inherit their favorable size or weaponry. After several generations of this type of sexual selection, the frequency of weaponry and large individuals increases in the population. Once these traits are common, only the largest individuals or those with the greatest weaponry succeed in intrasexual competitions and reproduce. Individuals with relatively small weaponry and size are incapable of winning contests and/or attracting mates, and are selected out of the population. This sequence demonstrates how certain traits increase their frequency in a population and also how they become exaggerated over time.

Not all competition involves violent contests before copulation; competition may also occur after insemination. Sperm competition may occur when females commonly mate with several males in the same breeding attempt. This form of competition occurs when sperm from two (or more) individuals compete to fertilize eggs within the same female (Birkhead & Hunter 1990). Sperm competition often includes: (i) the production of large ejaculates that can out-compete the smaller quantity of sperm of rival males within the female (Shapiro *et al.* 1994); (ii) sperm morphologies that increase the chances of egg fertilization (Birkhead & Hunter 1990; LaMunyon & Ward 2002); and (iii) the production of copulatory plugs to prevent sperm leakage and copulation by other males (Birkhead & Hunter 1990). Numerous behaviors by males may also evolve to ensure successful fertilization: (i) mate guarding, which prevents competitors from inseminating the same female; (ii) endurance rivalry which allows reproductive activity to persist during large parts of the season; (iii) scrambling activity aimed at locating mates swiftly before competitors have opportunities for copulation; (iv) avoidance of superior competitors in order to increase chances of mating; and (v) rape, i.e. forced sexual intercourse (Andersson 1994; Andersson & Iwasa 1996).

The other major mechanism of sexual selection is mate choice – the process by which either sex selects to mate with particular individuals from a larger sample. Mate choice often involves signal communication between the two sexes. The information included in these signals conveys aspects about the signaler that may be important to the receiver when selecting an acceptable mate. This information may relate to genetic quality, physical prowess, territory possession, foraging efficiency, parental ability, etc. (Andersson & Iwasa 1996). Sexual selection on organisms to signal individual quality to potential mates has caused, in some instances, an exaggeration of behaviors and/or physical ornamentation (Andersson 1994; Andersson & Iwasa 1996; Stearns & Hoekstra 2000). As mentioned previously, females are typically the choosy sex since they have lower reproductive potential and typically invest more in raising offspring than the males of most species. Males are commonly the sex that evolves characteristics to signal individual quality.

There is general consensus that there are three, non-mutually exclusive mechanisms by which female preferences (through intrasexual competition and mate choice) may arise in populations: (i) indirect benefits - the ‘good genes’ and ‘handicap principle’; (ii) direct benefits – ‘good parent’; and (iii) sensory bias. Each mechanism is capable of explaining how mate choice can honestly select for high quality mates and, hence, increase overall reproductive success. Once mate preferences are established in a population, sexual selection can cause the exaggeration of female preferences and elaboration of male ornamentation through ‘Fisherian runaway’. The following sections consist of a discussion of these mechanisms before beginning a brief literature review of sexual selection studies focused on my study system, zebra finches.

1.1.1 – Indirect benefits

Indirect benefits come in the form of genes that increase offspring fitness (Stearns & Hoekstra 2000). The ‘good genes’ theory and ‘handicap principle’ explain how female preferences for indirect benefits (genetic quality) can evolve. The premise of the ‘good genes’ theory is that organisms should prefer mates that signal the possession of genes for superior survival ability (Iwasa *et al.* 1991; Andersson & Iwasa 1996; Stearns & Hoekstra 2000; Kokko 2001). Individuals should select mates that will maximize their lifetime fitness by producing fit offspring – signals of genetic quality aid in the selection of the best mate. Evidence of this mechanism appears in systems with heritable variation in qualities such as longevity, enhanced growth, and fecundity of offspring (Kokko 2001). An example of this theory in action lies in the mate selection of female guppies (*Poecilia reticulata*). Female guppies preferentially mate with large males because they produce longer-lived offspring than smaller males (Watt *et al.* 2001). Similarly, male guppies have exhibited sexual preferences for the largest females; microsatellite DNA genotyping showed that the preferred larger females had the greatest fecundity (Herdman *et al.* 2004). These studies suggest that guppies select mates because of their ‘good genes’ which produce more, superior offspring.

Zahavi’s ‘handicap principle’ adds another component to the ‘good genes’ theory (Zahavi 1975; Zahavi 1977). The ‘handicap principle’ emphasizes the underlying cost of the ornamental trait as its important signaling function (Zahavi 1975; Zahavi 1977; Iwasa *et al.* 1991). Exaggerated behaviors or physical ornamentation that seem costly to the bearer are theorized to signal their genetic quality/superior survival ability in spite of the possession of the severe handicap imposed by the costly character.

1.1.2 – Direct benefits

Direct benefits are those that provide immediate phenotypic benefits to a potential mate (Stearns & Hoekstra 2000). Females may select mates that provide these immediate phenotypic benefits to her and her offspring in order to increase the probability of survival. Signals of good parenting, protective ability from predators, or the possession of a quality territory are examples of direct benefits that males may advertise to attract females. For example, brighter yellow blue tit males (*Parus caeruleus*) are more sexually attractive to females, apparently because they advertise good parenting ability (Senar *et al.* 2002).

These birds acquire the pigments that produce the yellow color in their feathers from their diet, and therefore, only the best foragers (and hence parental providers) can produce the brightest yellow feathers. Another example of mate selection for direct benefits is that larger male sculpins (*Cottis bairdi*) are more sexually attractive to females, because they are more effective egg guardians (i.e. better parents) against predators (Brown 1981).

1.1.3 – Sensory bias

Sensory biases are arbitrary mating preferences that are not the result of sexual selection, having arisen in some other context (Stearns & Hoekstra 2000). Organisms may inherit sensory capacities from ancestors that bias the characteristics they prefer in potential mates (Ryan & Keddy-Hector 1992; Andersson & Iwasa 1996; Stearns & Hoekstra 2000). These biases may be caused by innate developmental processes rather than adaptations of mate choice. Guppies may provide an example of female choice by sensory bias. Female guppies have sexual preferences for males with larger, more chromatic orange spots. One proposal is that this preference originated because it allowed females to select the highest quality mates. An alternative hypothesis is that the origin of this preference is a pleiotropic effect of a sensory bias for the color orange, which may have arisen in the context of food detection (Rodd *et al.* 2002). In other words, male guppies evolved orange pigmentation to take advantage of female guppies' bias for (non-sexual) orange objects, like food.

This kind of mate choice mechanism may generate selection pressures as strong as the previously discussed mechanisms.

1.1.4 – Exaggeration of preferences and traits

In sections 1.1.1 through 1.1.3, I explained how female preferences may evolve. Here I describe how these preferences and their respective preferred characteristic(s) may become elaborated over evolutionary time.

Almost 75 years ago, Fisher proposed a theory that explained how female preferences and male sexual ornaments may evolve in concert (Fisher 1930). Fisher's theory states that females select males with an attractive character. The female selects this attractive male because he will produce attractive male offspring that will enjoy high mating success. Additionally, their female offspring will inherit the preference genes of their mother which will also proliferate in the population due to the linkage with the attractive male genes. After several generations of mating success, the attractive male trait and female preference for that trait will become abundant and exaggerated due to sexual selection pressure (Fisher 1930; Pomiankowski *et al.* 1991; Stearns & Hoekstra 2000; Kokko 2001). Thus, female preferences will become more selective and male sexual ornaments will become more extravagant. Male character exaggeration and the correlated female preference genes will 'runaway' in the population until they are halted by the costs of natural selection (Fisher 1930).

1.1.5 – Sexual selection by female choice

In most species females select their mates and males evolve traits to attract females (Darwin 1859). Sexual selection pressure forces males to evolve signals of individual quality; stronger pressure forces the production of more exaggerated signals and sometimes a large quantity of signals. Females select mates that signal the best genetic quality, provide the most direct benefits, and/or most appeal to their sensory system (Andersson & Iwasa 1996; Stearns & Hoekstra 2000; Kokko 2001). Female choice is also pressured by sexual selection to produce the fittest and most attractive offspring in order to increase lifetime fitness. After several generations of sexual selection pressure, female choice may become more selective and male signals of quality may become exaggerated (Fisher 1930). This happens because only the choosiest females and most decorated males produce fit and attractive offspring that survive and successfully reproduce. Exaggeration of female choice and male ornamentation is eventually halted by costs of natural selection.

The rest of this chapter will be devoted to a review of several forms of male sexual ornamentation that can be evaluated by females. Specifically, I will focus on the types of sexual decorations that have evolved in male zebra finches, carotenoid- and melanin-based pigmentation. I will also review fluctuating asymmetry and its relevance to mate choice, a topic that has already been researched a great deal with respect to zebra finches. Finally, I will explore the theory underlying the evolution of multiple sexual ornaments, i.e. why do male zebra finches possess so many sexual decorations? A discussion of these types of sexual ornamentation is necessary to understand completely the mating system dynamics of zebra finches.

1.2 – Sexual selection and color

Since Darwin formed his theory of sexual selection to explain the evolution of sexually dimorphic traits, biologists have been fascinated with the study of exaggerated ornamentation (Darwin 1871). Bright coloration is an example of exaggerated ornamentation (Andersson 1994; Andersson & Iwasa 1996). Recently, researchers have begun to uncover the information signaled by variation in ornamental color. In particular, they have focused on how the pigments that produce colors are obtained and what information they signal. Brightly colored ornamentation may signal one or more of the following: species, sex, age, 'good genes' (Zahavi 1975; Pomiankowski 1987a; Andersson & Iwasa 1996), social dominance (Esa & Alatalo 1993; Andersson & Iwasa 1996), foraging efficiency (Kodric-Brown & Brown 1984; Olson & Owens 1998; Møller *et al.* 2000; Hill *et al.* 2002; McGraw *et al.* 2003), parasite resistance (Hamilton & Zuk 1982), immunocompetence (Folstad & Karter 1992; Olson & Owens 1998; Møller *et al.* 2000; McGraw 2003; McGraw *et al.* 2003), nutritional condition (Hill & Montgomerie 1994; Olson & Owens 1998; McGraw *et al.* 2003), potential for paternal care (Hill 1991; Smiseth *et al.* 2001), and the physiological ability to deposit pigments into body tissue (McGraw *et al.* 2003). There are three primary types of coloration that animals produce: carotenoid-, melanin-, and structural-based coloration. Male zebra finches display two of these types of coloration in their sexual ornamentation, carotenoid- and melanin-based coloration.

1.2.1 – Carotenoid pigmentation

Carotenoids are a group of more than 600 different molecules synthesized by plants, algae, bacteria, and fungi (Fox 1976). They can be subdivided into xanthophylls and carotenes based on characteristics of their molecular structure (Møller *et al.* 2000). No animals are capable of synthesizing carotenoids, so the ability to express carotenoid-based coloration is directly linked to the ability to acquire carotenoids from dietary sources and deposit them into the integument (Fox 1976; McGraw *et al.* 2003). Once ingested, carotenoids must be transformed several times through oxidative alterations before the correct biological precursor is available for incorporation into body tissue (Møller *et al.* 2000). Carotenoid pigments are responsible for the bright red, orange, and yellow coloration seen in a variety of taxa, e.g. birds, fish, and mammals (Fox 1976; Badyaev 2000). Male zebra finches display carotenoid-based coloration in their red bills. This type of coloration may function as a signal of sex, age, relatedness, sexual attractiveness, or as a warning to other organisms (Fox 1976; Hill 1999a; Møller *et al.* 2000). Carotenoid-based coloration is thought to be greatly affected by sexual selection as it is involved in much sexual dichromatism in birds (Badyaev 2000).

There is no general consensus as to the precise information signaled by carotenoids, as this type of pigmentation has been demonstrated to correlate with a number of different characteristics. Simple logic suggests that one type of information that carotenoid coloration may convey is foraging efficiency – carotenoids are rare in nature and can only be obtained from dietary resources. Thus, the best foragers can obtain the most of these pigments and perhaps produce the brightest ornaments (Kodric-Brown & Brown 1984; Olson & Owens 1998; Badyaev 2000; Møller *et al.* 2000; McGraw *et al.* 2003). A study on wild house finches (*Carpodacus mexicanus*) found a positive correlation between the amount of carotenoids in the gut and in feathers growing during molt – providing significant evidence for the relationship between diet and appearance (Hill *et al.* 2002). Also, zebra finches with higher plasma carotenoid concentrations exhibited brighter red bills (McGraw *et al.* 2003). However, male zebra finches with the same diet as female zebra finches had significantly more plasma carotenoids (McGraw *et al.* 2003). This result suggests that there is an important, and unstudied, physiological component to carotenoid utilization and deposition.

An alternative hypothesis by Hamilton and Zuk states that the possession of brightly colored ornaments signals parasite and/or disease resistance genes (Hamilton & Zuk 1982). Only disease-free, healthy individuals are capable of maintaining bright ornamentation. Recent research has provided some validation of this hypothesis as parasitized individuals were found to possess duller carotenoid ornamentation than unparasitized ones (McGraw & Hill 2000). Thus, brightly colored carotenoid ornamentation should be a preferred trait because it signals a healthy mate with an efficient immune system and the potential for producing disease-resistant offspring (Hamilton & Zuk 1982; Lozano 1994).

A related proposal for the information content of carotenoid-based coloration, the immunocompetence handicap, stresses one particular cost to this type of ornamentation that may signal individual quality. This hypothesis states that testosterone stimulates secondary sexual character development, but it also impairs the functioning of the immune system. Thus only the best individuals may produce bright ornamentation and persist with an impaired immune system (Folstad & Karter 1992; Hill 1999a; Hill 1999b; Møller *et al.* 2000). There is controversy about the immunocompetence hypothesis as studies have found conflicting results, suggesting it may not apply to all species. In some instances immune responses were found to be positively correlated with ornament size or brightness, in other cases the relationship was negative (Zuk *et al.* 1995; Gonzalez *et al.* 1999; Faivre *et al.* 2003; Kilpimaa *et al.* 2004). A recent study with zebra finches demonstrated that individuals with a lower plasma concentration of carotenoids also had a less responsive immune system. This study provides support for the hypothesis that individuals with the highest concentration of plasma carotenoids also possess more effective immune systems (Blount *et al.* 2003).

Another unrelated cost of carotenoids is their direct toxicity to the owner if consumed in large amounts (Olson & Owens 1998). This kind of toxicity can result in death or a severe degenerative disease unless the organism has evolved a physiological tolerance or pays the high cost of carotenoid metabolism.

Thus, individuals possessing high levels of carotenoid-based ornamentation may be signaling one of two things - individual quality, through their tolerance of this toxicity, or an attractive handicap for carrying the toxin load.

Carotenoids have a well documented role in free-radical absorption that suggests they may be important in the prevention of degenerative diseases such as cancer, heart disease, and cataracts (Bendich 1993; Olson 1993; Olson & Owens 1998). Therefore, carotenoids may signal general health to potential mates, and thus the direct benefits of a healthy mate and good parent. In support of this notion, house finches with brighter plumage grew feathers more quickly and molted earlier than conspecifics will duller plumage (Hill & Montgomerie 1994). American kestrels (*Falco sparverius*) exhibited a positive correlation between carotenoids and plasma protein levels – a signal of a healthy body condition (Bortolotti *et al.* 1996). Zebra finches with redder bills (carotenoid pigmentation) were found to be in better physical condition and to be more active (Birkhead *et al.* 1998). Additionally, carotenoids support the production of steroid hormones that regulate reproduction. So, individuals displaying large amounts of carotenoids may be advertising their capability as successful mates (Bendich 1993; Olson & Owens 1998). Other beneficial physiological contributions made by carotenoids include: wound healing, antioxidant properties, vitamin A precursors, and water balance, among many others (Olson & Owens 1998).

Competitive ability has also been considered to be correlated to carotenoid-based ornamentation, but conflicting results have been reported. The status signaling hypothesis proposes that conspicuous male plumage serves as an honest indicator of social status within a population. Red-shouldered widowbirds (*Euplectes axillaries*) with larger carotenoid epaulettes established territories more quickly and dominated feeding sites to the exclusion of others with smaller epaulettes (Pryke & Andersson 2003). In contrast, zebra finch bill color had no effect on competitive ability as males chose to feed equally as much in the presence of red- and orange-billed conspecific males (Etman *et al.* 2001). However, male zebra finches wearing plastic, red leg bands (simulated carotenoid pigmentation) exhibited dominance over males wearing plastic, green leg bands, suggesting that even the appearance of carotenoid ornamentation may signal high social status (Cuthill *et al.* 1997). Finally, the status signaling hypothesis proposal does not hold true in house finches as it was found that carotenoid-based plumage color had no effect on the win/loss outcome of dominance trials (McGraw & Hill 2000). It appears that carotenoid-based pigmentation may signify social status and competitive ability, but only in select species. With regard to zebra finches, carotenoid-based ornamentation has an ambiguous role in social dominance. The two previously mentioned studies examining the relation between carotenoid-based pigmentation and zebra finch social dominance produced contrasting results (Cuthill *et al.* 1997; Etman *et al.* 2001).

1.2.2 – Melanin pigmentation

Melanin pigments are large molecules arranged in the form of polymers with many functional carboxyl groups (Fox 1976). They are synthesized by animals as by-products of amino-acid catabolism, thus they are not acquired solely from dietary sources like carotenoids (Fox 1976; Badyaev 2000). Melanins are responsible for producing the earth-toned pigmentation (blacks, grays, browns, and rusts) seen in many animals, e.g. birds, fish, and mammals. There are two derivatives of melanin: eumelanin is responsible for producing black, gray and brown colors, whereas phaeomelanin produces rust and dark red coloration. Male zebra finches display melanin-based coloration in their cheek patches (phaeomelanin) and in their chest plumage (eumelanin). With reference to birds, melanin deposition depends on the duration of melanocyte activity in growing feather and the interaction of the melanocyte with the epidermis (Nickerson 1944; Badyaev 2000).

The appearance of melanin in physical ornamentation is under tight genetic control and is not easily altered by environmental variation, including diet and parasitism (Fox 1976; Veiga & Puerta 1996; Hill & Brawner 1998; Badyaev 2000; McGraw & Hill 2000). In these studies, it was shown that vitamin deficiencies and/or parasitism had no significant effect on the expression of melanin-based ornamentation; opposite results were discussed earlier in reference to carotenoid-based ornaments. Carotenoid-based pigmentation is also responsible for a larger proportion of sexual dichromatism in birds than is melanin-based pigmentation, suggesting that carotenoids are more heavily involved in sexual selection (Badyaev 2000). Thus, it has been hypothesized that carotenoid- and melanin-based ornaments signal different information to other animals. Melanin-based ornaments seem to be a less likely, but possible candidate for signals of genotypic quality, but more likely as signals of status and dominance (Møller 1987; Hill & Brawner 1998; Senar 1999; Badyaev 2000; McGraw & Hill 2000; Senar *et al.* 2003). There are several hypotheses about how melanin-based ornaments can honestly signal social status and dominance; however, none of them can be applied to all species (Senar 1999). Some of these hypotheses include: (i) only dominant individuals can survive the predation risk associated with displaying large melanin ornaments (Balph *et al.* 1979; Fugle & Rothstein 1987); (ii) the production of large badges can have immunosuppressive effects due to the role of testosterone in ornament production (Owens & Hartley 1991; Johnstone & Norris 1993); and (iii) signals of dominance are only honest if dominant behavior accompanies the morphological cue (Rohwer 1977; Rohwer & Rohwer 1978). A relatively recent review describes a large number of avian species where melanin-based plumage is related to social dominance (Senar 1999). In only a handful of species, though, does melanin-based plumage appear to be related to sexual attractiveness.

