

INTRALOCUS SEXUAL CONFLICT AS INDICATED BY MATE CHOICE IN THE ZEBRA
FINCH (*TAENIOPYGIA GUTTATA*)

A Thesis

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Master of Arts

by

Wakana Kirihata

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Abstract

Intralocus sexual conflict, or the conflict that occurs between the sexes due to their shared genome, has recently begun attracting great attention. Increasing evidence suggest that this conflict may be more widespread than previously thought. Using a mate choice paradigm, we explored this conflict in a vertebrate species, the zebra finch (*Taeniopygia guttata*). Beak color may be under genetic conflict in this species because females prefer red-beaked males, while males prefer orange-beaked females, and this trait is highly correlated between the sexes. If intralocus sexual conflict is present, we predicted that males and females would choose partners possessing dissimilar beak colors, possibly combating the effects of this genetic conflict and thus maximizing the fitness of both sons and daughters. Understanding this phenomenon will allow us to gain valuable insight into the evolution of sexual traits and a reason and mechanism for keeping genetic diversity in a population.

Biographical Sketch

Wakana Kirihata earned her Bachelor of Science degree in Applied Mathematics from Columbia University Fu Foundation School of Engineering and Applied Science in May of 2010. In August of 2010, she joined the graduate program at Cornell University to study sexual conflict in zebra finches under the guidance of Dr. Elizabeth Adkins-Regan in the department of Psychology.

Wakana Kirihata has been the recipient of numerous grants during her graduate career, including the American Ornithologists' Union Research Award, Emory University Prosocial Workshop Travel Grant, Psychology Graduate Research Grant, and the Cornell Chapter of Sigma Xi Grant. She was also given an Honorable Mention for the NSF Graduate Research Fellowship Program in 2012.

Wakana Kirihata has presented her research at various conferences and workshops, including the Animal Behavior Society Conference at the University of New Mexico and the Workshop on the Biology of Prosocial Behavior at Emory University. Additionally, she has published her research in the journal *Biosurveillance and Biosecurity* with the work she completed during an internship at IBM Almaden Research Center during the summer of 2008.

Wakana Kirihata's thesis, *Intralocus sexual conflict as indicated by mate choice in the zebra finch (Taeniopygia guttata)*, was supervised by Dr. Elizabeth Adkins-Regan.

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Introduction

Sexual conflict is a widespread phenomenon seen across taxa. This conflict occurs because males and females often have conflicting interests in reproduction due to divergent life history traits (Arnqvist and Rowe, 2005). As a result of these differences, males and females often disagree on many aspects of reproduction, including mating frequency and relative parental investment.

Sexual conflict can be divided into two types: interlocus and intralocus. Until recently, there has been a great emphasis on interlocus sexual conflict, or conflict between alleles at different loci that enhance one sex's reproductive success at the expense of the other (Bonduriansky and Chenoweth, 2009). This type of conflict can result in a coevolutionary arms race between the sexes, in which males evolve traits to maximize their reproductive success even at the expense of females, while females evolve traits to resist (Arnqvist and Rowe, 2005). For example, in *Drosophila melanogaster*, males have evolved seminal fluid that is transferred to the females during mating, which increases the reproductive success of males by increasing both egg production and laying in the female, but at the same time it decreases female lifespan and future fertility (Chapman et al., 1995). As a result, females may evolve behavioral or morphological counteradaptations to reduce these negative effects (van Doorn, 2009).

Though interlocus sexual conflict has been studied extensively across taxa, conflict at the level of the genome has been largely ignored. Recently, however, intralocus sexual conflict, or conflict between the sexes over the optimal value of a trait encoded by the same set of genes, has begun attracting increasing attention (Bonduriansky and Chenoweth, 2009). Intralocus sexual conflict is expected to manifest when a trait that promotes high

fitness in one sex results in low fitness in the other, and when this trait is highly correlated between the sexes. For example, selection on males for increased testosterone can result in a correlated response in females, negatively affecting their fecundity (Rutkowska et al., 2005). According to traditional sexual selection, individuals will choose the highest quality mates to produce offspring of the best quality. In contrast, intralocus sexual conflict indicates that mating with the highest quality partner may not always be the best strategy, due to possible detrimental effects on offspring of the opposite sex. Therefore, we predicted that males and females would choose to mate with partners that will minimize intralocus sexual conflict and maximize fitness for both daughters and sons.

Thus far, experimental studies on intralocus sexual conflict have focused on invertebrates, so we wanted to explore this phenomenon in a vertebrate species (Bonduriansky and Rowe, 2005). The zebra finch (*Taeniopygia guttata*) is an ideal species to begin this process for the following reasons. First, beak color is highly correlated between parent and offspring of the same and opposite sex, suggesting a common genetic basis (See **Table I**). Using heritability estimates between parent and offspring, Price (1996) found the genetic correlation between the sexes to be 0.81. Price and Burley (1993) also included heritability estimates between full and half siblings, and found the genetic correlation between the sexes to be 0.91.

Table I: Parent-offspring beak color heritability estimates in 2 different studies, where * indicates significance.