Dominance, however, may be correlated with mating success and genetic quality in some species. Therefore, it is possible that melanin-based plumage may be an indirect indicator of genetic quality and sexual attractiveness. Female black grouse (*Tetrao tetrix*) select mates at leks where the males violently compete for copulation attempts with females. Carotenoid- and melanin-based plumage, when examined alone, had no significant effect on female choice in this population (Alatalo *et al.* 1991). The winners of these competitions were shown to acquire significantly more copulations, produce more offspring, and live longer than the losers of the male-male competitions (Alatalo *et al.* 1991). The long-time consensus is that complementary signals (behavioral interactions) are required for melanin-based coloration to indicate forms of phenotypic quality since there has been no definitive evidence that melanin-based plumage signals individual quality (Møller 1987; Senar 1999; Badyaev 2000). However, a recent hypothesis demonstrates how melanin-based ornamentation can serve as an honest advertisement of individual quality.

Macro- and microminerals (e.g. Ca, Zn, Cu, Fe) are obtained from dietary sources and are critical regulatory factors in the biosynthesis of melanin-based pigmentation (McGraw 2003). However, these metal ions are also toxic to the body when accumulated in high concentrations. These toxically high accumulations have been reported in horses, fish, and in captive and wild birds (Harper & Skinner 1998). The carboxyl groups of melanin molecules also bind to these metal ions and store them in melanocytes. Thus, by the exhibition of large melanin ornaments animals may be revealing the physiological tolerance they have evolved to the damaging high mineral concentrations (McGraw 2003). Previously, carotenoids were shown to be harmful if accumulated in high concentrations (Olson & Owens 1998); this is similar to the toxic effects of metal ions discussed here. Hence, displays of both carotenoid- and melanin-based ornamentation may serve as reliable indicators of individual quality by physiological tolerance to direct toxicity.

1.2.3 – Mate choice and sexual coloration

In previous sections, carotenoid pigments were shown to signal several facets of individual quality, many of which may relate to mate preferences. Melanin pigmentation is not believed to be as involved in mate choice and has been demonstrated to primarily signal social status and possibly a physiological tolerance to metal toxicity. Male guppies possess both carotenoid and melanin pigments and females have been found to evaluate only the carotenoid-based ornaments when selecting a mate (Kodric-Brown 1993; Brooks & Caithness 1995). Below, I provide a brief review of mate choice studies where carotenoid pigmentation plays a significant role as a sexually preferred characteristic. Establishing this fact is necessary here as carotenoid pigmentation (male bill color) has been shown to play an important role in the mate preferences of female zebra finches (Burley & Coopersmith 1987; Blount *et al.* 2003; McGraw *et al.* 2003).

Females of many bird species prefer brightly-ornamented males (due to carotenoid pigmentation); some examples are zebra finches (Burley & Coopersmith 1987; Blount *et al.* 2003), house finches (Hill 1990; Hill 1991; Hill 1992), American goldfinches (*Carduelis tristis*) (Johnson *et al.* 1993), and yellowhammers (*Emberiza citronella*) (Sundberg 1995). Several fish species demonstrate similar preferences: guppies (Endler 1980; Houde & Endler 1990; Kodric-Brown 1993; Brooks & Caithness 1995), pupfish (*Cyprinodon rubrofluviatilis*) (Kodric-Brown 1983; Kodric-Brown 1993), and sticklebacks (*Gasterosteus aculeatus*) (Milinski & Bakker 1990). The species listed above are only a small fraction of the animal species that use carotenoid ornamentation in mate selection. Review papers about this topic have gone so far as to point out the one or two studies that have not found a positive correlation between carotenoid ornamentation and sexual attractiveness (Collins & Ten Cate 1996; Olson & Owens 1998; Hill 1999a).

Despite widespread results that label the brightest individuals as the most attractive, often research produces contradictory results. One such case involves zebra finches, a species in which males that possess the brightest red bills are the most attractive. Two studies, by the same laboratory, have found results that contradict this previously held notion and have suggested other male phenotypes that may be better predictors of sexual attractiveness. The first of these studies suggests that male display rate is a better predictor of attractiveness than is bright red bill color (Collins & Ten Cate 1996). They state that male bill color is probably important in mate choice, but that in their experiment, male display rate was found to be more significant in mate selection. The second study by this lab pinpoints male song rate as the better predictor of male attractiveness (Collins *et al.* 1994). They admit, though, that their small sample size may be masking the importance of bill color in mate choice. This is probably the case as all other published studies, to the best of my knowledge, have reported that male zebra finch bill color is the most significant predictor of sexual attractiveness (Burley & Coopersmith 1987; Blount *et al.* 2003; McGraw *et al.* 2003). Complex bird vocalizations, though, have long been hypothesized to function in mate choice and have been proven to be the most important criterion in some species (Catchpole 1987). Therefore, it may be possible that male zebra finch song rate may also have a significant role in female choice (Collins *et al.* 1994; Zann 1996).

Some mate choice studies artificially manipulate the magnitude of sexual ornamentation by brightening color or enlarging the ornament's size and then testing for the effects of the manipulation on sexual attractiveness. Of particular interest to this study are the experiments with colored leg bands and male attractiveness in zebra finches. The reasoning behind this method takes advantage of a previously known preference exhibited by female zebra finches – bills with large amounts of red, carotenoid-based pigmentation (Burley & Coopersmith 1987; Blount *et al.* 2003; McGraw *et al.* 2003). Therefore, female zebra finches may prefer a seemingly arbitrary male trait that mimics carotenoid pigmentation, red-colored leg bands. Pioneering work by Nancy Burley found that male zebra finches wearing red leg bands were more sexually attractive and produced more offspring than males wearing orange or light green bands (Burley 1986). Replication of this study has proven to be difficult though, as it is thought that other male characteristics or behaviors may have caused interference. One research team pointed out that preference for attractive leg band colors may be masked under conditions of strong male-male competition for nest boxes (Ratcliffe & Boag 1987). These researchers claim that male activity level, nest box possession, or other natural ornamental traits (which were not matched between the treatments) may have been used by the females in mate selection, thus complicating their results. Another study found that male zebra finches wearing red leg bands had dominance over males wearing light green leg bands when housed together (Cuthill *et al.* 1997). These studies add support to the notion that female zebra finches have preferences for males possessing large amounts of carotenoid-based coloration, either natural (bill) or artificial (leg bands).

Another confounding factor surrounding color preferences is the often overlooked fact that other animals do not view color in the same manner as humans (Bennett *et al.* 1994). For example, zebra finches are capable of detecting ultraviolet light because they possess the retinal cone cells specific to that range of wavelengths. Humans can not detect ultraviolet light. There has been experimental evidence that suggests zebra finches use ultraviolet light in species and mate recognition (Bennett *et al.* 1996; Hunt *et al.* 1997). Most light sources in mate choice experimental rooms do not emit ultraviolet wavelengths that would be present in natural mate choice situations. This potentially alters the appearance and color perception of the test subjects. In these experiments, females only demonstrated preferences for hypothesized attractive phenotypes when ultraviolet light was present in the room (Bennett *et al.* 1996; Hunt *et al.* 1997). Therefore, consideration of experimental design and lighting is very important in avian mate choice studies, particularly those that involve color perception.

Elaborate sexual ornamentation evolves in part because certain preferable qualities are passed on to offspring. Females (and males) select mates that will produce the highest quality offspring attractive to members of the opposite sex

(Wynn & Price 1993). Several studies have reinforced the idea that there is high heritability of sexual ornamentation. House crickets (*Acheta domesticus*) exhibit high heritability of preferred male sexual traits, $h^2=0.76$ (Hedrick 1988). A few studies of captive zebra finches have found that bill color has wide-ranging heritability estimates (from $h^2=0.23$ to 0.73) between parent and offspring (Price & Burley 1993; Price 1996). A different study on zebra finches found no significant heritability for bill color (Burley & Bartels 1990). Two other ornaments, breast and eye stripes, of captive zebra finches have shown significant heritability estimates (Burley & Bartels 1990). Among house finches there is a positive correlation between the plumage coloration of father and sons which indicates significant heritability of the trait (Hill 1991). Finally, it was found that male guppies significantly inherit their father's attractiveness which is genetically correlated with ornamentation (Brooks 2000).

All of these ornamental heritability experiments involved captive animals where natural environmental conditions that may affect the production of these ornaments were absent, e.g. limited food supply, predators, harsh weather conditions, etc. Captive conditions may increase heritability estimates as all organisms are living in identical environments where factors such as limited food supply and predation are unable to have their 'natural' effects. It is therefore probable that these heritability estimates may be higher than would be observed under natural environmental conditions.

1.3 – Sexual selection and symmetry

Secondary sexual ornaments can be greatly exaggerated traits, which may be very expensive to produce. These ornaments may be intricate in design and thus, there are many ways to disrupt their development to perfect expression. One of these possible disruptions is fluctuating asymmetry, random deviations from perfect symmetry which arise in the development of a trait that would otherwise be bilaterally symmetrical (Van Valen 1962). It is thought that these asymmetries arise due to the organism's inability to cope with environmental and genetic stresses during development (Van Valen 1962; Møller & Pomiankowski 1993a; Swaddle & Witter 1994). Levels of fluctuating asymmetry are believed to be indicators of genetic quality since they reflect the whole genome's ability to tolerate environmental and developmental stress. Theoretically, high quality individuals buffer against stresses better than low quality individuals and therefore are more likely to produce more symmetric characters (Møller 1990; Møller & Pomiankowski 1993a; Andersson & Iwasa 1996; Swaddle 1996). Sexual ornaments display greater absolute and relative degrees of fluctuating asymmetry than non-ornamental traits (Møller & Höglund 1991). This is expected since sexual ornaments are more costly to produce than non-ornamental traits and are at the limits of physiological production. Therefore, bilateral symmetry of sexual ornamentation is an indicator of individual genetic quality. Also, the degree of fluctuating asymmetry in sexual ornaments has been shown, in some species, to have a negative relation to the size of the ornament, whereas this pattern is not observed in non-ornamental traits (Møller 1990;

Møller 1991; Møller & Höglund 1991; Balmford *et al.* 1993). Therefore, the magnitude of fluctuating asymmetry in large sexual ornaments may be a reliable reflection of genotypic quality (Møller 1990; Møller 1991; Møller & Höglund 1991).

The actual information that fluctuating asymmetry signals is controversial; some studies have found that it conveys nutritional condition, sexual attractiveness, or dominance whereas similar studies have not (Møller 1991; Møller & Pomiankowski 1993a; Swaddle & Witter 1994; Swaddle & Cuthill 1994a; Dufour & Weatherhead 1998; Simmons *et al.* 1999). A recent review points out that there has been a chronological decline in the number of published studies that support the notion that bilateral symmetry portrays individual quality. This marked decline, they point out, may be due to publication bias, a less critical approach to research, or improper statistical analyses (Simmons *et al.* 1999). Another potential problem that has been recognized in symmetry studies is the potential for measurement error, especially in analyses of avian wing lengths. It was found that there were significant measurement biases of avian wings in the results obtained by right handed, left handed, and ambidextrous individuals (Helm & Albrecht 2000). Measurements of fluctuating asymmetry are small, so even the smallest measurement errors could significantly impact the results of relevant studies. Despite the controversies and potential problems surrounding studies of fluctuating asymmetry, there has been a great amount of work done about fluctuating asymmetry that has produced interesting results.

Female barn swallows (*Hirundo rustica*) preferentially mate with males that possess the longest tail feathers (Møller 1988; Møller 1989). This preference may be working under a 'good genes' mechanism (specifically a handicap) as it was subsequently found that males with artificially elongated tails were less efficient in prey capture and grew shorter tail feathers in the following annual molt (Møller 1989). An additional signal of male barn swallow tail feathers may be their level of fluctuating asymmetry. It was found that the preferred phenotype (longer tail feathers) also had a strong correlation with smaller levels of fluctuating asymmetry (Møller 1990; Møller 1991). Also, males with artificially increased tail asymmetry less efficiently navigated a test maze by frequently contacting the walls of the maze – asymmetry may have a flight cost that affects fitness (Møller 1991). This has led to the suggestion that it is natural selection, not sexual selection, that selects for more symmetrical feathers (Balmford *et al.* 1993). Female barn swallows may possibly select males with the handicap of long tails and then use the correlated tail symmetry as a confirmation of male quality.

Nutritional stress can cause large developmental asymmetries in the primary feathers and chest plumage of molting European starlings (*Sturnus vulgaris*) (Swaddle & Witter 1994). Food deprived starlings grew significantly more asymmetrical primary feathers than normally fed subjects. The starlings with the most symmetrical primary feathers also had the spottiest chest plumage – an attractive trait. Also, the starlings that grew the most symmetrical feathers had the largest fat reserves (Swaddle & Witter 1994). All of these results indicate that low levels of fluctuating asymmetry may signal good nutritional health to others.

Conflicting results have been found regarding correlations between character symmetry and social dominance. Male Japanese scorpionflies (*Panorpa japonica*) with low levels of forewing asymmetry were found to be more likely to win intrasexual contests over food (Thornhill 1992). In contrast, barn swallows with the most symmetrical tail feathers were found to have no competitive edge over less symmetrical males when fighting over access to females (Møller 1992). The most asymmetrical European starling females were found to win significantly more dominance interactions than symmetrical males. This result however has been suggested to be due to experimental housing and nutritional conditions during molt (Swaddle & Witter 1994). Most recently, bilateral symmetry of four body characters was found to have no correlation with social dominance in red-winged blackbirds (*Agelaius phoeniceus*) (Dufour & Weatherhead 1998). The relation between asymmetry and social dominance is complex, and it is likely that this relationship varies across species.

As previously discussed, bilateral symmetry of sexual and non-sexual ornaments can signal developmental stability, nutritional condition, and (questionably) social dominance. Therefore, there may be sexual selection pressure for organisms to produce symmetrical traits, ornamental or not. It has already been discussed that negative correlations have been observed for sexual ornament size and asymmetry in some species (Møller & Höglund 1991) – this indicates that ornament size as well as symmetry may be viable indicators of individual quality since the largest ornaments have the greatest bilateral symmetry. What follows is a brief discussion of mate choice studies involving manipulated sexual ornaments as well as arbitrary ornament symmetry.

Two mate choice studies involving barn swallows demonstrated that males with experimentally decreased levels of asymmetry had a shorter pre-mating period, an earlier egg laying date, as well as more offspring produced than males with experimentally increased levels of asymmetry (Møller 1992; Møller 1993). Before this study, it had already been found that female barn swallows prefer to mate with males that possess the longest tail feathers (Møller 1988; Møller 1989). In one study, males were split into four treatments, two treatments had their outer tail feathers painted to appear symmetrical and the other two treatments had the same feathers painted to appear asymmetrical (Møller 1992). In the second study, males were divided into treatment groups that altered the length and fluctuating asymmetry of their tail feathers. Females consistently exhibited sexual preferences for males possessing the longest, most symmetrical tail feathers (Møller 1993). However, there may be a problem with this study due to the largely, unnatural exaggerated feather lengths and asymmetry used.

Mate choice studies with zebra finch leg bands have already been discussed whereby females preferentially mate with males wearing red leg bands (Burley 1986). Female zebra finches also display significant preferences for males wearing symmetric arrangements of plastic leg bands (Swaddle & Cuthill 1994b; Swaddle 1996). Males wore two orange leg bands and two green leg bands at all times (two bands on each leg); the arrangement of how these bands were worn created the different treatments. Six different arrangements of leg bands were tested for female preference: two asymmetric, two cross-asymmetric, and two symmetric. Females significantly preferred the symmetric males in both experiments (Swaddle & Cuthill 1994b; Swaddle 1996). The second experiment went a step further by testing for reproductive success of the different treatments. Since the difference between the treatment groups was arbitrary and not specific to the males, the test was primarily examining maternal effects. It was found that the symmetric treatment males produced significantly more independent fledglings (Swaddle 1996). This indicates that female-based paternal investment was increased by the mothers for the apparently symmetric males, due to the males' superior attractiveness. Female zebra finches have also shown sexual preferences for males possessing artificially manipulated symmetric chest plumage, an intricate sexual ornament (Swaddle & Cuthill 1994a). Stimulus males in this experiment had feathers strategically trimmed to give their chest bar plumage either a symmetric or asymmetric appearance. In choice experiments, females displayed strong sexual preferences for males from the symmetric treatment groups (Swaddle & Cuthill 1994a).

There have been a number of zebra finch mate choice studies that have shown females to significantly prefer males possessing symmetrical sexual and arbitrary traits. Males possessing symmetrical characters signal several potential aspects of individual phenotypic as well as genotypic quality. In summary, only the best individuals can tolerate environmental stresses during development and still produce bilaterally symmetric traits. Small levels of asymmetry have also been shown to signal good health and nutritional condition, a possible signal of the direct benefits. There is also some support that individuals displaying symmetric sexual ornamentation may be socially dominant.

Trait symmetry, sexual coloration, body size, and other sexual characters may all play significant roles in the mating systems of some species. The signaling content of each of these characteristics has been discussed previously, but not in conjunction. In the following section, the evolution of multiple sexual traits will be discussed as well as its significance to my study system.

1.4 – Sexual selection and multiple ornaments

Males of many species possess multiple sexual ornaments and/or perform multiple behavioral displays during courtship (Burley 1981; Kodric-Brown 1993; Savalli 1994; Brooks & Caithness 1995; Dale & Slagsvold 1996; Buchanan & Catchpole 1997). Models have suggested that multiple ornaments and behaviors may evolve for multiple mate preferences for separate ornaments, or alternatively for a single preference (Møller & Pomiankowski 1993b; Iwasa & Pomiankowski 1994; Johnstone 1995; Brooks & Couldridge 1999). A verbal model predicts three reasons that male birds may evolve more than one sexual ornament (Møller & Pomiankowski 1993b). (i) The multiple message hypothesis – different ornaments signal different characteristics about the condition of the individual, or appeal to a variety of female preferences (Coleman *et al.* 2004), e.g. different components of a sexual display; (ii) The redundant signal hypothesis – the combined signal of several traits will provide a more honest indication of individual quality, or some traits may amplify the signals of others (Brooks 1996); and (iii) The unreliable signal hypothesis – one or more ornaments do not currently have signaling function and only exist because they are uncostly to produce. These hypotheses predict that multiple sexual ornaments should be commonly found in species under intense sexual selection, and there should be more evidence for condition dependence in the ornaments of species with single as opposed to multiple ornaments (Møller & Pomiankowski 1993b; Iwasa & Pomiankowski 1994). A mathematical model has demonstrated that the handicap process can select for multiple preferences and sexual ornaments but only if the cost of mate choice is low. As the costs of mate choice increase the process is predicted to lead to the evolution of one indicator of quality (Iwasa & Pomiankowski 1994). Accordingly, a recent mathematical model of choice based on multiple ornaments hypothesized that choosers should prioritize which cues are being assessed based on the costs of mate choice, indicating that not all ornaments are of equal signaling value (Fawcett & Johnstone 2003). It is difficult to obtain a full understanding of a mating system in species that possess multiple sexual ornaments. Uncovering the signaling content of each ornament or combination of ornaments is difficult to isolate in mate choice experiments. Also, to fully understand a mating system one must determine which ornaments are the most critical in mate assessment.