Heritabilities	Father	Mother
Daughter (Price, 1996)	0.23 (0.37*)	0.53* (0.57*)
Son (Price, 1996)	0.58* (0.42*)	0.56* (0.41*)
Daughter (Price and Burley, 1993)	0.54*	0.33
Son (Price and Burley, 1993)	0.66*	0.70*

Second, females often prefer red-beaked males, whereas males prefer orange-beaked females, resulting in opposing optimal beak colors for the sexes and potential intralocus sexual conflict (Burley and Coopersmith, 1987). However, there is conflicting evidence in the literature on whether or not female zebra finches actually prefer redder beaks, independent of other sexual traits (Collins et al., 1994; Simons and Verhulst, 2011). In addition, there is evidence for low between-female agreement in choosing males based on beak color, making assortative mating a possibility (Forstmeier and Birkhead, 2004). Finally, beak color has been found to be positively correlated with important life history traits such as survival, reproductive success, and immune functioning in male birds, while negatively correlated in females, again opening up the possibility to sexually antagonistic selection (Price and Burley, 1994). Because of the high genetic correlation of beak color between the sexes, and the opposing selection on this trait, it is highly likely that zebra finch beak color is undergoing intralocus sexual conflict.

Zebra finches are biparental and monogamous with very little extra-pair paternity, making mate choice important for both sexes (Zann, 1996). Thus far, most mate choice experiments have focused mainly on female choice, but there is increasing evidence that male mate choice may be important in many breeding systems, especially in sexually and

socially monogamous species (Edward and Chapman, 2011). Therefore, we decided to test both male and female mate choice in our experiment.

If intralocus sexual conflict were present, we would expect males and females to choose in ways to maximize the fitness of both sons and daughters. **Fig 1** illustrates our fitness predictions for both daughters and sons based on parent beak colors. According to a study by Burley and Coopersmith (1987), there is directional selection for red beaks in males, however, there seems to be an opposing stabilizing selection for intermediately orange beak colors in females. Therefore, we would predict daughters to be of highest quality when the parents possess dissimilar beak colors. However, sons would be of highest quality when their parents both possess red beak colors. For our mate choice trials, we would expect orange-beaked females to choose red-beaked males and red-beaked females to choose orange-beaked males. Males on the other hand should all choose red-beaked females for sons, but orange-beaked females for daughters, and this will depend on the male's own beak color and the quality of the female.

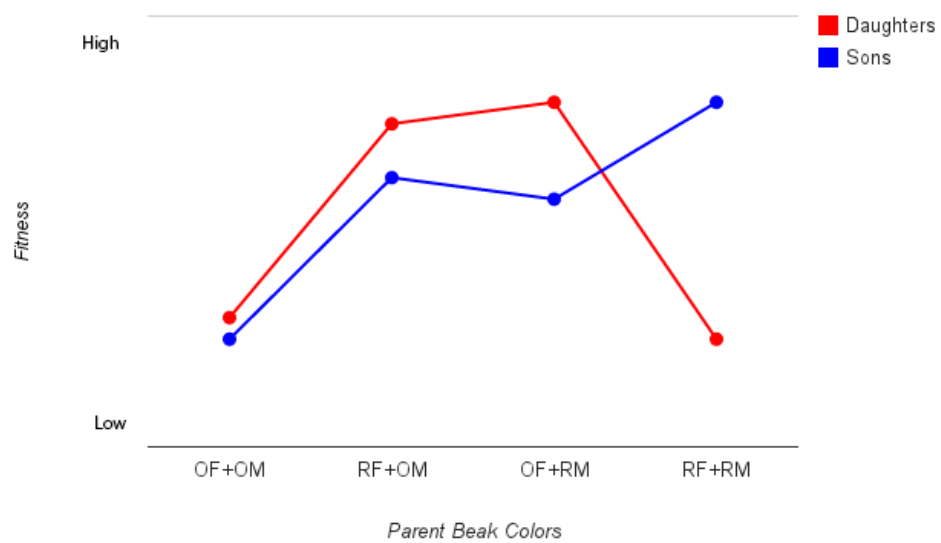


Fig 1: Fitness predictions based on parent beak colors (where OF = orange-beaked female, OM = orange-beaked male, RF = red-beaked female, RM = red-beaked male). Higher fitness daughters are expected when parents have dissimilar beak colors, where for males, red-beaked parents result in the highest fitness.

Methods

Subjects and stimuli

For our study subjects, we originally had 10 adult zebra finches with wild-type plumage from each of our 4 groups, but we have slightly lower sample sizes in both of the female subject groups because a few did not survive the length of the experiment (orange-beaked females $n=8$; red-beaked females $n=9$; orange-beaked males $n=10$; red-beaked males $n=10$). We used the top 10th and bottom 10th percentiles of beak color PC1 distributions in each sex as our red and orange subjects birds, respectively (See *Beak color measurements*). Our stimulus birds were taken from the 25th to the 75th percentiles of the beak color PC1 distributions, and consisted of 40 birds of each sex with wild-type plumage, for a total of 20 stimulus pairs (males $n=40$; females $n=40$). Both subject and stimulus birds consisted of experienced and non-experienced breeders of varying ages with known pairing history. All efforts were made to not use birds from a previous pair together within a trial.

All birds in our laboratory population are generally kept in multi-sex rooms in large aviaries with an ambient temperature of 72 degrees F, with humidity fluctuating daily between 30% and 70% and a light cycle of 14L:10D. All birds were fed ad libitum on a commercial finch seed mix (Kaytee Forti-Diet Finch), and fresh water was provided daily. Starting a few months before the actual mate choice trials, experimental subjects and stimuli were moved to single-sex rooms, in order to increase their motivation to pair with the opposite sex and to avoid previously paired birds from interacting with one another. All birds were monitored daily, and all parts of this experiment were approved by the Cornell University IACUC.

Beak color measurements

Using a spectrometer, we first quantified the distribution of beak colors in our laboratory population, and selected subject birds from the extremes of this range. Using readings from the spectrometer, we chose to extract hue as the maximum slope greater than 500nm, brightness as mean reflectance averaged along the visible avian spectrum (260-720nm), and red chroma as the percentage of reflectance in the red range (650-720nm) over total reflectance in the avian visible spectrum (260-720nm) (Method of Ardia et al., 2010). Repeatability within individuals was high for all parameters of interest: Hue ($R=0.91$; $*p<0.0001$), red chroma ($R=0.762$; $*p<0.0001$), brightness ($R=0.792$; $*p<0.0001$). For this reason, we averaged these values over 5 independent spectrometric measurements to get one value for each parameter of interest in each bird. Consistent with past literature, both red chroma and hue were higher in male zebra finches, while brightness was higher in female zebra finches (Ardia et al., 2010; Bolund et al., 2007). Using the method of McGraw et al. (2003), we collapsed these 3 variables using principal component analysis and used PC1 to summarize our color data. PC1 explains 72.7% of the variability in beak color in our laboratory population. Higher PC1 values indicate higher hue, higher red chroma, but lower brightness. The frequency distributions we found in our laboratory population are consistent with what we would expect in a species that may be undergoing intralocus sexual conflict (See **Fig 2**).

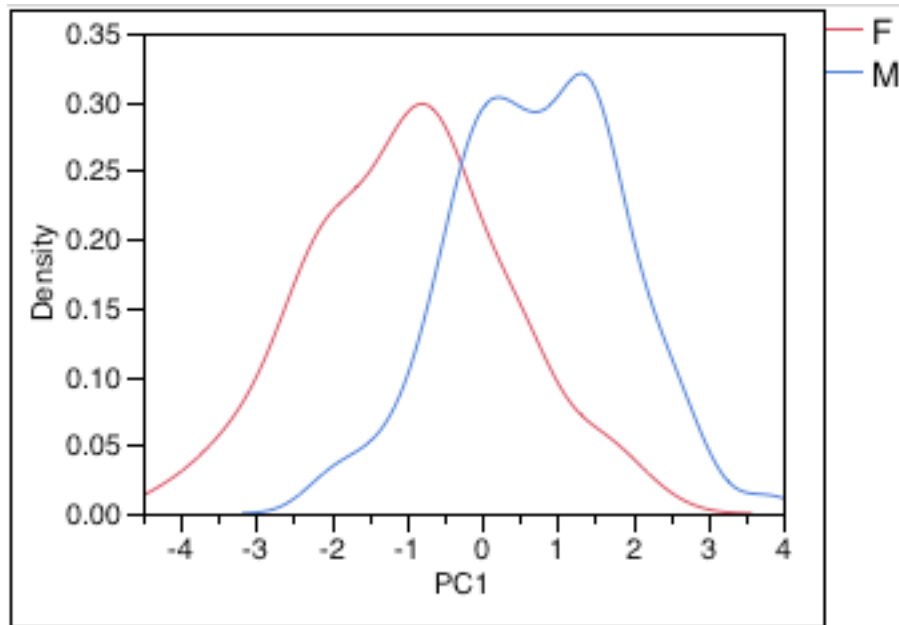


Fig 2: Beak color PC1 frequency distributions. There was an overlap in male (M: $n=173$) and female (F: $n=133$) beak colors, but males on average had higher PC1 values, indicating higher red chroma, higher hue, but lower brightness. This overlap in distributions may indicate that both male and female beak colors are not reaching their optimal values due to genetic correlation between the sexes. Intra-locus sexual conflict is predicted if optimal fitness values for the sexes are on opposite ends of this spectrum.

Experimental manipulation of stimuli

The beak colors of the stimulus birds were experimentally manipulated using paint with minimum odor and toxicity (Benjamin Moore Natura Interior Waterborne paint). We ordered paint colors using the Munsell color measurements found in a previous study (Burley and Coopersmith, 1987). The values for our paint were Munsell 1.25YR 6/12 and 8.75R 4/12, for our orange and red colors, respectively. In order for the paint colors to be in the natural range of beak color in both male and female zebra finches, our red paint is the most naturally red male beak color, while the orange paint is the most naturally orange female beak color. In addition, because display rate can have a significant effect on female preference, we matched our stimulus males by their song rate, also known as display rate. We placed male birds with 3 different females on 3 consecutive days for 5 minutes each and video recorded the encounter. We calculated song rate as the duration of time that the male spent singing in this 5-minute period.