Male guppies possess many different physical and behavioral cues that could theoretically be used in mate choice: carotenoid (orange) spots, melanin (black) spots, iridescent coloration, gonopodium size, fin sizes, social dominance, and courtship intensity (Kodric-Brown 1993; Brooks & Caithness 1995). In two experiments that tested for correlations between male sexual traits and sexual attractiveness, several characters were found to be positively associated with being chosen. Carotenoid pigmentation was found to be correlated with mating success in both experiments (Kodric-Brown 1993; Brooks & Caithness 1995), and social dominance and courtship intensity were significant predictors of attractiveness in the one study in which each were examined (Kodric-Brown 1993). The finding from the first experiment in which only carotenoid-based ornamentation was used in mate choice provides support for the unreliable signal hypothesis as there seemed to be a number of unused, arbitrary ornaments (Brooks & Caithness 1995). The second experiment, where both physical and behavioral cues were highly significant in mate choice seems to comply with the multiple message hypothesis, because each ornament/behavior signaled a different component of individual quality. Another mate choice study with guppies found that female preferences for orange and black male coloration responded to selection independently. This would suggest that there are two distinct evolutionary preferences for their respective ornaments (Brooks & Couldridge 1999). Finally, there is a hypothesis that melanin ornaments serve as signal amplifiers – ornaments that accentuate the pattern or expression of another ornament (Brooks 1996). Natural variation in melanin area is not correlated with female response. However, when males' melanin ornaments in guppies are reduced their sexual attractiveness also decreases. This result suggests that melanin ornaments may be accentuating the expression and appearance of another ornament, carotenoid-based coloration (Brooks 1996).

Other recent studies provide evidence for multiple mating preferences in fiddler crabs (*Uca annulipes*) (Backwell & Passmore 1996), pied flycatchers (*Ficedula hypoleuca*) (Dale & Slagsvold 1996), sedge warblers (*Acrocephalus schoenobaenus*) (Buchanan & Catchpole 1997), yellow-shouldered widowbirds (*Euplectes macrourus*) (Savalli 1994), pigeons (*Columba livea*) (Burley 1981), and northern cardinals (*Cardinalis cardinalis*) (Jawor *et al.* 2004). Females in these species evaluate different suites of mate characteristics before choosing a sexual partner. Female satin bowerbirds have a multistage mate choice process where they evaluate several male displays at different times (Coleman *et al.* 2004). This technique of mate evaluation may be an explanation for the evolution of multifaceted male sexual display patterns. Different populations of the same species may evaluate potential mates differently, as they are under different natural and sexual selection pressures. These pressures cause the evolution of appearance, behavior, and preferences of individuals within a population.

Multiple sexual ornaments are found in many species, some of which are mentioned above. The presence of multiple sexual ornaments may indicate high sexual selection pressure within a population to signal individual quality. In some mating systems different ornaments signal different individual qualities, in other systems ornaments may serve as redundant signals or have no signaling function at all. Mating preferences may exist for attractive combinations of sexual traits, connected series of displays, or complementary amplifier traits that are not selected for individually but in combination with others. These ideas have broad implications to much sexual selection research, including my study system with zebra finches.

1.5 – Sexual selection and this study

Wild-type zebra finches were used in mate choice trials in this experiment. These birds are monogamous and sexually dimorphic, in which the males are more ornamented than the females (Zann 1996). Males are known to compete for female attention and perform ritualized displays and song during courtship. If disinterested in the courting male, females will ignore or desert the male or react violently if the male attempts rape. Females, if interested, also partake in song and courtship dances typically involving spins and hops between neighboring branches. Due to these behaviors, zebra finch mate choice is simple to gauge in laboratory situations – the total number of display hops and time spent in proximity to potential mates are the most often used methods to determine the 'chosen' male (Swaddle & Cuthill 1994a; Bennett *et al.* 1996; Blount *et al.* 2003).

Male zebra finches have a suite of ornamental characteristics that may be related to sexual attractiveness. One carotenoid-based male ornament is a bright red bill; females' bills are a duller orange color. The pigments required to form this bright red color are obtained from dietary sources (McGraw *et al.* 2003). However, as mentioned previously, there may be an additional physiological component that plays a significant role in pigment deposition. Females prefer males that possess the brightest red bills (Burley & Coopersmith 1987; Blount *et al.* 2003; McGraw *et al.* 2003). Males also display several melanin-based ornaments that have not been analyzed with regards to mate choice, to the best of my knowledge. Phaeomelanin pigments are used to form the rust color in males' cheek patch. Eumelanin pigments are used to form the dark chest badge and assortment of chest bars (Fox 1976; Badyaev 2000; McGraw 2003). In this study, these melanin-based ornaments and bill color were analyzed for their appearance and size in relation to sexual attractiveness.

Two measures of bilateral symmetry were examined in this experiment to test for a correlation with sexual attractiveness. Female zebra finches display preferences for character symmetry – chest bar plumage (Swaddle & Cuthill 1994a) and leg band arrangements (Swaddle & Cuthill 1994b; Swaddle 1996). In this experiment, I analyzed the length of primary feathers IV and VI (position from distal edge) for measures of fluctuating asymmetry. Primary feather length is also an indicator of body size, so this examination would reveal any preference for male body size. Finally, males with the greatest display rates have been reported to be the most attractive (Collins *et al.* 1994; Collins & Ten Cate 1996). Therefore, I tested for correlations between male display rates and the extent of female preference.

Since male zebra finches display a large number of ornamental characteristics and behaviors during courtship, these phenotypes can be analyzed for their signaling significance during female mate choice; e.g. a bright red bill may be of greater significance to a choosy female than a male with a high display rate. Alternatively, certain ornaments may simply signal different qualities of the bearer that may be important but simply not applicable to mate choice; e.g. some aspects of carotenoid versus melanin ornaments. Finally, some display traits of males may not have any signaling function at all. This experiment attempted to discover which male phenotypes or combination of phenotypes is most significantly correlated with sexual attractiveness.

This experiment had an extended duration of 10 days that has never been used in any other zebra finch mate choice studies, to the best of my knowledge. Most sexual selection studies with these birds last only a few hours (Burley & Coopersmith 1987; Wynn & Price 1993; Collins *et al.* 1994; Swaddle & Cuthill 1994a; Swaddle & Cuthill 1994b; Bennett *et al.* 1996; Hunt *et al.* 1997). Ten day choice trials allowed more than sufficient time to observe changes in mate preference over the course of the experiment. A thorough mate evaluation may last longer than an hour or a day, so a mating preference and/or the extent of preference might change over time. Certain characteristics might be used to make quick mate choice decisions, whereas after a period of time other traits or a combination of traits may be the focus. For example, bright red bill color may take signaling precedence in one hour zebra finch mate choice studies as the significant predictor of attractiveness. However, if that experiment were continued for a few days or more, then bill color in combination with the amount of melanin-based plumage on the chest may factor into the mating decision. In summary, an examination of mating preferences in combination with physical correlates of male attractiveness should answer a number of interesting sexual selection questions.

I had three predictions concerning the mating preferences and behavior of the females in this experiment. (i) Throughout the experiment, the females would exhibit sexual preferences for the stimulus males possessing the brightest red bills. Previous research has shown that bill color is the most significant male characteristic evaluated by females when choosing a mate, and thus will have the most significant correlation with sexual attractiveness. (ii) Male phenotypes other than bill color (e.g. display rate and fluctuating asymmetry) would be more significantly involved in the mate choice decisions of the females as the experiment progressed. Models have predicted that as females have more evaluation time, they will have a greater chance to assess more than one phenotype. (iii) The melanin-based ornaments (cheek patch, chest bars, and chest badge) of the stimulus males would have relatively weak associations with male sexual attractiveness. Previous research indicates that these ornaments do not have significant roles in mate selection.

CHAPTER 2

COSTS OF MATE CHOICE

2.1 - What are costs of mate choice?

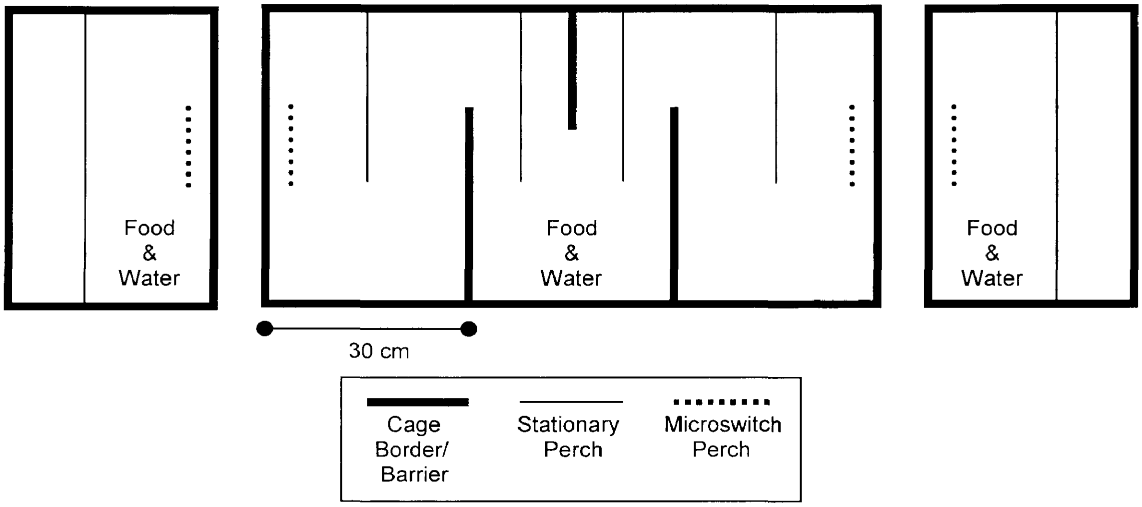
The evolution of mating preferences and preferred traits within populations may be limited or determined by costs associated with mate choice (Pomiankowski 1987b; Lima & Dill 1990; Höglund & Sheldon 1998). It was not until the mid-1980s that researchers realized the importance of understanding how costs affected mate choice. Mate choice (and sexual selection) has associated costs and should be viewed in the same context as any other life-history trait. For example, trade-offs and allocation of resources to sexual advertisements and mate choice behaviors may be comparable to those associated with optimal foraging or offspring production (Höglund & Sheldon 1988; Kokko 1997).

Costs of mate choice that have been documented in the past twenty years include: vulnerability to predation (Pomiankowski 1987b; Lima & Dill 1990; Magnhagen 1991), time and energy expenditure (Pomiankowski 1987b; Sullivan 1994; Andersson & Iwasa 1996; Gibson & Langen 1996), the risk of injury from con- and/or heterospecifics (Pomiankowski 1987b; Magnhagen 1991; Andersson 1994; Reynolds & Côté 1995), the risk of contracting diseases or parasites (Boots & Knell 2002), lost mating opportunities, reduced parental care

(Pomiankowski 1987b; Andersson & Iwasa 1996), the risk of losing an acceptable mate to competitors if choice is delayed (Pomiankowski 1987b; Andersson & Iwasa 1996; Gibson & Langen 1996), and the impairment of the immune system (Kilpimaa *et al.* 2004). The majority of research about costs of mate choice has focused on their proximate effects, primarily choosiness (Slagsvold & Dale 1991; Berglund 1993; Hedrick & Dill 1993; Godin & Briggs 1996). However, more recent research reveals the impact that costs of mate choice may have on the evolution of a mating system (Kokko *et al.* 2002; Fawcett & Johnstone 2003).

Mate choice costs play an important role in my thesis research about zebra finch sexual selection. Much research has already been performed concerning female choice in zebra finches, leading to information about sexual behavior and mate preferences. However, no research project, to the best of my knowledge, has targeted the study of mate sampling costs and their effect on zebra finch mating systems. My project attempted to simulate mate choice situations where one zebra finch female chose between two stimulus males at ends of a choice chamber. In one treatment (high costs of mate sampling), the female had to maneuver three wooden baffles to reach either end of the choice chamber (figure 2). In the other treatment (low costs of mate sampling), the chamber lacked the three obstacles and the female was able to travel freely in her cage (figure 2). Thus, females in the high cost treatment had to expend more energy and time to gain visual access to the stimulus males and make a mate choice decision. This type of mate choice cost may have proximate effects on

FIGURE 2



Plan view of a high cost female choice chamber (81 x 39 x 31 cm) with two adjacent stimulus male cages (29 x 41 x 23 cm). Low cost choice chambers are identical minus the three barriers in the middle of the high cost choice chamber.

female behavior and mate preference. For example, females that undergo high costs of mate choice may not be choosy in mate selection (Kokko *et al.* 2002). This may result in a preference for a relatively unattractive, low quality mate. Conversely, females undergoing low costs of mate choice may be more discriminatory and, theoretically, be able to inexpensively select the most attractive mate. This kind of behavior, repeated over several generations, has been predicted to have a significant impact on the evolution of mating preferences and sexual ornamentation (Kokko *et al.* 2002).

Mate choice costs may also have evolutionary effects on a mating system. Depending on the costliness of mate choice in the environment, female mate selection strategies will respond accordingly, e.g. high mate choice costs may select for more restrictive, less choosy mate searching strategies. These types of mate choice strategies may result in a change in the appearance and/or fitness of individuals in the population. This type of scenario will be discussed later. The remainder of this chapter will be devoted to a review of how mate choice costs are important to mating system dynamics and evolution.

2.2 – Predation risk

Vulnerability to predation has been by far the most widely studied cost of mate choice, to date (Pomiankowski 1987b; Lima & Dill 1990; Andersson & Iwasa 1996). There are several possible reasons for this investigational bias: (i) mortality is the ultimate cost that any organism can pay, and therefore the risk of predation is an obvious cost to consider; (ii) the threat of predation is universal to almost every organism (except top-level predators); and (iii) predation risk is relatively straight-forward to manipulate and/or quantify.

Mate choice may be risky when it involves widespread searching activity that increases the probability of encountering a predator (Gwynne 1987). Courtship behavior, lekking, or proximity to brightly-colored members of the opposite sex are components of mate choice activity that may potentially attract predators (Breden & Stoner 1987; Gibson & Bachman 1992; Rowe 1994). Endler (1987), Real (1990), and Crowley *et al.* (1991) were among the first researchers to consider predation as a legitimate factor affecting mate choice. It was found that male guppies courted less often and reduced their number of conspicuous, sexual display elements in the presence of a pike cichlid (*Crenicichla alta*) predator and/or under high light, maximum predation-risk conditions (Endler 1987). A search theory and mate choice model states that, 'increased search costs reduce the threshold critical value for mate acceptability' (Real 1990). Predation was the target of a dynamic-game model that predicted mating skew to decrease under instances of predation risk (Crowley *et al.* 1991). Results from these groundbreaking studies imply that the risk of predation can affect mate choice strategy and sexual advertisement. These findings sparked an abundance of mate choice studies with manipulations of predation risk.

2.2.1 – Predators as cues of predation risk

The most obvious way to introduce predation risk into mate choice experiments is to present a predator to the participants. This is the most commonly used method in this line of testing. In most cases the predator is housed in a separate, but adjacent apparatus to the species under examination. Arrangements like this allow for the perception of the predator as it is in plain sight and for the prevention of the loss of test subjects. Female sand gobies (*Pomatoschistus minutus*) have been shown to decrease their preference for the more sexually attractive, large and brightly colored males when a codfish (*Gadus morhua*) predator occupies a neighboring aquarium (Forsgren 1992). Also in the presence of a codfish predator, male pipefish (*Syngnathus typhle*) radically altered their approach to mate choice – their extent of preference for the larger, more attractive females decreased as well as their overall amount of courtship displays and copulations (Berglund 1993). The populations of sand gobies and pipefish mentioned above evolved in coexistence with their respective predators, and the modification of their mate choice behavior has theoretically evolved in response to that predation threat. The following studies, all involving guppies, were carried out to verify that these types of behavioral adjustments may evolve in response to the presence of predators over time.

Two populations of guppies from the Quaré River that differed only in their natural predation regime were studied in an experiment that tested for the effects of predation risk on sexual activity and preference. Females from a population with naturally high levels of predation reduced their overall sexual activity and mating preference for the more attractive, brightly colored males with the presence of a pike cichlid predator in a nearby holding tank. The presence of the predator had no effect on the behavior of the females naïve to predation risk (Godin & Briggs 1996). A similar experiment obtained the same general results when two piscivorous predators were placed in the same tank as the guppies (Magurran & Seghers 1990). Finally, it was found that populations under high and low predation pressures were genetically differentiated for female preference (Breden & Stoner 1987). Offspring of wild-caught guppies from two high-predation populations and two low-predation populations (all separated by less than five km) were raised in captivity in identical environments (in the absence of their parents). These female offspring exhibited different mating preferences – females from the low-predation populations preferred the more brightly colored males whereas females from the high-predation populations preferred the more drab males. Brightly colored individuals are more conspicuous to predators and are at a higher risk of mortality by predation (Godin & McDonough 2003).

Therefore, it makes sense that the high-predation female offspring would not demonstrate a preference for brightly colored males. Persisting with bright coloration in a high predation environment, however, may serve as a viability indicator, according to the 'handicap principle' (Zahavi 1975). The fact that preferences for dull individuals dominate in the previously mentioned high predation populations suggests that the predation pressure was too great for such handicaps to evolve. Thus, it makes sense that an intense predation pressure would select for more drably colored individuals and by association, sexual preferences for drably colored conspecifics.

2.2.2 – Environmental cues of predation risk

The perception of a predation threat need not be caused by the presence of a predator itself; it can also be simulated by aspects of the environment. For example, Endler's (1987) study on guppies assumed that both pike cichlids and light intensity could serve as justifiable measures of predation risk. Endler found that male guppies reduced their sexual display when light intensities were at their highest. This is presumably because pike cichlids and other predators hunt visually, and so these guppies have been selected to be as inconspicuous as possible in the presence of predators and to only perform sexual displays at night when light levels are at a minimum.

Other species, distantly related to fish, have also shown strong preferences to remain inconspicuous to possible predators when seeking out mates. Female house crickets preferentially mate with males performing long call bouts (Hedrick 1986), and mate searching places female crickets at a great predation risk, especially in open areas (Sakaluk & Belwood 1984). Playback recordings of male call bouts were used in an experiment to imitate the presence of attractive (long call bout length) and unattractive (short call bout length) male crickets at different ends of a choice arena. To gain access to the attractive stimulus, females would have to cross an open area of a choice arena; whereas access to the unattractive stimulus was through pathways of varying degrees of cover. Females preferentially traveled to the unattractive male, 'predator-free' stimulus end of the choice chamber instead of the attractive male, potentially dangerous side (Hedrick & Dill 1993).