Experimental apparatus and procedure

Beak color preferences for potential mates were assessed using an apparatus containing a chamber for the subject bird adjacent to 2 separate chambers for stimulus birds (experimentally painted red vs. orange), and measuring the time spent near each of the stimuli (See **Fig 3**). The stimulus cages were surrounded by opaque sound-reducing quilted fiberglass (Sound Seal, Oshex Associates, Inc.) to exclude song quality as a potential confound and to prevent auditory and visual intrasexual competition between stimulus birds. Subject and stimulus birds were allowed to interact through a small glass window (10cm x 10cm) made of borosilicate float glass (Schott Borofloat 33) that had reasonable

light transmittance in the avian visual range, including the ultraviolet range. In addition, special fluorescent light bulbs (Indoor Sunshine, Sunlight Sciences: 95 CRI, 5300-5500 K, 35 kHz) that mimic natural sunlight were used during mate choice trials. We made sure to use a light bulb with a high flicker rate (>30 kHz, at which point flicker is imperceptible), as it has been shown that flicker rate can have a great effect on mate choice experiments in birds (Evans et al., 2006). Finally, because zebra finches are colonial breeders, the testing room contained an aviary full of paired birds that none of the experimental birds were familiar with, creating a more natural environment for the subject birds to make their decisions. These background birds were behind a curtain behind the stimulus birds, and could be heard, but not seen by the experimental birds.

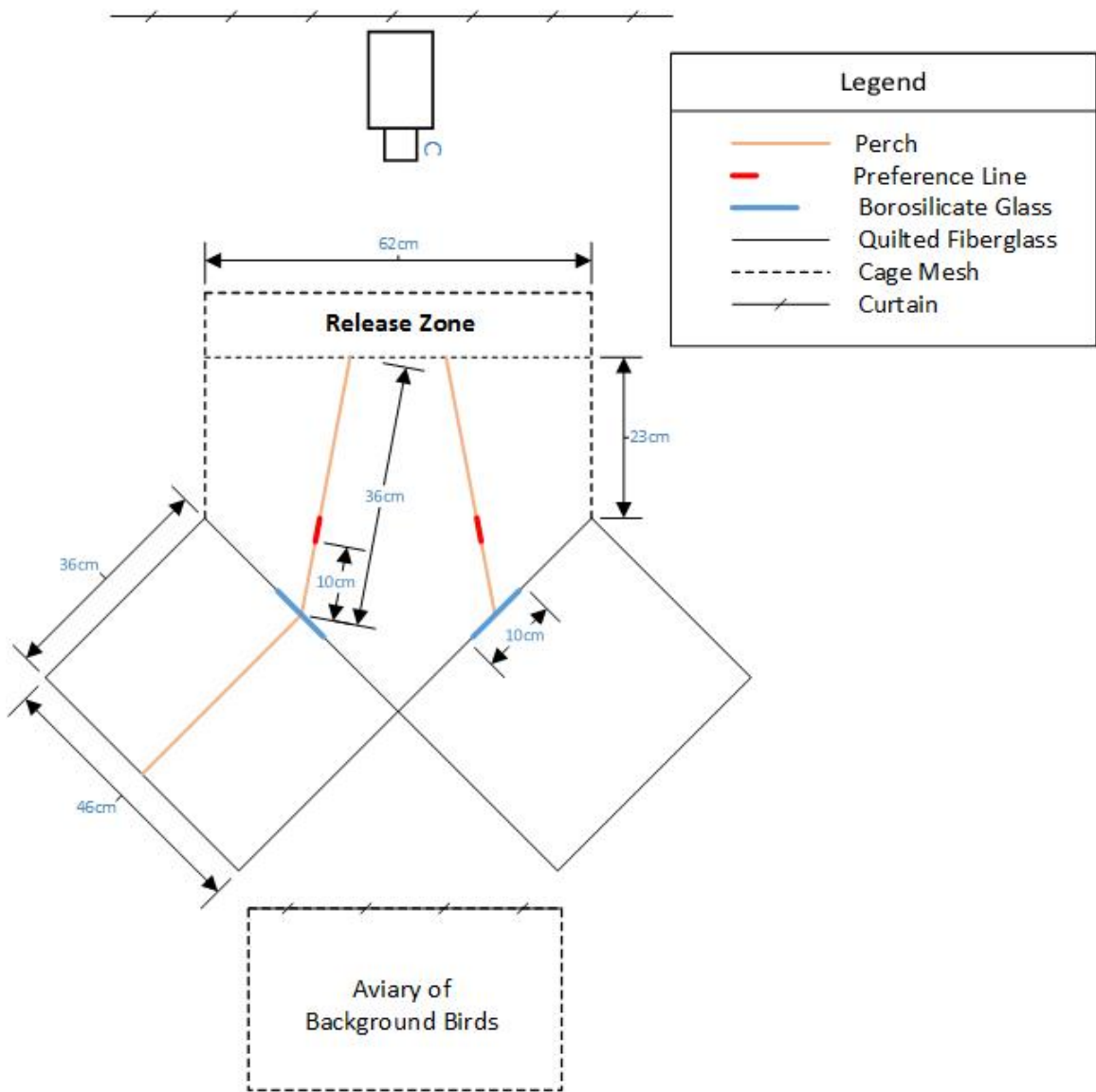


Fig 3: Schematic diagram of mate choice apparatus.

To minimize extraneous variance between stimulus birds, the same pair was used for 2 (1 red, 1 orange) subject birds. Each subject was exposed to 4 different stimulus pairs on 2 consecutive days of 2 consecutive weeks, for a total of 4 trials. We alternated stimulus beak color side between trials. In total, we had 40 stimulus birds (20 stimulus pairs) to use. Each stimulus pair was only reused once, and the painted colors were reversed the second time around.

Each mate choice trial lasted for 40 minutes. All mate choice trials were run between 8:00am and 12:00pm from January to September of 2012. The stimulus birds were first caught into a small, fully enclosed nestbox and we painted their beaks approximately 10 minutes before a trial. Then these stimulus birds were released into the stimulus cages of the mate choice apparatus without any additional handling. The subject bird was caught in a similar fashion and placed into a fully enclosed nestbox. This nestbox was then placed in the release zone of the apparatus, and the experimenter would pull a string from behind a curtain in front of the release zone to open up the nestbox. In this way, the subject bird was released into the apparatus with minimal intervention and handling. A camera was set to record in front of the release zone before the subject bird was released, and once the bird was released, the 40-minute time period would begin.

All videos were coded using ELAN 4.6.1. (Max Planck Institute for Psycholinguistics Nijmegen, The Netherlands), a program that allowed us to look at the videos frame by frame. We coded videos by marking the times at which one foot of the subject bird crossed the red preference line onto the side closer to one of the stimulus birds, and continued until the subject bird either left the perch or one foot crossed to the other side of the red

preference line. We collected and analyzed the time spent with the left stimulus bird versus time spent with the right stimulus bird.

Statistical analyses

All statistical analyses were performed using JMP Version 9.0.1 (2010 SAS Institute Inc.). Parametric tests were applied to all preference data (Shapiro-Wilk test for normality: all $ps > 0.1$). We calculated preference for orange beaks independently for each trial as the total amount of time spent with the orange stimulus bird divided by the total amount of time spent with either stimulus bird. Preferences for orange beaks were averaged across the 4 trials for each subject bird. We used one-way ANOVAs to determine differences between subject bird groups. Statistical analyses for male and female subject birds were performed separately. In addition, we used one-sample t tests (two-tailed) with a random expectation of 0.5 to determine whether or not each subject group had a preference for a certain beak color. We also carried out a GLMM to assess differences in preference for orange beaks between all four of the subject groups by sex and color, with subject bird included as a random effect and using original stimulus bird beak color as covariates. In this way, we were able to assess whether subject birds were choosing based on other traits besides the painted beak color that may be correlated with the original beak color.

Because there was great variability in beak color preference in red-beaked males, we decided to look at preference strength as the deviation from a random expectation of 0.5. We again compared differences between subject groups using one-way ANOVAs.

Results

Consistent with our predictions, we found that orange-beaked females significantly preferred red-beaked males over orange-beaked males, as indicated by a significant difference from a random preference of 0.5 (See **Fig 4**). We also found a significant difference between the two beak color subject groups in their preference for orange beaks, where the orange-beaked females had a stronger preference for red-beaked males, compared to the red-beaked females. However, preference for orange beaks in the red-beaked females did not significantly differ from a random preference of 0.5.

We were not able to find a significant difference between beak color groups in preference for orange beaks in male birds (See **Fig 5**). We also were not able to see significant differences from a random preference of 0.5 in neither of our male beak color subject groups. However, we observed that in our red-beaked males in particular, there was great variability in what beak color each male was choosing. Therefore, we decided to look at preference strength, which can be defined as how strongly the subject male chose a beak color, regardless of color. We found that red-beaked males had a much stronger preference when choosing a beak color compared to the orange-beaked males (See **Fig 6**). We were not able to detect a similar significant difference in preference strength between our female subject groups (See **Fig 7**).

Because we did not measure other traits that could potentially correlate with the natural beak colors of our stimulus birds, we ran a GLMM with all four of our subject groups by sex and color using the natural beak colors of stimulus birds as covariates to see if there were any correlations between our preference data and the natural beak color of our stimulus birds (See **Fig 8**). We found no correlation between the natural beak color of

the stimulus birds painted red and preference for orange. Similarly, no correlation was found between the natural beak color of the stimulus birds painted orange and our preference data. The interaction between the two stimulus beak colors was also non-significant. Subject color and the interaction between subject sex and color did have significant effects on preference for orange beaks. However, subject sex was non-significant (See **Table II**).