2.2.3 – Lekking and the sexual asymmetry of predation risk

Field studies of mate choice are far more difficult to perform than arranged laboratory tests, but there are obvious advantages to observing animals' behavior in their natural environment. One might expect lekking behavior to be very costly in terms of mate choice due to the necessary traveling back and forth to the leks and the vulnerability associated with being part of a noticeable grouping of prey in a lek. In a field study, researchers attempted to measure the mate choice costs of female sage grouse (*Centrocercus urophasianus*), a species in which the females travel to leks repeatedly and spend time with several different males before mating. They found that hens that visited leks more than once (compared to one short visit for mating) experienced an estimated reduction in annual survival of less than 0.1% due to predation (Gibson

& Bachman 1992). This inconsequential cost was not due to an abnormally low number of predators present, for the golden eagle (*Aquila chrysaetos*) population was typical of this region. Due to the low predation cost, they concluded that the benefits of traveling to the lek several times and assessing many males greatly outweigh the reported risk of predation.

Finally, the risk of predation may be different for subsets of a population. This asymmetry can affect the dynamic of mating systems by altering individual behavior and decision making. For example, female guppies may perceive themselves to be at greater risk of predation than males (Magurran & Nowak 1991). Females devoted a larger proportion of their time to adaptive anti-predator behavioral responses – they inspected the predator frequently and schooled more often than males. Predators of guppies more frequently and efficiently hunt larger individuals in laboratory tests (Liley 1989). Females are the larger sex in this species of guppy and so are probably under greater predation risk than males. The difference in security between the sexes produces a conflict where males can afford to court continuously and be more selective where females must limit their preferences and be less active in mate choice behaviors.

2.2.4 – Predation risk due to copulation

Copulation, itself, may be costly in that it may be conspicuous in the eyes of predator and/or prey. Orb-web spiders (*Argiope keyserlingi*) are a sexually cannibalistic species in which during and after copulation, females sometimes devour their mates (Herberstein *et al.* 2002). Males visit the webs of females where females choose to copulate with or reject the suitor. Webs that contained a courting or copulating pair attracted more mantid predators (*Archimantis lattistylus*) and captured less prey items per hour than webs with only the resident female (Herberstein *et al.* 2002). Thus, the females' risk of predation increased and foraging efficiency decreased as a result of sexual activity. Copulation has also been shown to attract predators in water striders (*Gerris buenoi)*. In these animals, females judge males by the vigor of their harassment activity and repel the mating attempts of unsatisfactory males. These pre-mating rituals, as well as copulation itself, occur on the surface of the water and produce an obvious visual disturbance known to attract predators (Rowe 1994).

A review of copulation and predatory risk, conducted prior to the two studies mentioned above, found that in four species (two birds, one amphibian, and one insect) copulation did not increase the risk of predation for either sex; in fact the risk may be less, in comparison to other activities (Gwynne 1989). However, the studies mentioned in the previous paragraph had significantly elevated risks of predation during copulation. The risks associated with copulation certainly vary across species, presumably due to differences in breeding ecology.

In summary, the risk of predation has been demonstrated to have significant effects on the dynamics and evolution of mating systems. The presence of predators, in many cases, limits the amount of safe sexual advertisement and the extent of mate choice. Also, it may direct the evolution of sexual ornamentation and mate preferences. Although predation risk is the most widely studied cost of mate choice, there are other potential costs that may have similar effects on mating system dynamics and evolution.

2.3 – Mate searching and energetic expenditure

Searching for a mate can impose several costs: the energetic travel costs of seeking out a mate (Pomiankowski 1987b; Real 1990); the subsequent health risks that travel costs may impose on the individual (Pomiankowski 1987b; Lima & Dill 1990); the cost of mate assessment (Fawcett & Johnstone 2003); and the mortality or injury risks that come with conspicuous mate searching (Lima & Dill 1990). There are three, non-mutually exclusive strategies of mate sampling that can be used in mate searching and choice; the optimal strategy depends on the ecology and mate choice costs associated with the population in question. (i) The best-of-*n* strategy is where the chooser samples a number of mates and then chooses the one of the highest perceived quality (Janetos 1980). (ii) The one-step decision strategy is where the chooser samples mates until one is encountered that is of higher quality than the expected quality of mates that could be found with continued sampling (Janetos 1980). (iii) The partner-hold strategy is where the chooser continually compares a number of potential mates, always remaining with the superior of two consecutive potential mates (Sullivan 1994). Models of mate search theory have attempted to derive the most favorable of these strategies for particular populations, but most have had difficulty quantifying costs and/or obtaining concurring results (Janetos 1980; Real 1990; Slagsvold & Dale 1991).

Female pied flycatchers prefer mates that possess nests higher up in trees, because predation rates are greatest close to the ground (Alatalo *et al.* 1986). In a test of choice involving search costs, it was found that female pied flycatchers had smaller preference skews when higher search costs were present in the environment (Alatalo *et al.* 1987). In the low cost treatment of this experiment, males occupying boxes of various heights were placed at higher density, whereas in the high cost treatment boxes were positioned at greater distances from one another. As inter-box distance increased, mate search costs also increased. When it was energetically costly to choose the best mate (with the best territory), females in this experiment greatly reduced their mating skew and sampled far fewer males.

The minor costs of predation (0.1% annual survival cost) associated with sage grouse lekking were briefly mentioned above. Next I will discuss the search costs documented in that study (Gibson & Bachman 1992). One might expect there to be substantial energetic costs in traveling to a lek on several occasions and assessing groups of males. Females may trade-off such energetic costs with energetic reserves for laying and incubating eggs. However, like predation costs, energetic costs of mate choice at leks is small, a little more than 1% of the female sage grouse's daily field metabolic rate (Gibson & Bachman 1992). These findings can be applied to many lekking species as the number of predators encountered and distance traveled is similar across species (Bradbury *et al.* 1989). Once again, Gibson and Bachman (1992) conclude that the benefit of acquiring a superior mate at leks greatly outweighs the mate choice costs for female sage grouse.

As a result of mate searching, one may sustain injuries from con- and/or heterospecifics, for example due to territorial aggression. Theoretically, increases in mate searching raises the probability that the chooser may sustain an injury. This hypothesis was studied in the field with redlip blennies (*Ophioblennius atlanticus*). In this species of fish, females make several long-distance trips over the course of a few days to leave eggs in a male's care for fertilization. Large males are the preferred mates as they have proven to be better, more experienced parents (Côté & Hunte 1989; Côté & Hunte 1993). On these mate choice trips females were commonly found to encroach on the territories of damselfish (*Stegastes fuscus*, *S. partitus*, and *Micropathodon chrysurus*) and sustain injuries from these residents (Reynolds & Côté 1995). Females that traveled greater distances to leave their eggs with the preferred larger males also possessed more scars from damselfish attacks (Reynolds & Côté 1995). This study supports the notion that search costs need to be considered life threatening as well as energetically costly.

Another way to view mate choice is as an information gathering process whereby females base their choices on information that is costly to obtain (Sullivan 1994; Wikelski *et al.* 2001). If information is costly, then choosers should select from only a subset of potential mates and base their decision on incomplete information (Kokko & Lindström 1997). In most cases, collecting all possible information will be costly, and therefore selection should act to maximize the information gathering ability of choosers, within natural limitations (Sullivan 1994). The mate choice behavior of marine iguanas (*Amblyrhynchus cristatus*) on the Galápagos archipelago was studied in the field to test how search costs and information gathering affected their sexual activity (Wikelski *et al.* 2001). Both male and female marine iguanas were dispersed at varying population densities on cliffs and intertidal zones. Females of this species sample many males and preferably mate with larger males possessing the highest display rates. It was found that the females choosing mates in areas with a high density of males lost significantly more weight than those females sampling in areas of lower density (Wikelski *et al.* 2001). Females in areas of lightly dispersed males chose less active mates, but did not pay the cost of weight loss attributed to the energetic behavior of postural changes in response to male attention. This cost of weight loss may also represent a constraint on the evolution of costly mate choice.

With specific regard to the costs of mate searching, the only consistent conclusion is that higher search costs should result in a lower mating skew, e.g. a more restricted mate search with less sampling. In practice, however, search costs are difficult to isolate and measure, especially in natural populations. Consequently, there have been very few attempts at executing studies about the costs of mate searching. My thesis research, however, attempted to quantify the costs of mate sampling in a controlled, laboratory environment.

2.4 – Health risks and time expenditure

Mate choice increases the chance that individuals are exposed to diseases, especially sexually transmitted ones, and that they may be contracted from potential mates (Boots & Knell 2002). It may be expected that, depending on the incidence of disease, selection would lead to more monogamous situations or at least reduced mate choice. However, a theoretical model holds that as long as choice carries a fitness benefit, highly risky behavior and mate choice can persist in the face of disease along with the coexistence of safer strategies that carry little to no cost (Boots & Knell 2002).

Several forms of sexual activity may impair the functioning of the immune system (Kilpimaa *et al.* 2004). It was found that sexual advertisement, mate choice, and/or copulation may have detrimental effects on the immune system. Unmated male pied flycatchers exhibited a stronger mating effort and a reduced humoral immune responsiveness relative to mated males (Kilpimaa *et al.* 2004).

As mentioned previously, mate choice can be viewed as a costly information gathering process. Selection should act to maximize the information gathering of choosers within prevailing time constraints (Sullivan 1994). This process can take time and attention away from other necessary activities such as foraging, territoriality, and parental care. Neglecting critical life-history interests can certainly be considered a cost, perhaps not an immediate one, but their disregard will ultimately cause a reduction in fitness. Energy and resources must be allocated optimally among all life history activities, according to life-history theory (Kokko 1997; Höglund & Sheldon 1998).

In summary, the health of individuals seeking a mate may suffer, especially if that individual is choosy. Choosing a mate may increase exposure to diseased individuals or may impair the immune system. Additionally, the time spent in choosing a mate may be at the expense of other necessary activities. Neglecting activities such as foraging or parental care may have consequences that decrease health and overall fitness.

2.5 – The evolutionary importance of mate choice costs

So far, I have discussed several costs of mate choice in a manner that elucidates only their immediate impact. Predation and the risk of injury have been demonstrated to decrease levels of sexual advertisement and mating skew. Search costs associated with mate choice may also decrease mating skew as well as change mate sampling strategies. Personal health may suffer as a result of mate choice – the increased exposure to diseased individuals as well as the toll that mate choice has on the immune system are two such costs. Finally, mate choice may cause the neglect of necessary life history activities. These are all proximate effects (of one generation) associated with mate choice. However, all of these costs can have a substantial evolutionary impact on mating systems (Kokko *et al.* 2002; Fawcett & Johnstone 2003).

Kokko *et al.*'s (2002) model demonstrates that the two primary mechanisms of sexual selection by which female preferences arise ('good genes' and 'Fisherian runaway') can operate simultaneously, with their contributing weights dependent upon the magnitude of mate choice costs present in the environment (Kokko *et al.* 2002; Radwan 2002). In populations with high environmental costs of choice the model predicts that the 'good genes' mechanism will carry more weight. This is because when environmental costliness is high, only the individuals of the highest genetic quality will survive to attract a mate and reproduce. Low quality individuals die before reproducing. Therefore, choice will be acting under the 'good genes' mechanism with females choosing males that produce offspring of high genetic quality. When environmental costliness is low, 'Fisherian runaway' dominates since the majority of individuals will be capable of survival and elaborate sexual advertisement. Therefore, exaggeration of sexual ornamentation will evolve and females will choose the males that will produce the most attractive offspring. These notions have been replicated in other mate choice models (Iwasa *et al.* 1991; Pomiankowski *et al.* 1991).

Kokko *et al.*'s (2002) model specifically predicts that when costs of mate choice are high: (i) mating should be relatively random since mate choice is risky and costly; (ii) survival will be correlated with mate quality since all males must face the same environmental costs and only the best will survive; and (iii) offspring production will be reduced due to the heightened energy allocation to mate choice. Alternatively when costs of mate choice are low, the model predicts that: (i) mating skews will be higher since mate evaluation is inexpensive and thus easier to select the most attractive mates; (ii) there may be a negative correlation between quality and survival, because even the highest quality individuals must advertise more to attract a mate even if it results in high mortality rates exceeding that in the low quality individuals; and (iii) offspring production will be increased since energy reserves will be saved for offspring production (Kokko *et al.* 2002). Whether costs of mate choice are high or low, the model expects female choice to be capable of producing offspring of high reproductive value either by low mortality, sexual attractiveness, or both.

Another model specifically targets mate choice and its evolutionary consequences, when it is a process involving the costly assessment of multiple cues. The assessment of some traits may be more costly than others. This model uses a simple case where a ‘chooser’ faces a discrimination task involving two cues which vary in their accuracy and cost to assess (Fawcett & Johnstone 2003). Results of the model include the following predictions: (i) mating skew should be reduced when mate choice costs are high; (ii) cues should be prioritized depending on how choosy an individual is; (iii) less accurate cues may sometimes be evaluated (when costs of choice are low); and (iv) the importance of particular cues depends on the abundance of desirable mates (Fawcett & Johnstone 2003). These predictions are applicable to mate choice experiments where the costs of mate choice can be manipulated.

In combination, these two models make some important predictions about the evolutionary and behavioral consequences of costs of mate choice. When mate choice costs are high, mating within populations is predicted to be more random. This has been shown in a number of studies (Slagsvold & Dale 1991; Berglund 1993; Hedrick & Dill 1993; Godin & Briggs 1996). Also, the presence of mate choice costs can affect the appearance and overall fitness of animals within a population after several generations. For example, over evolutionary time high costs of mate choice can sharply reduce the number of sexual ornaments or conspicuous display elements possessed by individuals. Under high costs of choice, display becomes too costly to produce and assess, so these elements are eliminated. The opposite is true when environmental costliness is low; the amount of display ornamentation and behaviors may increase as their production and assessment is relatively inexpensive. Finally, the viability of offspring is predicted to be higher when mate choice costs are high. This is because, presumably, only individuals of high genetic quality survive to produce offspring under situations of high mate choice costs. Therefore, only offspring of individuals with high genetic quality will be produced. Alternatively, when mate choice costs are low, offspring are hypothesized to be of greater physical attractiveness but not necessarily of high genetic quality. When mate choice costs are low, males are under intense sexual selection pressure to evolve attractive, sexual ornamentation. Even individuals of low genetic quality can afford this ornamentation since environmental costliness is low. Therefore, low quality individuals may be selected to mate (instead of high quality individuals) simply because they have afforded attractive sexual ornamentation which will be inherited by their offspring. Thus, offspring produced under situations of low environmental choice costs may be attractive but not of high genetic quality. Demonstrations of these ideas are not available as no long-term studies of mate choice costs have ever been performed; this is a direction that needs to be explored as it is of central importance to sexual selection theory.

2.6 – Mate choice costs and this study

Mate choice costs play an important role in my thesis research with zebra finch sexual selection. Specifically, my project attempted to test the effect(s) that energetic costs of mate sampling had on mate selection and breeding performance. Energetic costliness of sampling was simulated by forcing females to traverse wall obstacles within a choice chamber to gain visual access to potential mates at separate ends. The cages simulating low energetic sampling costs lacked these obstacles and allowed for inexpensive mate assessment (an attempt at calculating the actual disparity in energetic expenditure between the two treatments can be found in the methods section). It is important to consider female choice with regard to zebra finches, because although the males typically initiate courtship, it is the females who make the final decision on whether or not to proceed with copulation and pair bond formation (Zann 1996).

Female mate preference in zebra finches is simple to recognize and quantify – females spend significantly more time in close proximity to preferred mates (Zann 1996). During this time, females may perform ritualized hopping displays between nearby perches in the presence of the male in order to communicate receptivity. Counting the number of hops on the closest perch to the stimulus male cage is a justifiable and commonly used measure of mate preference in zebra finch mate choice studies (Bennett *et al.* 1996). Another commonly used measure to quantify preference is the amount of time spent in 'display zones' nearest the stimulus males (Swaddle & Cuthill 1994b; Blount *et al.* 2003).

I had six predictions concerning the effects of sampling costs on the mating preferences and reproduction in zebra finches. The models mentioned in the previous section work under the assumption that both females and males endure the environmental costs of choice. However, in my experimental set-up only the females underwent this cost. My predictions were still based on these models; however, some of my predictions were customized to the premise of my experiment: (i) Higher energetic costs of mate sampling would result in more random preferences; i.e. lower preference skews. (ii) Higher energetic costs of mate sampling would result in a more restrictive mate searching strategy in which the females searched for potential mates relatively less. (iii) Higher energetic costs of mate sampling would result in less active sexual display activity by the choosing females. (iv) Higher energetic costs of mate sampling would result in a greater relative weight loss by the high cost females. (v) A larger quantity of viable offspring would be produced by the low cost breeding pairs since those females were predicted to more often select the superior male. Also, energy gain is positively correlated with fitness and population growth in zebra finches (Lemon 1991). Theoretically, females from the low cost treatment would expend less energy in mate choice and would be able to allocate more resources to offspring production. (vi) A higher perceived predation risk during breeding would result in delayed reproductive progress and lower reproductive output. To test this prediction, I observed reproductive behavior in two different breeding environments that varied in their level of cover, and presumably perceived predation risk (figure 3). An open, wire cage represented a more ‘vulnerable, high-predation' breeding environment, and an enclosed, wooden cage represented a more 'secure, low-predation' breeding environment. To test these predictions, I conducted mating trials and allowed one generation of breeding.

FIGURE 3

Photographs of an open wire breeding cage (left) (64 x 46 x 33 cm) and an enclosed, wooden breeding cage (right) (81 x 39 x 31 cm). A nest box is located on the left side of both cages.

CHAPTER 3

METHODOLOGY

3.1 - Costs of mate sampling

In this experiment I used 32 adult female and 64 adult male wild-type zebra finches, obtained from three or more separate commercial breeders. All birds were virgin, in good physical condition, and approximately the same age. All individuals were unfamiliar with birds of the opposite sex. Before the choice experiment began, I housed the birds in single-sex group cages (64 x 46 x 33 cm) on a constant 14:10 h light:dark photoperiod at approximately 20°C with food and water available *ad libitum*. All birds wore an individually-numbered, aluminum identification band on one leg.

This study began with 32 mate choice trials. In each trial, one female chose between two stimulus males. The 32 mate choice trials were equally divided into two treatment groups, low and high energetic costs of mate sampling. The energetic costs of mate sampling were manipulated by experimentally altering the ease with which the female could visit either of the two males at opposite ends of her choice chamber. Females in the high cost treatment had to traverse three barriers in the middle of their cages in order to obtain visual access to either male. Thus, these females paid a presumed energetic cost of mate sampling. The choice chambers in the low cost treatment lacked these three obstacles, which allowed these females to inexpensively (relative to high cost females) visit all areas of their cages to assess the stimulus males.

The mate choice cages were wooden chambers (81 x 39 x 31 cm) with completely enclosed tops, backs, and bottoms. The front of each chamber was comprised of steel bars. The two sides had large plexiglass windows to allow visual access to males in smaller, steel-bar cages (29 x 41 x 23 cm) at both ends of the female choice chamber (figure 2). Two stationary perches, a seed dish, and a water supply were located in the middle of the female choice chamber. At both ends of the female cage were another stationary perch and a recording perch (separated by 10 cm) attached to a microswitch (Coulburn Instruments, Inc., model V3L-2106-D8) linked through a switchboard (Coulburn Instruments, Inc., model H03-04) and a group of hardware links (Coulburn Instruments, Inc., model H02-08) to a PC. This microswitch recorded when a female hopped on or off the recording perch; i.e. when microswitch was opened or closed. Therefore, the microswitch perches allowed me to record remotely the number of hops each female performed in front of either stimulus male (Swaddle & Cuthill 1994b). The male cages contained food and water dishes, a stationary perch, and a microswitch perch that logged male display activity in an identical manner to the female display perches. The number of hops on the microswitch perches was used to infer the rate of male display activity. The female and male cages were situated so that when both the female and a stimulus male occupied their microswitch perches, the birds were no more than 15 cm apart.

The mate choice trials lasted 10 days. The experiment was conducted in two blocks of 16 females, as I only had enough equipment for 16 female choice chambers to run at one time. Sixteen trials (eight high cost and eight low cost) were performed between 14 June 2003 and 23 June 2003, and the remaining 16 (eight high cost and eight low cost) were performed between 30 June 2003 and 9 July 2003. Mate choice in this study was quantified by the number of hops females performed in front of each stimulus male. The male that received the most female display hops was assumed to be the most sexually attractive to that female, i.e. the 'chosen' male. This is a justifiable assumption as field observations have led to the conclusion that amount of time spent in proximity to potential mates indicates eventual mate preference (Zann 1996).

In the past, female mate choice in zebra finches has been quantified by two methods, either the time spent or the number of courtship hops near stimulus males. I collected data that could be applied to analyses by each of these methods, but decided to quantify mate choice only by the number of courtship hops. Previous experiments that quantified zebra finch mate choice by the amount of time spent near stimulus males did not last more than a few hours (Burley & Coopersmith 1987; Wynn & Price 1993; Collins *et al.* 1994; Swaddle & Cuthill 1994a; Swaddle & Cuthill 1994b; Bennett *et al.* 1996; Hunt *et al.* 1997). This short period of time allowed for video analysis of the mate choice experiment whereby non-sexual activity (sleeping, preening, etc.) performed near the stimulus males could be disregarded. The duration of my experiment (10 days) made this type of video analysis impractical; I had to rely on the data logged by the computer. Therefore, I would have been unable to eliminate non-sexual activity that may have added noise to my data. Zebra finches are known to fall asleep and execute long bouts of preening during experiments, potentially on the microswitch perches of my mate choice setup. The possibility of this happening eliminated the reliable use of mate choice quantification by time spent near the stimulus males.

The duration of my experiment (10 days) allowed me to analyze several facets of mate choice over an extended period of time. To the best of my knowledge, this is the longest recorded mate choice experiment involving zebra finches. I was able to determine if mate preference or the extent of mate preference changed during the experiment. Also, I tested for correlations between male phenotypes and attractiveness at different intervals of time throughout the experiment. I limited these types of analyses to three time markers: 1 hour, 1 day, and 10 days. I chose the 1 hour time interval, because a large proportion of zebra finch mate choice experiments have lasted for approximately one hour. Therefore, I could compare my results with already published results. The choices of 1 and 10 days are somewhat arbitrary, but the purpose was that they represented a moderate and an extreme extended period of time.

I placed all experimental birds in their cages the evening before commencing the mate choice trials. This was to ensure that the birds became accustomed to the experimental cages before the trials began. The birds were in visual isolation until the next morning as curtains covered the plexiglass windows at both ends of the female cages. I ran the experiment under a 14:10 h light:dark photoperiod. I used Graphic State (Coulbourn Instruments, Inc.) software version 2.101 (at a sampling rate of 0.1 s) to simultaneously record the display activity of all 48 birds (16 female, 32 male) during each block of the experiment. I lifted the curtains between the females and males when the lights turned on. Upon entering the experimental room, I always lowered the curtains between the females and males to prevent the formation of any negative association between my presence and any of the experimental birds. Three hours after 'dawn', when the lights turned on, females were caught and weighed to the nearest 0.01 g on a digital scale. Body mass data allowed me to interpret the effects of energetic costs of mate sampling (or lack thereof) on the condition of the females throughout the experiment. Recording the mass of 16 females took approximately 15 minutes each day.

Daily, at three hours, six hours, and nine hours after 'dawn' I randomly decided whether to switch the position of the stimulus males relative to the female chamber, or to leave them in place. This procedure safeguarded against the possibility that any female might exhibit a side bias towards one end of her cage instead of the male located at that end. Also, by changing the location of the males, the females were forced to search their environments for the 'new' location of any particular male. Hence, females would pay a mate sampling cost. If the males remained in the same position, I disturbed the males as if I had switched their positions. Therefore, three times each day, the relative positions of the males were either switched or sham-switched. Switching/sham-switching the position of the 32 males took approximately 10 minutes on each occasion. After weighing the females and/or switching/sham-switching the males' positions, I lifted the curtains and left the room. I halted data collection 12 hours after 'dawn' each day and lowered the curtains until the next morning. At this time, I refilled each male's food and water supply. Females were also given water *ad libitum*; however, their food supply was limited (10 g per day) to increase the probability that the energetic cost of mate sampling could not simply be overcome by excess nutritional intake. For one week prior to the experiment, I measured the exact amount of food eaten (to the nearest 0.01 g) by two female zebra finches in order to find out how much food to supply during the experiment. I found that amount to be 3.33 g (± 0.59 g) per bird, which is nearly identical to published data (Zann 1996). Ten grams of food is more than a zebra finch's daily diet requires, but this amount was carefully decided upon to prevent starvation and to allow for comfortable feeding out of the deep seed dishes used in this experiment.

After 10 days of choice trials, I summed the number of courtship hops performed by each female towards each stimulus male over the 10 day period and assigned a 'chosen' male and an 'unchosen' male. The 'chosen' male was the male that received the most courtship hops by the female and was assumed to be the most sexually attractive to that female. This male was placed in a cage with the female for breeding (section 3.2).

Two females from the high cost treatment died during experimentation, one in each experimental block. This resulted in sample sizes of N=14 from the high cost treatment and N=16 from the low cost treatment.

3.2 – Reproductive performance

After the 10 days of mate choice trials, I placed each experimental female and the respective 'chosen' male in a breeding cage, to examine the associations between mate sampling costs and reproduction. Each female and her 'chosen' male from the first block of the experiment were housed in wire cages (64 x 46 x 33 cm) where they were provided with a nest box (11 x 11 x 13 cm), hay for nest building, food and water *ad libitum*, and cuttlebone. Breeding birds from the second block of the experiment were housed in the wooden-sided cages used as female choice chambers (low cost) (81 x 39 x 31 cm) and were also provided with a nest box (13 x 10 x 9 cm), hay, food and water *ad libitum*, and cuttlebone.

I monitored nest building progress, egg laying, and offspring development at least once per week for more than eight months. Therefore, each week I was able to check for nest construction and count the number of eggs, hatchlings, and fledglings in each breeding cage. Six weeks after fledging, all offspring were separated from their parents and placed in single-sex cages as they were nutritionally independent. After five months, high-calcium grit and open water bowls were added to the cages of all breeding pairs with the hope of increasing their breeding success.

The two types of breeding cages used in this study differ in their openness to the environment and, therefore likely affected the perceived predation risk (Lima & Dill 1990; Hedrick & Dill 1993). Breeding pairs from the first block of the experiment were placed in more open cages than pairs from the second block. The perception of predation risk by the breeding birds has been shown to affect their breeding progress and reproductive output (Cresswell 1997; Groothuis & Schwabl 2002; Doligez & Clobert 2003). Consistent with results from these studies, I predicted that breeding pairs from the 'vulnerable, high-predation' cages would have relatively delayed reproduction and a lower reproductive output.

3.3 – Quantification of mate sampling costs

In this experiment, I assumed that the high cost females incurred a significantly higher energetic cost of mate sampling than the low cost females. Quantifying the energetic costs of mate choice has proven difficult in the past, as most studies have been performed in the field. However, this experiment was conducted in a more controlled environment, making it easier to estimate energetic costs. The average perch-to-perch flight cost of zebra finches has been reported as 2.24 watts (joules/second) (Hambly *et al.* 2002). This estimation is applicable to my study as the females typically maneuvered their choice chambers by hopping from perch to perch. Therefore, I observed female zebra finches in their experimental cages and used a stopwatch to find their average mate sampling time. The relative difference in the time of travel between the microswitch perches of each treatment's choice chambers provided an estimation of the relative energetic costs of mate sampling for the two treatments.

Following the completion of the experiment, I observed females traveling between the two microswitch perches in the female cage of each treatment group. The time to travel (in the air) from one end of the choice cage to the other was 0.323 s (±0.16 s) in the low cost set-up (cost: 2.24 W x 0.323 s = 0.724 J). Travel time (in the air) in the high cost treatment was approximately 2.23 s (±0.3 s) (cost: 2.24 W x 2.23 s = 5 J). There is a highly significant difference between the sampling times of the treatment groups (2 sample t-test, $t_{21}=21.491$, $P<0.00001$). This crude analysis suggests that mate sampling could be approximately seven times more energetically costly in the high cost treatment compared with the low cost treatment. In reality, the relative biological cost may be greater as females from the low cost treatment may simultaneously sample both males without traveling. Conversely, females from the high cost treatment must travel the length of the cage to sample both males.

I also recorded the mean travel time of five females between the microswitch perch and the neighboring stationary perch within the choice cages. I found this time to be approximately 0.15 s (cost: 2.24 W x 0.15 s = 0.336 J). The point of this analysis was to quantify the cost of courtship hopping for the females in this experiment.

3.4 - Male correlates of attractiveness

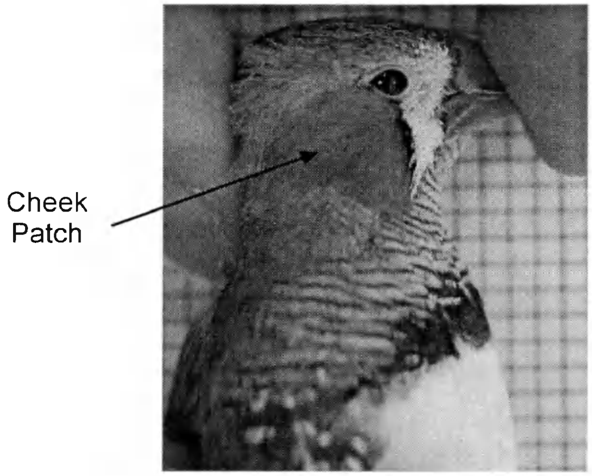
One month after the completion of the mate choice experiments, I collected and analyzed six phenotypes of each stimulus male to test for associations between these characteristics and sexual attractiveness. The phenotypes that were analyzed were: bill color, body size (estimated from primary feather length), cheek patch size, number of chest bars, chest badge size, and fluctuating asymmetry of primary feathers. All data were collected blind to experimental treatments.

(1) *Male bill color.* I used a hand-held reflectance spectrophotometer (Ocean Optics Inc., USB 2000 UV-VIS spectrophotometer) to determine the dominant wavelength of light reflected from the bill of each male. I took two measurements from each male. Ocean Optics software was used to analyze the data and record the average peak wavelength value from the two measurements.

(2) *Primary feather length.* Primary feathers IV and VI (position from distal edge) were plucked from both the left and right wings of each male. Length was measured with calipers to the nearest 0.001 cm. Feather length was used as an indicator of overall body size and as a measure of bilateral symmetry. The average of three measurements was used for each feather.

(3) *Cheek patch size.* I took digital photographs (Olympus Camedia E-20N, 5.0 megapixels) of the males' right cheek patch (figure 4) against a background of graph paper (to calibrate software). The camera was mounted a fixed distance from the bird and was perpendicular to both the bird and graph

FIGURE 4



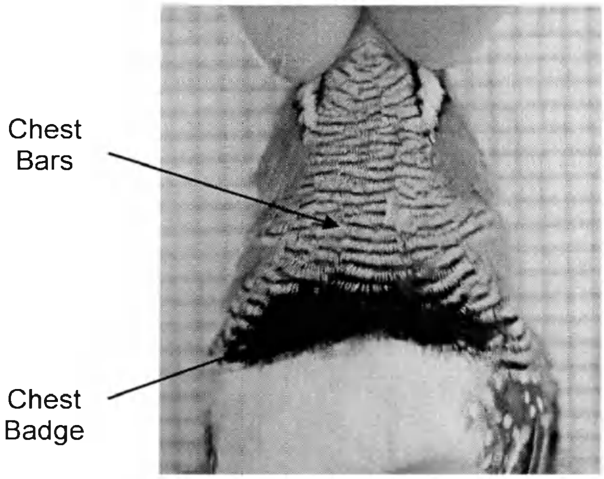
Photograph of a male zebra finch cheek patch. Each square of graph paper represents one mm^2.

paper. The birds were held in a standardized position by one researcher, JP Swaddle. Scion Image software was used to digitize the images and determine the internal area of the cheek patches. The average of two measurements was used for each male.

(4) *Chest bars*. Digital photographs were taken of the males' chest area (figure 5). A bilateral line was drawn down the chests of these black and white printouts (HP Lasterjet 5000N, 1200 dpi). The number of chest bars in intersection with this transect line were counted and used as a measure of chest bar quantity. The average of two counts was used for each male.

(5) *Chest badge*. The same black and white printouts from the chest bar analysis were used in this procedure. Pairs of males from the same choice trial were compared (blind to experimental outcome) to subjectively determine which male had the larger chest badge (figure 5). Two independent judgments were made for each comparison. Repeats never contradicted each other.

FIGURE 5



Photograph of a male zebra finch chest region. Each square of graph paper represents one mm^2.

Two males died before character measurements were taken. All measurements were taken from the dead birds and used in character analyses. The characters taken from these birds were within the normal range of characters taken from the live birds.

3.5 – Statistical analyses

I used SPSS 10.1 for the repeated-measures ANOVA analyses and Microsoft Excel for the 2 sample t-tests and correlation analyses in my experiment. Two-tailed tests were used in all analyses, and an alpha value of 0.05 was used to interpret significance in all cases. Bonferroni correction for multiple comparisons may be applicable to a number of my analyses. I did not apply the correction to any results, but do mention its potential effects when relevant.

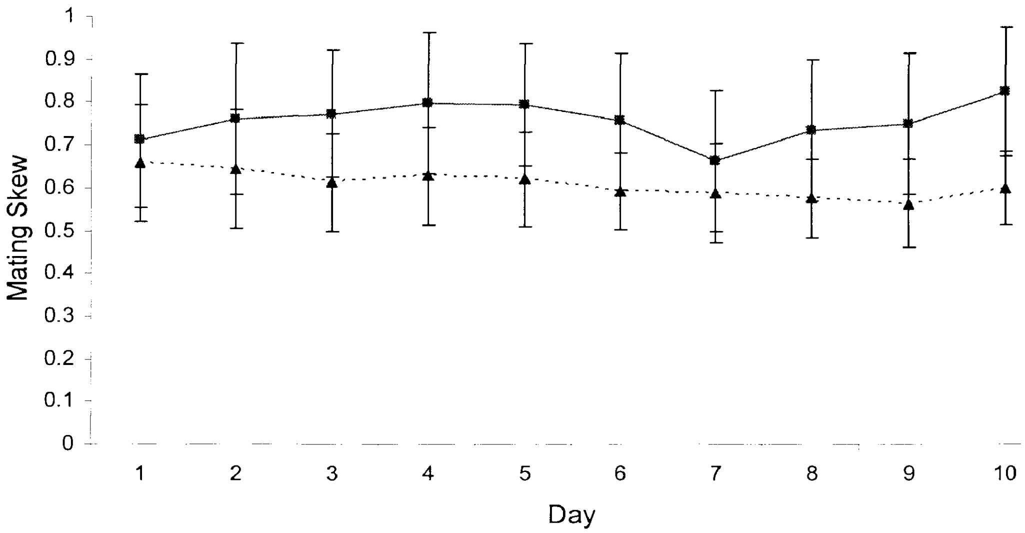
CHAPTER 4

RESULTS

4.1 – Costs of mate sampling and mating skew

Mating skew was defined as the proportion of hops directed towards a male during a specific time interval. For example, a mating skew of 52% during a time interval would mean that the female performed 52% of her hops in front of that particular male (and 48% in front of the alternate male). With a repeated-measures ANOVA (with day as the within-subject factor and treatment group as the between-subject factor), I found that the high cost treatment had a significantly larger overall mating skew over the course of the entire experiment, when considering each day as a data point (repeated-measures ANOVA, group effect, $F_{1,24}$=15.322, P=0.001, figure 6). I found that both treatments significantly varied their mating skew (by day) over the course of the experiment (day effect, $F_{9,216}$=2.968, P=0.002, figure 6). Specifically, females from the low cost treatment decreased their mating skew from day one to day nine (t_{28}=2.227, P=0.034, figure 6), and females from the high cost treatment decreased their mating skew from day four to day seven (t_{25}=2.128, P=0.043, figure 6) and increased their mating skew from day seven to day ten (t_{24}=2.66, P=0.014, figure 6). However, there were no differences in the manner of temporal variation of mating skew between the treatments (day-by-group interaction, $F_{9,216}$=1.581, P=0.122, figure 6).

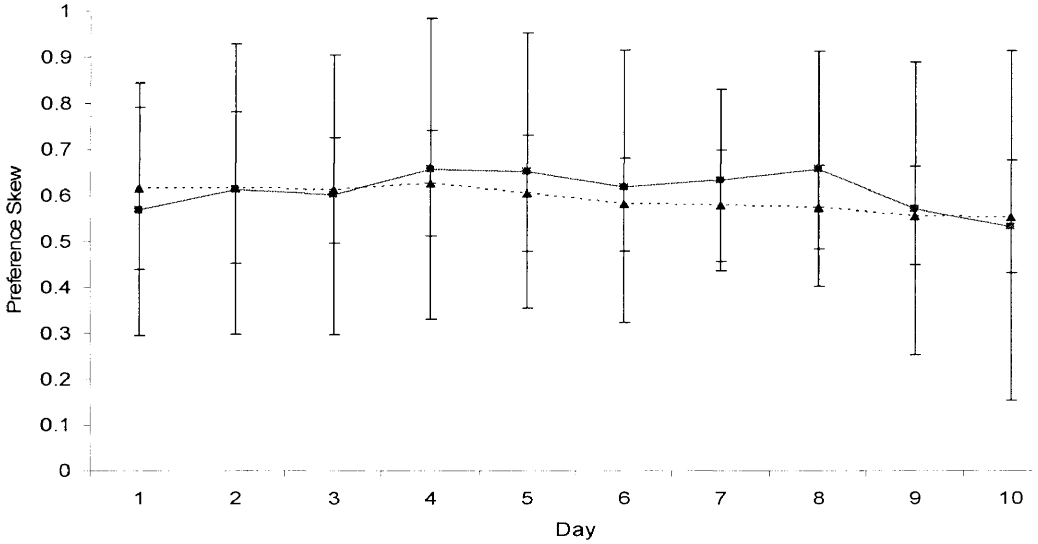
FIGURE 6



Mean female mating skew (±s.d.), by day, over the course of the 10 day experiment. The solid line represents the high cost treatment group. The dotted line represents the low cost treatment group. Both treatment groups varied their mating skew (by day) over the course of the experiment; the low cost females decreased their mating skew from day one to day nine and the high cost females decreased their mating skew from day four to day seven and increased their mating skew from day seven to day ten. The high cost treatment group had a larger overall mating skew when each day was considered a data point.