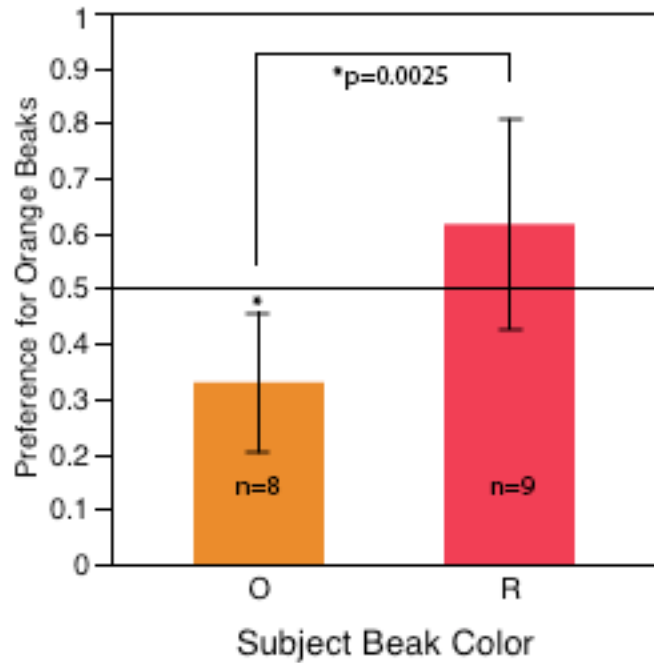


Fig 4: Female preference for orange beaks by subject beak color (ANOVA: $F(1,15)=13.1095$, $*p=0.0025$). Line at 0.5 indicates no preference. Preference for orange beaks significantly differed from 0.5 in orange-beaked females as indicated by * (two-tailed t test: $mean=0.3299$, $t(7)=-3.8033$, $*p=0.0067$). Preference for orange beaks did not significantly differ from 0.5 in red-beaked females (two-tailed t test: $mean=0.6168$, $t(8)=1.8503$, $p=0.1014$). Each error bar is constructed using 1 standard deviation from the mean.

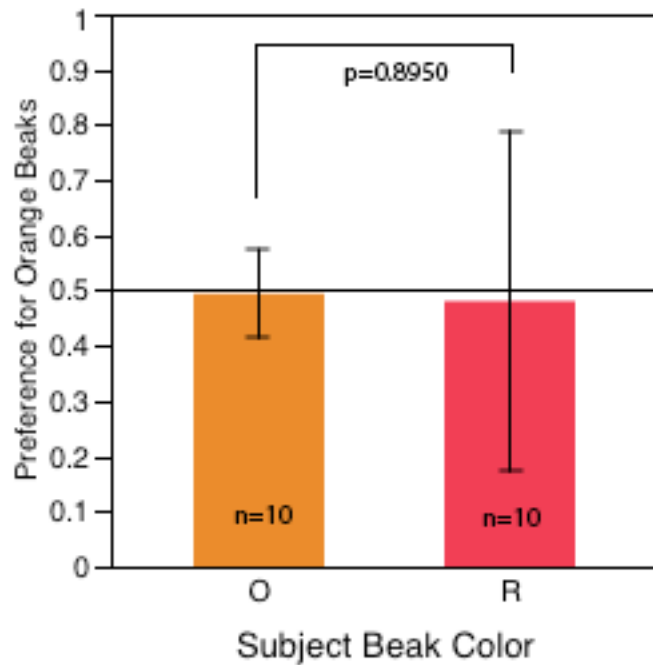


Fig 5: Male preference for orange beaks by subject beak color (ANOVA: $F(1,18)=0.0179$, $p=0.8950$). Line at 0.5 indicates no preference. Neither the preference in orange-beaked males (two-tailed t test: $mean=0.4943$, $t(9)=-0.2250$, $p=0.8270$) nor red-beaked males (two-tailed t test: $mean=0.4808$, $t(9)=-0.1968$, $p=0.8484$) significantly differed from 0.5. Each error bar is constructed using 1 standard deviation from the mean.

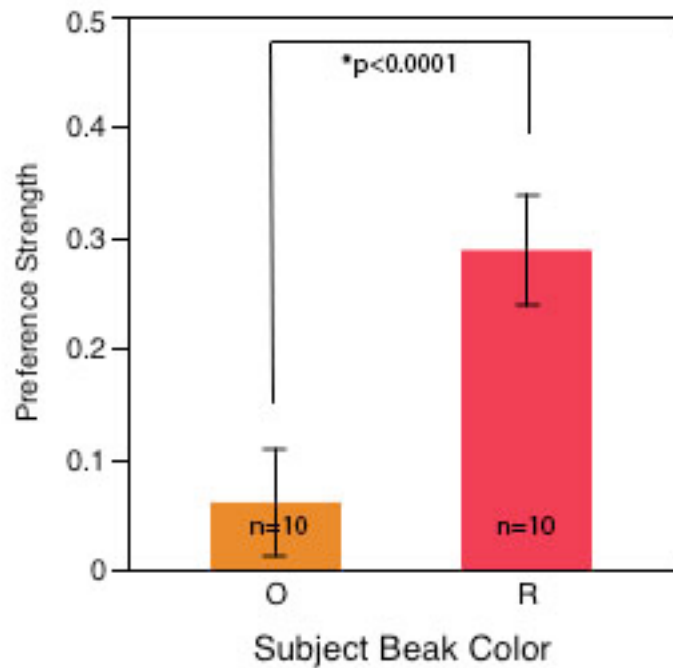


Fig 6: Male preference strength for either color measured as the deviation from 0.5 (ANOVA: $F(1,18)=106.7990$, $*p<0.0001$). Each error bar is constructed using 1 standard deviation from the mean.