The previous analysis of mating skew did not identify a preference for the male 'chosen' overall, i.e. preference for one male versus the other may change over the experiment. Therefore, I analyzed preference skew (with regard to the 'chosen' male) for each treatment, by day, over the course of the experiment (figure 7). I performed this analysis based on the male that had the largest

FIGURE 7

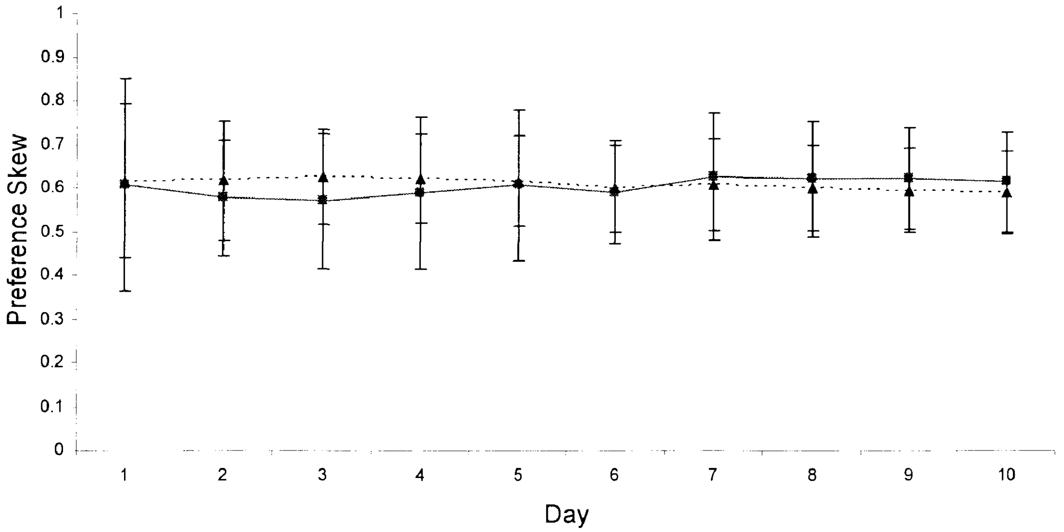


Mean female preference skew (±s.d.) for the eventually 'chosen' male (non-cumulative data points). The solid line represents the high cost treatment group. The dotted line represents the low cost treatment group. There were no differences between the treatment groups.

preference skew after 10 days, i.e. the 'chosen' male. With a repeated-measures ANOVA (as before), I found that there was no overall difference in 'chosen' male preference skew between the treatment groups (group effect, $F_{1,24}$=0.325, P=0.574, figure 7). I also found that the treatment groups did not differ significantly in their 'chosen' male preference skew (by day) over the course of the experiment (day effect, $F_{9,216}$=0.774, P=0.641, figure 7).

I performed a similar analysis with each data point as a cumulative measurement. In other words, the 'chosen' male preference skew plotted for each day was an inclusive measurement of preference for all preceding days. With a repeated-measures ANOVA (as before), I found that there was no overall difference in cumulative 'chosen' male preference skew between the treatment groups (group effect, $F_{1,24}$=0.005, P=0.943, figure 8). Also, the treatment groups did not differ significantly in their cumulative 'chosen' male preference skew (by day) over the course of the experiment (day effect, $F_{9,216}$=0.131, P=0.999, figure 8).

FIGURE 8

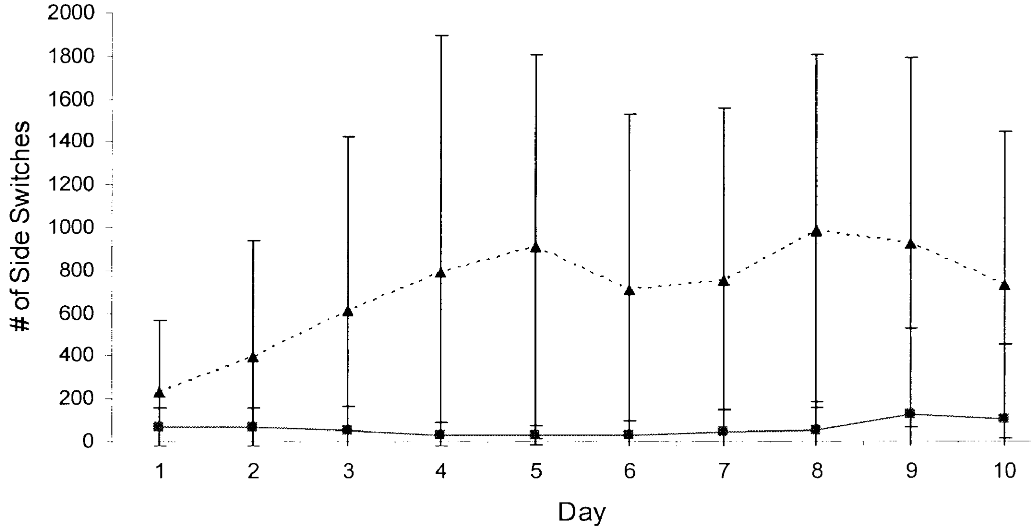


Mean cumulative female preference skew (±s.d.) for the eventually 'chosen' male. The solid line represents the high cost treatment group. The dotted line represents the low cost treatment group. There were no differences between the treatment groups.

4.2 – Costs of mate sampling and extent of female courtship activity

I analyzed female hopping activity at both ends of the choice chamber to determine how often the females traveled to opposite ends of the choice chamber each day. This analysis would reveal a crude measure of female energetic expenditure during the experiment. I found that the high cost females switched ends of the choice chamber 60.6 times (±133.5) each day, and the low cost females switched ends of the choice chamber 705.8 times (±710.6) each day (t_{16}=3.561, P=0.003, figure 9).

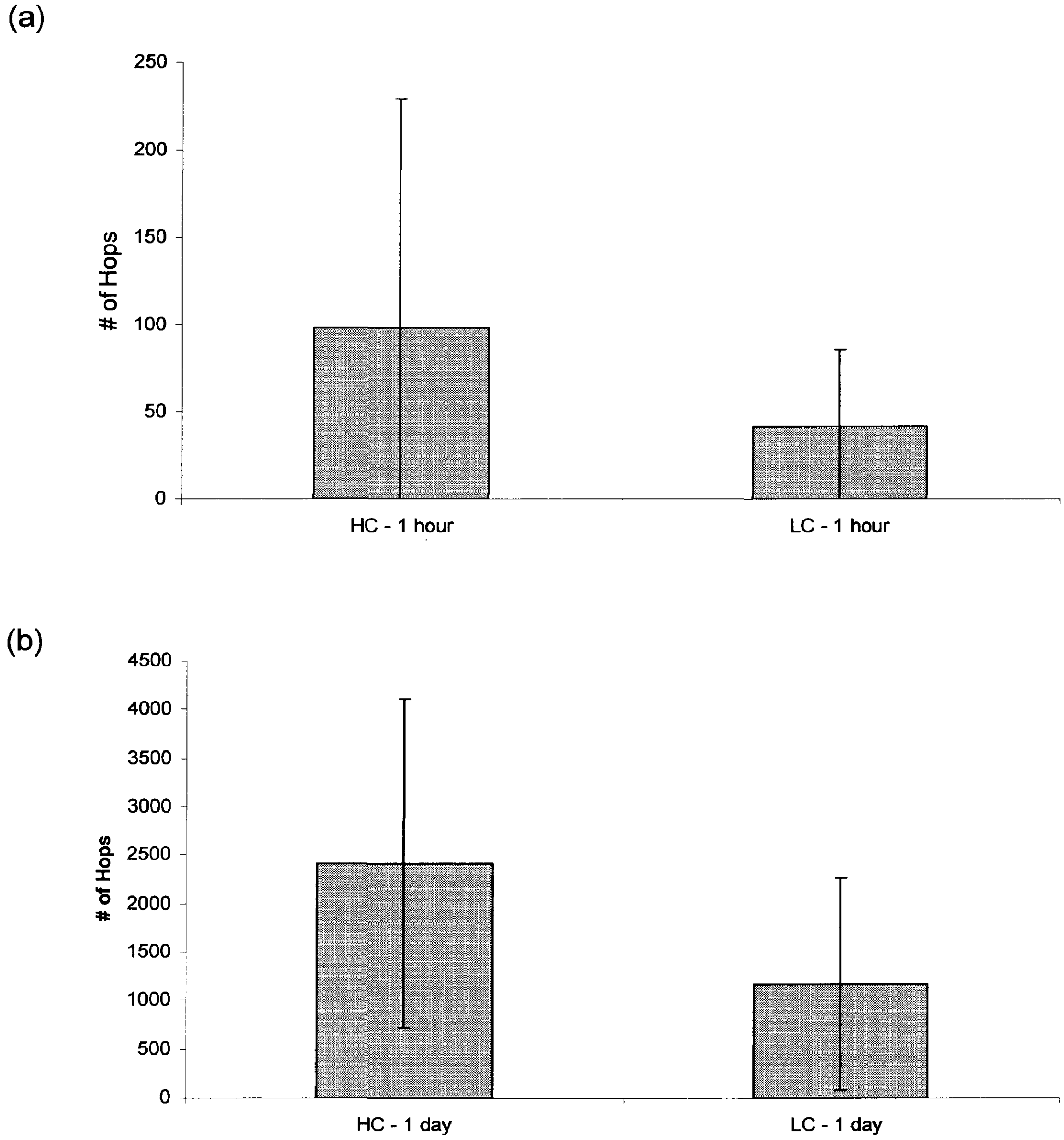
FIGURE 9



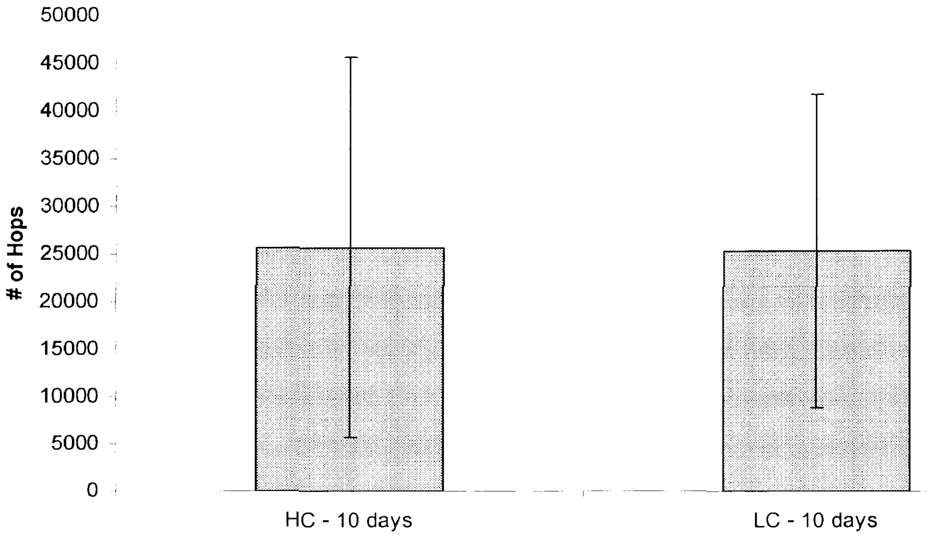
Mean female side switching (±s.d.) activity over the course of the 10 day experiment. The solid line represents the high cost treatment group. The dotted line represents the low cost treatment group. The low cost females switched sides significantly more often each day than the high cost females.

I also analyzed female courtship activity by counting the number of times they hopped on their microswitch perches. During the first hour of the experiment, there was no difference in the amount of hopping between the treatment groups (t_{16}=1.561, P=0.138, figure 10a). During the first complete day of the experiment, females from the high cost treatment performed more hops on display perches than low cost females (t_{22}=2.367, P=0.027, figure 10b). Over the entire 10 day experiment, there was no overall difference in the amount of female hopping between the treatment groups (t_{25}=0.045, P=0.964, figure 10c).

FIGURE 10


(a)
# of Hops
250
200
150
100
50
0
HC - 1 hour
LC - 1 hour
(b)
# of Hops
4500
4000
3500
3000
2500
2000
1500
1000
500
0
HC - 1 day
LC - 1 day

(c)

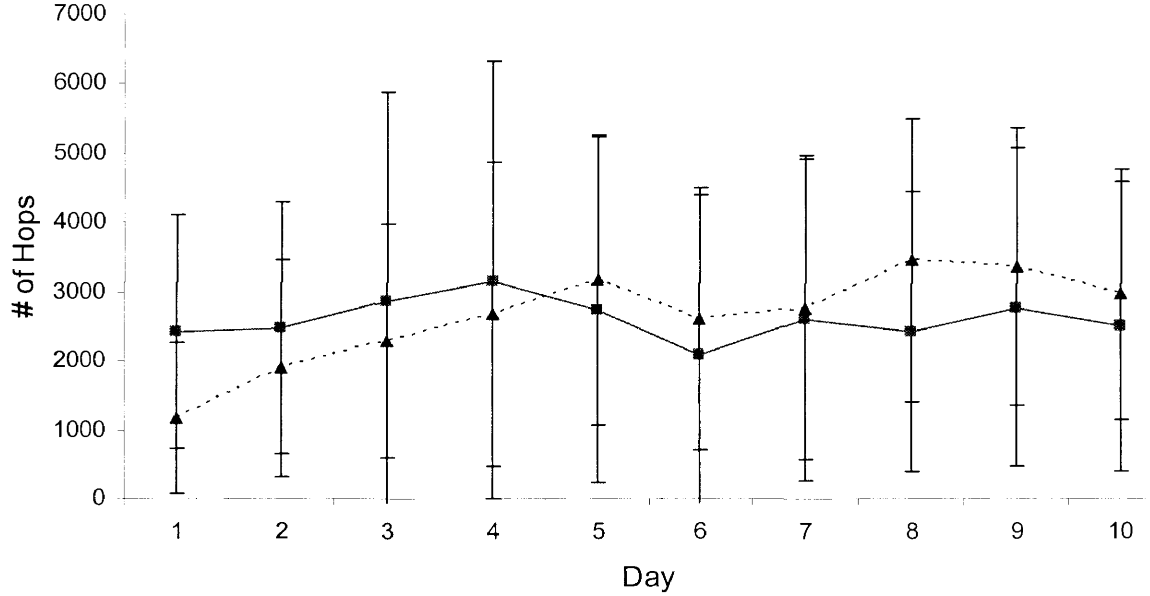


Mean female hopping activity (±s.d.) for each treatment group during (a) the first hour, (b) the first day, and (c) the entire experiment. High cost females performed more courtship hops than low cost females on day one of the experiment.

With a repeated-measures ANOVA (as before), I found that there was no overall difference in hopping activity between the treatment groups (group effect, $F_{1,24}$=0.23, P=0.636, figure 11). All females varied their hopping activity from day to day (day effect, $F_{9,216}$=2.362, P=0.015, figure 11). There was a difference in the manner of temporal variation of hopping activity between the treatment groups (day-by-group interaction, $F_{9,216}$=3.106, P=0.002, figure 11).

I recorded female activity on the display perches in four time blocks during each day: 0-3 hours after 'dawn', 3-6 hours after 'dawn', 6-9 hours after 'dawn', and 9-12 hours after 'dawn'. These data allowed me to examine 'time of day' effects on female activity throughout the experiment. With a repeated-measures ANOVA (with time block as the within-subject factor and treatment group as the between-subject factor), I found that there was no significant difference in overall

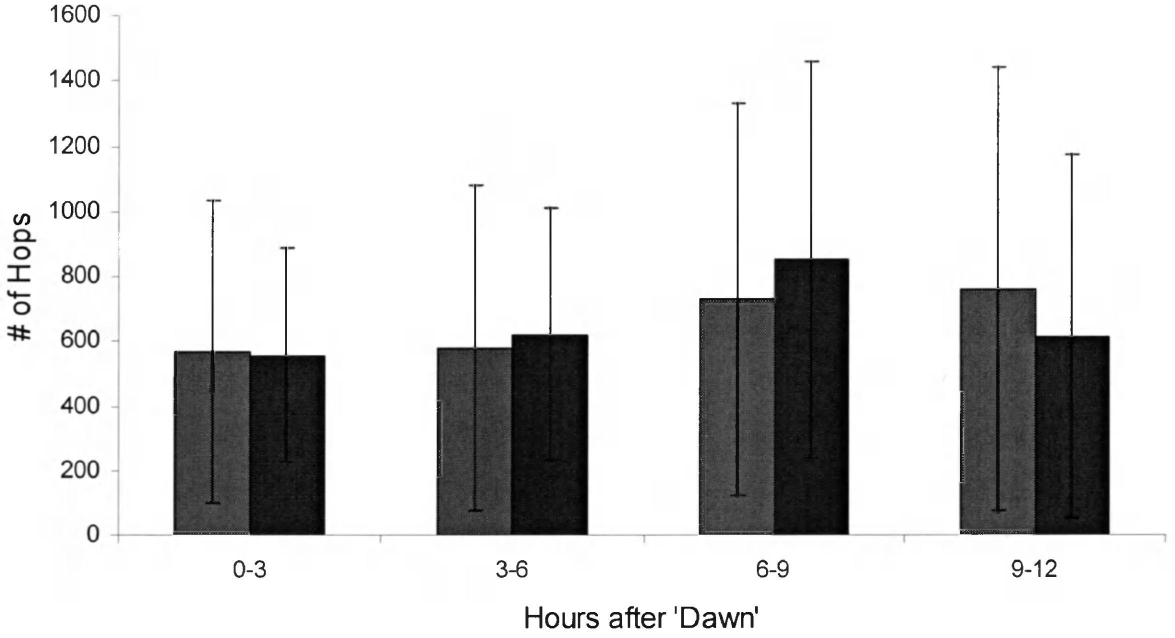
FIGURE 11



Mean female hopping activity (±s.d.), by day, over the course of the experiment. The solid line represents the high cost treatment group. The dotted line represents the low cost treatment group. All females significantly varied their hopping activity by day. There was a difference in the temporal pattern of hopping activity between the treatment groups.

female hopping activity between the treatment groups (group effect, $F_{1,28}=0$, $P=0.987$, figure 12). The female activity from both treatment groups differed between the time blocks (time block effect $F_{3,84}=3.577$, $P=0.017$, figure 12). Specifically, females hopped significantly more in time block three than in time block two (repeated-measures ANOVA limited to comparison of time block two and three, time block effect, $F_{1,28}=15.273$, $P=0.001$, figure 12).

FIGURE 12



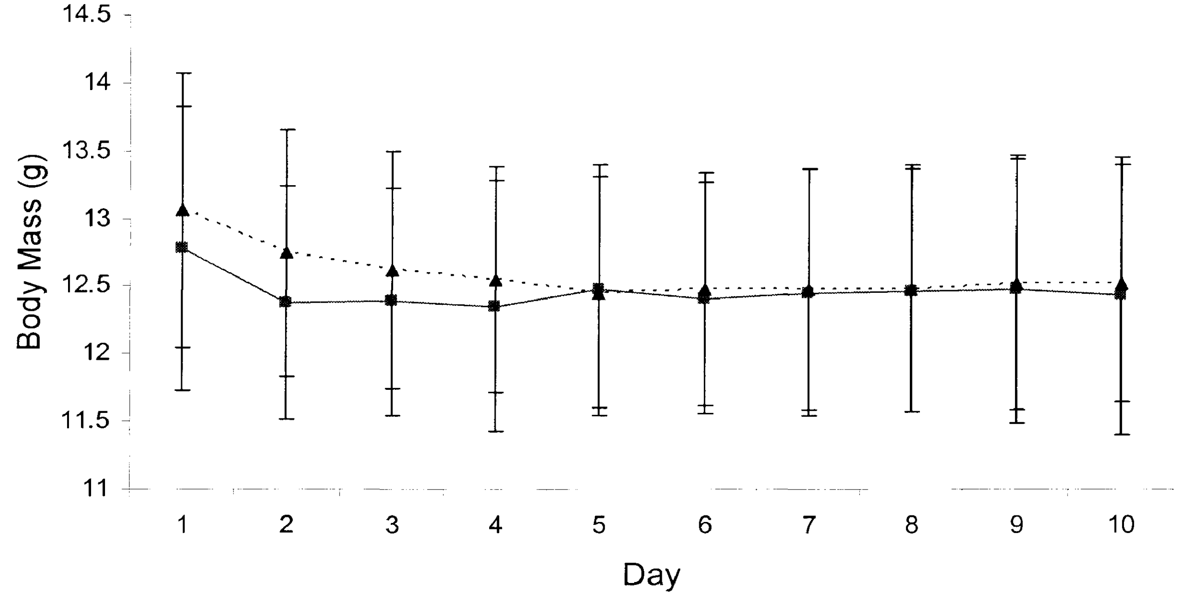
Mean female hopping activity (±s.d.) during each three-hour time block (for each treatment group). The light bars represent the high cost treatment group, and the dark bars represent the low cost treatment group. The x-axis signifies the four time blocks during the experimental days (0-3, 3-6, 6-9, and 9-12 hours after 'dawn'). Both treatment groups varied their display activity over the four time blocks, specifically between time blocks two and three.

4.3 – Costs of mate sampling and female body mass

Two females from the high cost treatment died during the experiment, reducing the sample size in this group to fourteen. Eleven of the 14 females from the high cost treatment and 13 of the 16 females from the low cost treatment lost body mass over the course of the mate choice experiment. Females from the high cost treatment had mean mass change of -0.35 g (±0.57 g), and females from the low cost treatment had a mean mass change of -0.54 g (±0.54 g) (figure 13). On average, females from the high cost treatment lost 2.6% (±4.2%) of their body mass, and females from the low cost treatment lost 4% (±4%) of their body mass (figure 13).

With a repeated-measures ANOVA (with day as the within-subject factor and treatment group as the between-subject factor), I found that there was no overall difference in within-individual mass change between the treatment groups (group effect, $F_{1,28}$=0.161, P=0.692, figure 13). All females significantly altered their mass during the experiment (day effect, $F_{9,252}$=9.531, P<0.001, figure 13), and there was a difference in the temporal pattern of mass change between the treatment groups. The low cost females lost mass from day two to day ten and the high cost females gained mass over that same time period (day-by-group interaction, $F_{9,252}$=1.999, P=0.04, figure 13).

FIGURE 13



Mean female body mass (±s.d.) over the course of the 10 day experiment. The solid line represents the high cost treatment group. The dotted line represents the low cost treatment group. Both treatment groups significantly changed body mass by day. The temporal variation of body mass change also varied between the treatment groups. Specifically, low cost females lost mass from day two to day ten, and high cost females gained mass during the same time period.

4.4 – Costs of mate sampling and reproductive performance

There were no significant differences between the breeding activities of the treatment groups following eight months of observation (table 1). However, there were two nearly significant trends in these analyses: (i) fledgling mortality was nearly greater in the low cost treatment group (% of fledglings that died before nutritional independence, t_8=2.091, P=0.07, table 1) and (ii) adult female mortality was nearly greater in the high cost treatment group; eight of the adult females from the high cost treatment (57%) and four from the low cost treatment (25%) died over the period of breeding observation (dead adult females per pair, t_{26}=1.816, P=0.081, table 1).

The number of days to clutch initiation (t_{14}=1.131, P=0.277, table 1), the number of eggs produced per pair (t_{27}=0.923, P=0.364, table 1), and the number of hatchlings produced per pair were no different between the treatment groups (t_{28}=0.392, P=0.697, table 1). Hatchling mortality (before leaving the nest) did not differ between the treatment groups (% of hatchlings that died before leaving the nest, t_9=0.59, P=0.569, table 1). Each treatment group produced nine fledglings over the length of breeding observation, 0.64 fledglings per pair (±1.34) in the high cost treatment and 0.56 fledglings per pair (±0.81) in the low cost treatment (fledglings per pair, t_{21}=0.195, P=0.847, table 1). The high cost treatment pairs produced eight independent fledglings, and low cost treatment pairs produced three independent fledglings (independent fledglings per pair, t_{17}=1, P=0.331, table 1).

TABLE 1

REPRODUCTIVE PERFORMANCE OF THE TREATMENT GROUPS

	High Cost	Low Cost	t Stat	P
Adult Female Mortality	0.57±0.51	0.25±0.45	1.186	0.081
Days to Clutch Initiation	35.1±23	54.8±56	1.131	0.277
Number of Eggs per Pair	5.1±3.4	6.4±4.6	0.923	0.364
Hatchlings per Pair	0.71±1.38	0.94±1.73	0.392	0.697
Hatchling Mortality	0.1±0.22	0.19±0.31	0.59	0.569
Fledglings per Pair	0.64±1.34	0.56±0.81	0.195	0.847
Fledgling Mortality	0.2±0.45	0.75±0.42	2.09	0.07
Ind. Fledglings per Pair	0.57±1.34	0.19±0.54	1	0.331

Breeding performance data comparison (±s.d.) between the treatment groups (high cost versus low cost). The t Stat and P value are direct comparisons between the treatment groups for that particular variable.

4.5 – Perceived predation risk of cages and reproductive performance

Breeding pairs in the enclosed, wooden cages were not more reproductively successful than pairs in the open, wire cages (table 2). The number of days to clutch initiation (t_{20}=0.468, P=0.645, table 2), the number of eggs produced per pair (t_{27}=1.255, P=0.22, table 2), and the number of hatchlings produced per pair (t_{18}=1.307, P=0.208, table 2) were no different between the breeding environments. Hatchling mortality did not differ between the two breeding environments (t_{9}=0.59, P=0.569, table 2). Breeding pairs from the wooden cages produced twice as many fledglings as pairs from the wire cages (0.8 ± 1.37 compared to 0.4 ± 0.63) (t_{20}=1.025, P=0.318, table 2). Fledgling mortality did not differ between the wire and wooden cages (t_{8}=0.578, P=0.579, table 2). Nine of the 12 fledglings from the wooden cages and two of six fledglings from the wire cages reached nutritional independence (t_{16}=1.294, P=0.214, table 2). Finally, adult female mortality in the wire cages (47%) was not different from the wooden cages (33%) (t_{28}=0.727, P=0.473, table 2).

TABLE 2

REPRODUCTIVE PERFORMANCE OF THE TWO CAGE TYPES

	Wire	Wooden	t Stat	P
Adult Female Mortality	0.47±0.52	0.33±0.49	0.727	0.473
Days to Clutch Initiation	40.3±27.3	47.9±52.2	0.468	0.645
Number of Eggs per Pair	4.9±4.3	6.7±3.8	1.255	0.22
Hatchlings per Pair	0.47±0.74	1.2±1.12	1.307	0.208
Hatchling Mortality	0.1±0.22	0.19±0.31	0.59	0.57
Fledglings per Pair	0.8±1.37	0.4±0.63	1.03	0.318
Fledgling Mortality	0.6±0.55	0.42±0.49	0.58	0.58
Ind. Fledglings per Pair	0.13±0.35	0.6±1.35	1.29	0.214

Breeding performance data comparison (±s.d.) between the two breeding environments (wire versus wooden). The t Stat and P value are results of a direct comparison between the breeding environments for that particular variable.

4.6 – Male correlates of attractiveness

With several repeated-measures ANOVAs (all with phenotype as the within-subject factor and treatment group as the between-subject factor), I tested for six phenotypic differences between all of the 'chosen' and 'unchosen' males over three time intervals (1^{st} hour, 1^{st} day, and 10 days) (table 3). I also tested for differences in the sexual preferences between the high and low cost treatment groups (table 4). These analyses would reveal which male phenotypes were most correlated with sexual attractiveness and also if the simulated costs of mate sampling had an effect on the females' mating preferences.

TABLE 3

MALE PHENOTYPIC DATA OF 'CHOSEN' AND 'UNCHOSEN' MALES

	'Chosen'	'Unchosen'	F	P
Bill Color - 1 h	661.8±17.9	662.4±21.3	0.152	0.699
Bill Color - 1 d	660.9±19.4	663.8±19.4	0.281	0.6
Bill Color - 10 d	654±16.3	670.7±18.7	14.045	0.001
Cheek patch size - 1 h	1.044±0.155	1.113±0.139	3.319	0.08
Cheek patch size - 1 d	1.061±0.169	1.087±0.137	0.791	0.381
Cheek patch size - 10 d	1.067±0.162	1.081±0.146	0.193	0.664
# Chest Bars - 1 h	26±4.4	25.1±3.8	0.539	0.47
# Chest Bars - 1 d	25.5±3.3	25.7±4.7	0.038	0.846
# Chest Bars - 10 d	26±3.1	25.2±4.8	1.044	0.316
Feather length (cm) - 1 h	4.748±0.124	4.781±0.122	1.178	0.289
Feather length (cm) - 1 d	4.756±0.116	4.775±0.133	0.07	0.794
Feather length (cm) - 10 d	4.76±0.136	4.771±0.111	0.12	0.732
Symmetry (%FA) - 1 h	0.024±0.014	0.026±0.035	0.175	0.68
Symmetry (%FA) - 1 d	0.02±0.014	0.028±0.035	1.649	0.211
Symmetry (%FA) - 10 d	0.023±0.015	0.026±0.035	0.077	0.784
Display (# hops) - 1 h	102.6±76.9	128.3±185.2	0.188	0.668
Display (# hops) - 1 d	1966±1683	1581±1096	1.33	0.259
Display (# hops) - 10 d	30054±18290	27500±18782	0.359	0.554

	'Chosen'	'Unchosen'	t Stat	P
Chest Badge (larger) - 1 h	17	11	1.61	0.113
Chest Badge (larger) - 1 d	15	15	0	1
Chest Badge (larger) – 10 d	11	19	2.11	0.039

Male phenotypic data of all 'chosen' and 'unchosen' males at 1 hour, 1 day, and 10 days. Bill color was measured in nanometers; cheek patches were measured in cm^2; chest badges were subjectively compared; the number of chest bars was counted; a mean of two feather lengths was used to estimate body size and fluctuating asymmetry; and the number of hops inferred display rate. The F value, t Stat, and P value are results of a direct comparison between the 'chosen' and 'unchosen' male phenotype. I expect 1 out of 20 analyses to be significant by chance; therefore, 1 or 2 of the significant results among these 21 analyses may be the result of multiple comparisons.

During the first hour of the experiment, the bill color preferences of the treatment groups were nearly statistically different ('chosen' status-by-group effect, $F_{1,26}$=3.749, P=0.064, table 4), with high cost females preferring males possessing duller red bills and low cost females preferring males with brighter red bills. Also during the first hour of the experiment, ‘unchosen’ males nearly had larger cheek patches than ‘chosen’ males (‘chosen’ status effect, $F_{1,26}$=3.319, P=0.08, table 3). There was a nearly significant difference in the preferences of the treatment groups with regard to male display rate during the first hour of the experiment. High cost females preferred males that performed relatively more display hops, and low cost females preferred males that performed relatively fewer display hops (‘chosen’ status-by-group effect, $F_{1,26}$=3.867, P=0.06, table 4). During the first day of the experiment, the cheek patch size preferences of the treatment groups were different; high cost females preferred males possessing relatively smaller cheek patches and low cost females preferred males with relatively larger cheek patches (‘chosen’ status-by-group effect, $F_{1,28}$=8.489, P=0.007, table 4). Over the course of the entire experiment, ‘unchosen’ males had brighter red bills than ‘chosen’ males (‘chosen’ status effect, $F_{1,28}$=14.045, P=0.001, table 3). Also over 10 days, there was a nearly significant difference in the chest bar preferences between the treatment groups. High cost females preferred males with relatively more chest bars and low cost females preferred males possessing relatively fewer chest bars (‘chosen’ status-by-group effect, $F_{1,28}$=3.124, P=0.088, table 4). Lastly, using a 2 sample t-test, I found that ‘unchosen’ males had relatively larger chest badges than ‘chosen’ males with regard to mating preferences over the course of the experiment (t_{58}=2.11, P=0.039, table 3).

TABLE 4

COMPARISON OF LOW COST AND HIGH COST PREFERENCES

	LC 'Chosen'	LC 'Unchosen'	HC 'Chosen'	HC 'Unchosen'	F	P
Bill Color - 1 h	661.7±20	653.5±22.6	661.8±15.5	674.2±12.1	3.749	0.064
Bill Color - 1 d	656.2±19.7	659±23.5	666.3±18.3	669.3±11.9	0	0.984
Bill Color - 10 d	649.1±17.1	666.1±22.4	659.7±13.9	676±12.8	0.005	0.942
Cheek patch size - 1 h	1.069±0.149	1.107±0.128	1.012±0.164	1.122±0.158	0.782	0.384
Cheek patch size - 1 d	1.125±0.142	1.02±0.127	0.987±0.171	1.129±0.14	8.489	0.007
Cheek patch size - 10 d	1.106±0.156	1.069±0.119	1.022±0.162	1.095±0.175	1.747	0.197
# Chest Bars - 1 h	26.3±4.7	24.4±3.8	25.5±4.01	26±3.84	1.549	0.224
# Chest Bars - 1 d	25.4±3.1	25.3±5.4	25.6±3.6	26.1±3.9	0.149	0.702
# Chest Bars - 10 d	25±3	25.7±5.4	27.1±2.9	24.6±4.1	3.124	0.088
Feather length (cm) - 1 h	4.736±0.139	4.752±0.113	4.762±0.107	4.82±0.128	0.188	0.669
Feather length (cm) - 1 d	4.76±0.113	4.728±0.137	4.75±0.123	4.823±0.114	2.107	0.159
Feather length (cm) - 10 d	4.725±0.13	4.768±0.117	4.8±0.135	4.775±0.11	0.459	0.504
Symmetry (%FA) - 1 h	0.026±0.015	0.022±0.018	0.022±0.013	0.031±0.05	0.727	0.402
Symmetry (%FA) - 1 d	0.02±0.015	0.028±0.018	0.02±0.014	0.029±0.046	0.134	0.718
Symmetry (%FA) - 10 d	0.026±0.016	0.022±0.017	0.02±0.014	0.03±0.048	1.511	0.23
Display (# hops) - 1 h	118.8±85.2	205.3±215.2	81±61.1	25.8±30.7	3.867	0.06
Display (# hops) - 1 d	2508±1898	1997±1122	1346±1177	1106±878	0.172	0.681
Display (# hops) - 10 d	33677±18515	33137±16253	25912±17779	21057±19958	0.23	0.635

	LC 'Chosen'	LC 'Unchosen'	HC 'Chosen'	HC 'Unchosen'	t Stat	P
Chest Badge (larger) - 1 h	10	6	7	5	0.215	0.832
Chest Badge (larger) - 1 d	8	8	7	7	0	1
Chest Badge (larger) - 10 d	8	8	3	11	1.66	0.108

Male phenotypic data of low cost 'chosen' and 'unchosen' males and high cost 'chosen' and 'unchosen' males. Bill color was measured in nanometers; cheek patches were measured in cm^2; chest badges were subjectively compared; the number of chest bars was counted; a mean of two feather lengths was used to estimate body size and fluctuating asymmetry; and the number of hops inferred display rate. The F value, t Stat, and P value are results of a direct comparison between the preferences of the treatment groups. Significant results indicate opposite preferences between of the treatment groups. I expect 1 out of 20 analyses to be significant by chance; therefore, the 1 significant result among these 21 analyses may be the result of multiple comparisons.

I analyzed several phenotypes of the stimulus males within individual choice trials to determine if the two opposing males were different (table 5). I found that there was little difference between opposing males with regard to bill color, cheek patch size, the number of chest bars, and body size (table 5). However, there was a great deal of phenotypic variability when comparing fluctuating asymmetry and display rate (table 5).

TABLE 5

WITHIN-TRIAL DIFFERENCES IN MALE PHENOTYPES

	Bill color	Cheek patch	Chest bars	Body size	Symmetry	Display 1h	Display 1d	Display 10d
Mean	3.45%	17.93%	15%	3.18%	76.80%	108.67%	71.75%	64.49%
S.D.	2.72%	12.65%	13%	2.40%	56.72%	70.80%	46.76%	45.66%

Mean relative difference of eight phenotypes between the two opposing males within individual choice trials. The relative difference was calculated by dividing the absolute difference between the phenotypes of the two males by the mean of the phenotypes of the two males. Bill color was measured in nanometers; cheek patches were measured in cm^2; the number of chest bars was counted; a mean of two feather lengths was used to estimate body size and fluctuating asymmetry; and the number of hops inferred display rate.

4.7 – Correlation of male phenotypes

I used a correlation analysis to test for significant associations between six male phenotypic characteristics: bill color, cheek patch size, number of chest bars, body size (estimated from primary feather length), fluctuating asymmetry of primary feathers, and display rate (after one hour, one day, and 10 days) (table 6). This test would determine, for example, if males with more chest bars also had larger cheek patches. I found that males with redder bills (largest reflectance wavelength) had a lower display rate during the first day of the experiment ($r=0.287$, $P=0.024$, table 6). I found that larger males (longer primary feathers) had larger cheek patches (r=0.301, P=0.017, table 6). I also found that male display rate on day one was significantly correlated with display rate over the entire experiment (r=0.596, P<0.0001, table 6).

TABLE 6

MALE PHENOTYPIC CORRELATIONS

	Bill	Cheek	Bars	Size	FA	1 h Disp	1 d Disp
Cheek	0.054	-	-	-	-	-	-
Bars	-0.058	0.212	-	-	-	-	-
Size	0.146	0.301	0.227	-	-	-	-
FA	0.155	-0.16	0.082	-0.212	-	-	-
1 h Disp	-0.245	-0.016	-0.087	-0.191	-0.097	-	-
1 d Disp	-0.287	0.061	0.082	-0.075	-0.16	0.215	-
10 d Disp	-0.253	-0.056	0.162	-0.19	0.075	0.078	0.596

Male phenotypic correlations of all males. Highlighted Pearson correlation coefficients are P<0.05. All rows of the correlation analysis have a sample size of N=60 except for the 1 hour display (N=56). I expect 1 out of 20 analyses to be significant by chance; therefore, 1 or 2 of the significant results among these 34 analyses may be the result of multiple comparisons.

CHAPTER 5

DISCUSSION

5.1 – Costs of mate sampling and mating skew

I predicted that higher energetic costs of mate sampling would result in high cost females selecting mates relatively randomly, i.e. smaller preference skews than low cost females (Berglund 1993; Andersson & Iwasa 1996; Kokko *et al.* 2002). I found no support for this prediction as high cost females formed stronger mating skews from day to day (figure 6), and when these preferences were analyzed with respect to male identity there were no significant differences between the treatment groups (figures 7 & 8).