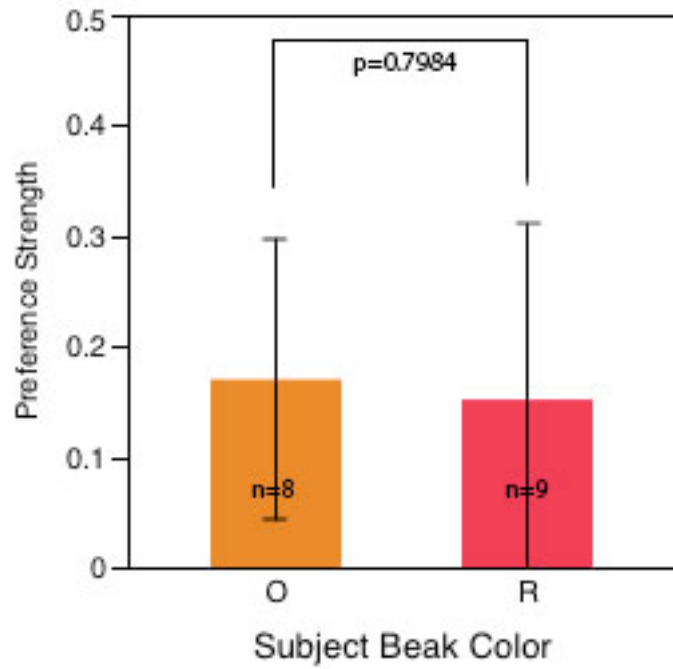


Fig 7: Female preference strength for either color measured as the deviation from 0.5 (ANOVA: $F(1,15)=0.0676$, $p=0.7984$). Each error bar is constructed using 1 standard deviation from the mean.

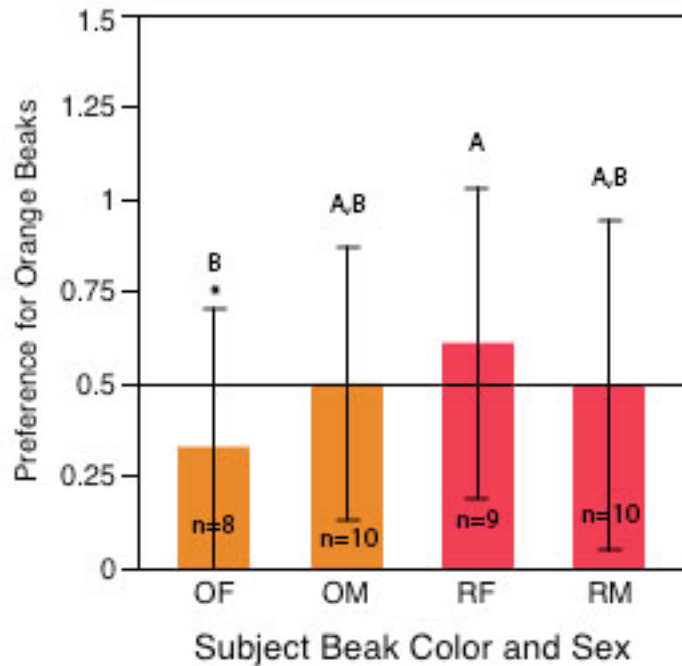


Fig 8: Male and female preference for orange beaks by subject beak color and sex (where OM = orange-beaked male, RM = red-beaked male, OF = orange-beaked female, RF = red-beaked female), controlling for natural beak color of the stimulus birds. Subject group did have a significant effect on preference for orange beaks. Groups not connected by the same letter are significantly different. Line at 0.5 indicates no preference and * indicates significant difference from 0.5. Each error bar is constructed using 1 standard deviation from the mean.

Table II: Results of GLMM testing the effect of subject sex and beak color, as well as the natural beak color of the stimulus birds on the preference for orange beaks, where * indicates significance.

Model Term	<i>F</i>	<i>df</i>	<i>p</i>
Subject Color	4.2872	1, 35	0.0468*
Subject Sex	0.0187	1, 35	0.8915
Subject Sex*Color	4.9596	3, 33	0.0331*
Orange Stimulus PC1	0.1601	1, 100	0.6899
Red Stimulus PC1	0.1499	1, 127	0.6993
Orange*Red Stimulus PC1	0.4609	1, 126	0.4984

Discussion

In this experiment, we found that orange-beaked females do indeed prefer red-beaked males over orange-beaked males. However, a similar preference for either beak color was not seen in the red-beaked females. Red beak color has been found to be negatively correlated with survival and reproductive success in female zebra finches, making it possible that orange-beaked females are of higher quality than red-beaked females (Price and Burley, 1994). For this reason, perhaps orange-beaked females can afford to be choosier, and are choosing to pair with red-beaked males. Contrary to beak color in females, red beak color has been found to be positively associated with survival and reproduction in male zebra finches, and therefore red-beaked males may be of higher quality than orange-beaked males (Price and Burley, 1994).

In males, we were not able to find a significant preference for orange or red beaks in either beak color subject group. However, when we look at the distribution of preference in red-beaked males, we found that it was binomial. It does seem that the red-beaked males are picking up on our manipulations and choosing orange- or red-beaked stimulus females. Therefore, we looked at preference strength to see if our subject groups differed in how strongly they preferred a beak color, whether it be red or orange. We found that red-beaked males had a much stronger preference for a certain beak color compared to the orange-beaked males. Similarly to the orange-beaked females, this may be explained by the fact that red-beaked males are of higher quality than the orange-beaked males, and perhaps the red-beaked males can then afford to be choosier. As discussed above, red beaks in males have been shown to be positively associated with survival, reproductive

success, and immune functioning (Price and Burley, 1994; Birkhead et al., 1998). Therefore, beak color may be an honest indicator of quality in the zebra finch.

We found low between-female and between-male agreement in what beak color to choose. Low between-female agreement in choosing beak color is consistent with a previous study by Forstmeier and Birkhead (2004). Our mate choice results are inconclusive because the fitness benefits of choosing to mate with a certain beak color may depend on whether the subject will have more sons or daughters. In addition, Burley and Coopersmith (1987) found that there seems to be directional selection for red beaks in males, but stabilizing selection for beak colors in the middle of the phenotypic range. As discussed in the introduction and as seen in **Fig 1**, we expect daughters of the highest quality when parents have dissimilar beak colors, while we expect higher quality sons with parents of red beaks.

If the above fitness predictions hold true, perhaps the reason why our higher quality orange-beaked females strongly preferred red-beaked males is because they can produce daughters of intermediately orange-colored beaks by choosing a red-beaked male. There is evidence in other species that higher quality females tend to produce more female offspring, and it may be beneficial for these higher quality orange-beaked females to choose higher quality red-beaked males that will result in intermediately orange-beaked daughters. For higher quality males, it may be more beneficial to have more sons with red-beaked females, but the results from our study are inconclusive as to why there is such low between-male agreement in choosing a beak color. Perhaps there are other traits that are driving these preferences. This experiment could be expanded by a more naturalistic breeding experiment to actually track the fitness success of different pairings of beak

colors and looking at the sex ratio of each clutch. In this way, we would gain insight into how the different beak color pairings may lead to actual fitness benefits for sons versus daughters in future generations.

Though our results in this experiment are promising, there are limitations to mate choice experiments such as ours. There are many traits that go into the mate choice of zebra finches besides beak color, and taking away these other factors may greatly affect our results. We found that there was low between-individual consistency when choosing a certain beak color. This within-group variability in preference could be driven by a trait that we did not measure, as zebra finches are known to choose based on many visual traits including, but not limited to display rate (Collins et al., 1994), band color (Hunt et al., 1997), and chest plumage (Swaddle and Cuthill, 1994).

Another potentially interesting research route is looking at the correlation between beak color and testosterone level, and how testosterone level may affect fitness in both male and female zebra finches. There have been numerous studies, both correlational and experimental, that have found a positive correlation between testosterone level and beak color, indicating that beak color may serve as an honest indicator of testosterone level (Cynx and Nottebohm, 1992; McGraw, 2006; Ardia et al., 2010). If this is true, there are many reasons why it may benefit both sexes of this species to be choosing mates based on this phenotypic trait.

In males, important fitness components including time to first nest, reproductive rate (Price and Burley, 1994), and song rate (Arnold, 1975) all increase with an increase in testosterone level. It has been found that female zebra finches prefer males with higher song rate (Collins et al., 1994). In female zebra finches, testosterone level has been found to

negatively correlate with important fitness components, including clutch size (Rutkowska et al., 2005) and survival (Price and Burley, 1994). However, evidence is still inconclusive in females because of the importance of testosterone in egg yolk for the survival, growth, and even sexual preference development in offspring (von Engelhardt et al., 2006; Adkins-Regan and Leung, 2006).

In conclusion, we found that orange-beaked females significantly preferred red-beaked over orange-beaked males, compared to red-beaked females. This same significant difference was not found in male subject birds. However, red-beaked males had a stronger preference for either red or orange beaks compared to orange-beaked males. Preference strength was significant in all four of our subject groups, indicating that beak color preference is consistent within an individual. It is difficult to predict how these preferences would translate into actual fitness benefits without a more naturalistic breeding experiment. Future work should concentrate on looking at survival and reproductive success of offspring from different beak color pairings, and the testosterone level correlates of various beak colors. Intralocus sexual conflict may be present in this species, but we were not able to find evidence for males and females choosing their mates in ways that would combat the potential detrimental effects.

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