The mating skew of both treatment groups changed over the course of the 10 day experiment (figure 6). These data suggest that the preferences were somewhat arbitrary, and that each day represents a sample from an arbitrary distribution of apparent preferences. I found that the high cost treatment had a larger overall mating skew, when considering each day as a data point (figure 6). However, these preferences may have been for different males on different days. I had to perform analyses that took regard to male identity to find out if these preferences were consistent.

I analyzed the 'chosen' male preference skew and found that neither treatment varied their 'chosen' male preference skew by day, and that there was no overall difference between the treatment groups (figures 7 & 8). Therefore, there is no support for the notion that high cost females exhibited more random mating preferences than low cost females. Also, since all females did not alter their 'chosen' male preference skew by day, there may be evidence that female zebra finches do not significantly change their mating preferences over (10 days) time (figures 7 & 8).

5.2 – Costs of mate sampling and extent of female courtship activity

I predicted that higher energetic costs of mate sampling would result in less active sexual courtship activity by high cost females (Alatalo *et al.* 1987; Pomiankowski 1987b; Real 1990; Sullivan 1994; Kokko & Lindström 1997; Wikelski *et al.* 2001), i.e. high cost females would perform fewer hops on the microswitch perches. I found no support for this prediction as there was no overall difference in hopping activity between the treatment groups (figures 10, 11 & 12). I also predicted that higher energetic costs of mate sampling would result in a more restrictive mate searching strategy whereby high cost females would less actively seek out potential mates (Janetos 1980; Pomiankowski 1987b; Lima & Dill 1990; Sullivan 1994; Gibson & Langen 1996; Kokko *et al.* 2002). I found significant support for this prediction as high cost females traveled the length of their cage much less often than low cost females (figure 9).

There was no overall difference in hopping activity between the treatment groups; however, high cost females performed more display hops on day one than low cost females (figures 10 & 11). This may be due to the nature of the female choice chambers. High cost females may have been effectively confined to the ends of the cages since those are the only locations that they could evaluate the stimulus males. Low cost females could see both males from any position in their cages, so they did not have to spend equal time on the microswitch perches to efficiently assess the males.

I found significant evidence that high cost females had a more restrictive mate sampling strategy than low cost females – low cost females switched ends of their cages much more frequently. The high cost females' tendency to remain at one end of the choice chamber is evidence that the costs of mate sampling effectively altered the manner in which they sampled mates (Janetos 1980; Sullivan 1994).

By combining hopping and side switching data with their respective energetic costs (section 3.3), I was able to estimate both groups' average daily energy expenditure on mate sampling. High cost females spent approximately 1187 J ± 1280 J, and low cost females spent approximately 1398 J ± 1006 J on mate sampling each day. Thus, both treatment groups spent approximately the same amount of energy in mate selection, even though their strategies of mate sampling were different (group comparison of energetic expenditure, t_{25}=0.498, P=0.623).

I conclude that the visual barriers in the 'high cost' female cages resulted in a more restrictive mate sampling (figure 9). My results may have a significant impact on mate choice studies where the 'chooser' must expend energy to gain visual access to the stimulus mates. When there are costs to sampling mates, the mate sampling strategy of the 'chooser' may be significantly altered.

5.3 – Costs of mate sampling and female body mass

I predicted that higher energetic costs of mate sampling would result in a greater relative body mass loss by the high cost females. I made this prediction because I thought that high cost females would expend relatively more energy during this experiment than low cost females (Janetos 1980; Real 1990; Sullivan 1994; Kokko *et al.* 2002). My prediction was not met as there was no overall difference in within-individual mass change between the treatment groups (figure 13). However, my results match a crude calculation of energetic expenditure due to mate sampling from the previous section. These data revealed that both treatment groups spent approximately the same amount of energy each day, so it makes sense that there was no difference in mass change between the groups.

From day five until day 10 of the experiment, the body mass trajectories of the treatment groups were nearly identical (figure 13). However, high cost females had a sharp drop in mass from day one to day two and then leveled off over the rest of the experiment, whereas low cost females had a steady drop in mass until day five and then leveled off until day ten (figure 13). I propose that after several days of experimentation, females from both treatment groups adopted mate sampling strategies, unique to their environments, which maintained their body mass at the same threshold level. In this case, low cost females slightly increased their courtship activity until day five, and high cost females did not noticeably change their mate sampling activity (figures 9 & 11). High cost females performed more courtship hops on day one than low cost females (figure 10b), which may account for the disparity in mass loss from day one to day two (figure 13). The fact that the courtship activity (total number of hops) and overall mass loss of high and low cost females were roughly the same after 10 days further suggests that both treatment groups developed mate sampling strategies in response to the inherent sampling costs of their environments. All data points to high cost females spending the majority of their time at one end of the cage with infrequent visits to the opposite side. In contrast, the low cost females did not exhibit a bias for one side of the choice chamber and made many trips to both ends of the cage each day. These strategies and their associated energetic expenditure seem to account for the changes in female body mass over the course of the experiment.

In conclusion, this study provides evidence that individuals may immediately adopt behavioral strategies to maintain their physical health (in this case, body mass) when environmental costs of mate choice dictate that a change is necessary (Janetos 1980; Real 1990; Sullivan 1994; Andersson & Iwasa 1996; Kokko *et al.* 2002; Fawcett & Johnstone 2003). Since mate sampling was energetically inexpensive for low cost females, they were able to switch sides of their choice chamber (sample mates) frequently. Mate sampling was energetically expensive for high cost females, so they adjusted to their environmental cost by sampling alternative males less often.

5.4 – Costs of mate sampling and reproductive performance

After the choice experiment, I placed each female and her 'chosen' male together in cages for breeding. I predicted that a larger quantity of viable offspring would be produced from the low cost treatment since those females were predicted to more often select the superior male (Andersson & Iwasa 1996; Kokko *et al.* 2002; Fawcett & Johnstone 2003). I found no support for this prediction (table 1).

There were no significant differences in the breeding performance of the high and low cost breeding pairs (table 1). However, the adult female mortality of the high cost treatment was almost significantly greater than the low cost treatment (table 1). This near significant result could make sense for two reasons. (i) The costs of mate sampling may have affected the health of high cost females. However, there was little difference in energetic expenditure between the treatment groups. (ii) The costs of mate sampling in the 'high cost' cages resulted in uninformed mate selection and subsequent violence directed towards the females. However, this is not the case here as aggression was rare and equally observed (two instances each) between the treatment groups. Therefore, the only explanation that I can offer for this nearly significant result is that the costs other than energy expenditure of the 'high cost' environments imposed upon the health of those females.

My original plan for this study was to continue for two or more generations of choice trials and subsequent breeding sessions. However, offspring production from the first breeding experiment was less plentiful than expected.

So, I was unable to test for the extended evolutionary effects of mate choice costs on reproductive performance. It would be interesting to continue this line of testing for several generations to see if and when the mate choice costs take effect.

5.5 – Perceived predation risk of cages and reproductive performance

I predicted that a higher perceived predation risk during breeding would result in delayed reproductive progress and lower reproductive output (Cresswell 1997; Groothuis & Schwabl 2002; Doligez & Clobert 2003). To test this prediction, I observed the reproductive behavior of 30 breeding pairs (16 low cost and 14 high cost) in two different breeding environments that varied in their level of cover, and presumably perceived predation risk (figure 3). To the best of my knowledge, this was the first experiment to examine the effects of perceived predation risk on breeding performance in a laboratory setting.

I did not observe any significant differences in the reproductive progress or output between the two breeding environments (table 2). However, I found several results to be consistently, however non-significantly, matched in the direction of my prediction, i.e. larger reproductive output in the enclosed, wooden cages. Breeding pairs from the wooden cages nearly produced more eggs, hatchlings, and independent fledglings than breeding pairs from the open, wire cages (table 2). Perhaps with a larger sample size, these differences in reproductive output may have been closer to significance and similar to the results provided by previous studies (Cresswell 1997; Groothuis & Schwabl 2002; Doligez & Clobert 2003).

My results provide speculative evidence that zebra finches may invest more energy and attention to offspring production and parental care when the perceived risk of predation is relatively low since there is little risk of losing offspring to a predator. Conversely, zebra finches may decrease their reproductive effort when the risk of predation is relatively high since there is a good chance that the energy and time devoted to offspring production may be sacrificed. Hence, predation risk may have a strong evolutionary effect on the breeding ecology of zebra finches, among other species.

5.6 – Male correlates of attractiveness

In this experiment, there were two ways that I analyzed male phenotypic correlates of attractiveness. (i) I combined the preferences of all females (high and low cost) and then compared the phenotypic attributes of all 'chosen' and 'unchosen' males (table 3). This method provided the largest sample size but may have produced questionable results if there were, in fact, significant differences between the preferences of the treatment groups. (ii) I compared the phenotypic attributes of the 'chosen' and 'unchosen' males from both treatment groups and then compared those differences between the treatment groups (table 4). This analysis determined if the simulated costs of mate sampling affected the sexual preferences of the females in the two treatments. I also compared the within-trial differences in male phenotypes, and found that there was little variability with regard to bill color, body size, cheek patch size, and the number of chest bars (table 5). So, the lack of choosiness with respect to these phenotypes may be due to an overall lack of variability between the stimulus males.

My first prediction was that females, throughout the experiment, would have sexual preferences for the males with the brightest red bill color (Burley & Coopersmith 1987; Hill 1991; Johnson *et al.* 1993; Sundberg 1995; Blount *et al.* 2003; McGraw *et al.* 2003). In many studies, male zebra finch bill color has proven to be the most significant male feature evaluated by females in choosing mates (Burley & Coopersmith 1987; Blount *et al.* 2003; McGraw *et al.* 2003). I found no evidence that females preferred males with the brightest bills. This lack of preference for brightly colored bills may be due to the fact that stimulus males, on average, only differed in bill color by 3.45% within trials (table 5). However, during several analyzed time intervals both low and high cost females had significant sexual preferences for males possessing duller red bills (tables 3 & 4). After ten days, both treatment groups had similar preferences - significant sexual preferences for males possessing duller red bills (high cost 'chosen' vs. 'unchosen' bill color: t_{26}=3.327, P=0.003; low cost 'chosen' vs. 'unchosen' bill color: t_{28}=2.414, P=0.023) (table 4). Only one analysis revealed a trend in the direction of my prediction – there was a non-significant sexual preference for males with brighter red bills in the low cost treatment during the first hour of the experiment (low cost 'chosen' vs. 'unchosen' bill color, t_{30}=1.088, P=0.285) (table 4).

Several mate choice studies involving zebra finches have found that bright red bill color is the most significant predictor of male sexual attractiveness (Burley & Coopersmith 1987; Blount *et al.* 2003; McGraw *et al.* 2003), so my results are surprising. These studies, however, lasted no more than a few hours. In my experiment, I found that the low cost females, during the first hour (the most comparable situation to other studies of zebra finch mate choice), had a non-significant tendency to favor males with the brightest red bill color but nearly significantly changed their preference for males with duller, red bills after an extended period of time (time by 'chosen' status effect, $F_{2,30}=3.099$, $P=0.06$, table 4). I propose that bright red bill color may be a significant factor in zebra finch mate choice when the evaluation time is brief, but its lone significance in mate choice diminishes when the evaluation time is extended. This hypothesis would imply that male phenotypes (other than bill color) become important in mate selection when the evaluation time lasts more than a few hours (Møller & Pomiankowski 1993b; Iwasa & Pomiankowski 1994; Johnstone 1995; Brooks & Couldridge 1999).

In chapter one, I discussed the importance of ultraviolet light to the color perception of animals and specifically to zebra finches (Bennett *et al.* 1994; Bennett *et al.* 1996; Hunt *et al.* 1997). The conditions of this experiment were not ideal, as the lighting that I used in the experimental rooms did not emit ultraviolet light. Therefore, when considering the mate preferences of the females in this experiment, one must keep in mind that their color perception may not have been exactly as it would have been under natural conditions. In addition to the lighting problems, the plexiglass windows between the males and females may have also filtered out light and subtly changed the natural appearance of the stimulus males. Bill color was the only male phenotype where color perception was analyzed in this experiment; however, the appearance of other ornaments may have been affected the lack of ultraviolet light.

My second prediction was that male phenotypes other than bill color would correlate more strongly with female mating decisions as the experiment progressed (Janetos 1980; Real 1990; Møller & Pomiankowski 1993b; Iwasa & Pomiankowski 1994; Sullivan 1994; Johnstone 1995; Brooks & Couldridge 1999). The logic behind this prediction was that as the experiment advanced, females would have a greater opportunity to evaluate more than one phenotype of the stimulus males and base their mating decision on this information. I found some evidence that females may select mates based on phenotypes other than bill color.

In the high cost treatment ('chosen' vs. 'unchosen'), there were several instances where phenotypes other than bill color were significantly associated with sexual attractiveness – greater display rate during the first hour, smaller cheek patch size on day one, and smaller relative chest badge size and more chest bars during the entire experiment (table 4). High cost females also consistently (but not statistically) preferred males with duller red bills, smaller cheek patches, less fluctuating asymmetry, and larger display rates over the three analyzed time markers (table 4).

There is not much evidence that sexual ornaments other than bill color had significant effects on the mating decisions of all females in this experiment (table 3). Only smaller relative chest badge size had a significant correlation with being chosen during the 10 day experiment (table 3). Low cost females did, however, exhibit several non-significant preference trends over the course of the entire experiment for duller red bills, smaller cheek patches, smaller body size, and less fluctuating asymmetry.

One common significant preference exists between these analyses – males possessing relatively smaller chest badges were found to be the most attractive after ten days by the high cost females and by the combined preferences of all females (tables 3 & 4). Chest badges and chest bars are adjacently situated ornaments on male zebra finches (figure 5). Therefore, a change in one of these ornaments may amplify or enhance the appearance of the other ornament (Brooks 1996). Specifically, in this case a reduction in chest badge size may amplify the apparent or actual area of the region of the chest containing the chest bars. Therefore, I hypothesize that small chest badges may be an attractive male ornament when they enhance the apparent size of the chest bar region. Melanin-based ornaments, like the chest badge and chest bars of male zebra finches, have been hypothesized to primarily signal social dominance, tolerance to metal toxicity, and perhaps indirectly sexual attractiveness (Møller 1987; Senar 1999; Badyaev 2000; McGraw 2003).

My third prediction was that the melanin-based ornaments of male zebra finches would have weak associations with sexual attractiveness. I made this prediction, because I thought that the melanin-based ornaments of zebra finches were more likely to be involved in social dominance signaling than in sexual selection (Møller 1987; Senar 1999; Badyaev 2000; McGraw 2003). There were significant and near significant correlations between melanin-based ornaments and sexual attractiveness in the preferences of each treatment group and in the combined preferences of all females (tables 3 & 4). Cheek patches were less involved in the mating decisions of the females in this experiment than were chest bars and badges (tables 3 & 4). I have two hypotheses to explain the different roles of these melanin-based ornaments. First, the melanin-based plumage in the male cheek patches evolved in some context other than mate choice – possibly age, size, status, and/or sex recognition. My second hypothesis, contrary to my prediction, is that the melanin-based plumage in the chest bars and badge may be important in attracting females by signaling some form of individual quality such as social dominance or physiological tolerance to metal toxicity (Møller 1987; Senar 1999; Badyaev 2000; McGraw 2003).

I found a few differences in the sexual preferences of the two treatment groups (table 4). Of note, high cost females had a unique sexual preference for males possessing small chest badges in combination with a large number of chest bars (table 4). To elaborate on my further discussion about these melanin-based ornaments - this combination of male ornaments is one that should be easily evaluated by females due to its size and striking appearance. Like bill color, chest badges and bars may be ornaments that can be used by females as quick references of individual quality during mate evaluation.

5.7 – Correlation of male phenotypes

I performed a correlation analysis to test for significant associations between six male phenotypic characteristics. I found that males' display rate after one day was significantly correlated to their display rate after 10 days (table 6). This indicates that the males in this experiment did not alter their display activity relative to each other over the course of the experiment. I found that males with the largest cheek patches had the largest body size (table 6). Therefore, cheek patch size may be a reliable signal of body size or age in male zebra finches. This correlation is predictable as one would expect ornament size to increase with body size. Cheek patch size may also grow to signal sexual maturity. The other melanin-based ornament in this analysis (chest bars) had a nearly significant association with body size, as well (table 6). Therefore, chest bars may also be a signal of body size and age. Additionally, the two analyzed melanin-based ornaments (cheek patch and chest bars) had a nearly significant correlation with one another (table 6). Therefore, there may be some individual component managing the expression of all melanin-based plumage. Finally, there was a negative correlation between bill color and display rate on the first day of the experiment (table 6). This may suggest that individuals with dull bills may display relatively more than those with brightly colored bills in order to acquire more female attention to compensate for the inadequate character.

If there are in fact no significant correlations between the suite of male zebra finch ornaments (after Bonferroni correction for multiple comparisons), then the multiple message hypothesis seems applicable to the multiple ornamentation of zebra finches (Møller & Pomiankowski 1993b). This hypothesis states that different ornaments evolve independently to signal different characteristics about the condition of the individual, or appeal to a variety of female preferences (Coleman *et al.* 2004). Theoretically, intense sexual selection pressure on male zebra finches resulted in the evolution of a number of sexual ornaments to signal different characteristics of condition and quality to females. For instance, bill color may signal general health or foraging efficiency to females and the amount chest bars may signal social dominance or a strong immune system. The combination of small chest badges and the number of chest bars was found to be attractive in several analyses. Therefore, I conclude that the combination of these melanin-based ornaments is important in signaling some facet(s) of individual quality to females. However cheek patches, another melanin-based ornament, do not appear to have a function in mate selection. I believe that this ornament may have evolved independently as a signal of sex, sexual maturity, and/or body size.

5.8 – Further discussion and future directions

This study, I believe, effectively demonstrated that costs of mate choice can have an immediate effect on the mate sampling behavior of zebra finches. Females from both treatment groups seemed to adapt behaviorally to equilibrate costs across the treatment groups to maintain body mass at the same level. These results provide evidence that costs of mate choice can affect mating behavior and the manner in which mates are sampled. However, I was unable to demonstrate that mate sampling costs can affect the choosiness of female zebra finches. This result, though, may be due to the lack of phenotypic variability between the stimulus males within choice trials.

I predicted that high cost females would produce smaller, lower quality clutches since they would less often select the more superior stimulus male and would have less energy to allocate to reproduction after costly mate selection. I also predicted that the perceived predation risk of the open, wire cages would negatively affect breeding performance. I found little to no indication that mate sampling costs (after one generation) or perceived predation risk affected breeding performance. There are a few possible explanations that may explain my results. (i) Several generations may be required for costs of mate sampling to have a significant impact on breeding performance. (ii) The laboratory breeding conditions were not suitable for normal reproductive output. (iii) Frequent, unavoidable disturbances to check breeding progress disrupted and diminished the output of the breeding pairs. One or all of these explanations may have contributed to my results not matching my predictions.

I did not find bright red bill color to be the most significant correlate of sexual attractiveness. Therefore, I proposed that bill color may be significant in male mate selection when evaluation time is brief, but other behaviors or ornaments may be judged once mate selection time is extended. I also hypothesized that the combination of small chest badges and a larger number of chest bars may be a factor to consider in zebra finch mate selection. I propose that male zebra finches advertise several facets of condition and quality with their suite of ornamental characteristics. There were no significant correlations between any of the analyzed morphologies, except cheek patch and body size which only indicates that cheek patches may be a signal of body size or sexual maturity.

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