

## **How do low-quality females know they're low-quality and do they always prefer low-quality mates?**

### **Introduction:**

The relatively young field of condition-dependent variation in female mate preferences has generally shown that variation in female quality causes fluctuations in female preference strength, but not usually in the direction of female preference (Cotton *et al.* 2006; Syriatowicz & Brooks 2004; Immonen *et al.* 2009). However, studies of human female mate preferences have demonstrated condition-dependent variation in the direction of female mate preferences; women who consider themselves to be of low phenotypic quality (i.e. low attractiveness) prefer to date less attractive men whereas women who perceive themselves as higher-quality individuals prefer to date more attractive men (Little *et al.* 2001; Buston & Emlen 2003). A recent study of wolf spiders found similar results; female spiders in poor condition following experimental malnourishment showed a shift in direction of preference to smaller males (Erlay *et al.* 2009).

Recent research involving the manipulation of female zebra finch condition has also shown variation in the direction of female mate preferences depending on female condition (Holveck & Riebel 2010). The zebra finch (*Taeniopygia guttata*) is a highly social Australian granivore which exhibits complex social dominance hierarchies and which has become the prototypical model for studying sexual selection and mate choice in sexually monogamous passerine species (Swaddle 1996; Rutstein *et al.* 2007). Because of the bidirectional mate selection in this species, females adjust their mate preferences based on the quality of males they are likely to attract and successfully retain as mates (Burley & Foster 2006). Low-quality females have been shown to prefer the calls of low-quality males, a preference reliably correlated to live male choice, whereas high-quality females were shown to prefer the calls of high-quality males (Holveck & Riebel 2010). This study illustrates the implications which rearing condition

has on the mate preferences of mature females, but it does not investigate the effects of less permanent variation in female condition. The general posit that low-quality zebra finch females prefer low-quality males must be further tested using alternate methods of quality manipulation before it is to be universally accepted. Fortunately, one such alternate method has been identified as the trimming of female flight feathers (Burley & Foster 2006). After experimental trimming (which resulted in reduced flight capabilities) followed by housing with other females, experimental females in otherwise good condition began associating with low-quality males more often than with high-quality males. Because these females associated with high-quality males more frequently before experimental treatment and also once their flight feathers grew back, these results indicate that flight-feather trimming resulted in temporary reduced preference strength. The experiment proposed here will investigate the universality of the claim that low-quality females prefer low-quality males by comparing the preferences for male calls of high-quality females before and after experimental flight feather trimming.

A potentially more interesting topic which deserves investigation is the elucidation of the mechanisms which grant female zebra finches some measure of determining their own quality, a process which in turn affects their mate preferences (Holveck & Riebel 2010). It has been hypothesized that the mechanisms underlying this determination either depend on physiological cues (such as metabolic rate and body mass) and/or relative quality-assessment following competitive non-sexual social interactions with conspecifics, although this hypothesis has not yet been tested (Verhulst *et al.* 2006; Holveck and Riebel 2010). The experiment proposed here intends to provide some indication of the mechanisms at play by comparing female preference data for females subjected to alternate social environments following experimental flight feather trimming. High-quality females initially shown to prefer high-quality males will undergo flight

feather trimming and be housed either solitarily (hereafter referred to as ‘self-assessment’ females) and thus denied potential competitive social interactions, or housed among other females (‘competitive-assessment’ females) and thereby subjected to competitive social interaction. If only the competitive-assessment females demonstrate a shift in preference direction, the results will suggest that competitive social interactions are necessary to provide females with sufficient information regarding their quality to affect a mating preference change. However, if a shift in preference direction is seen in the self-assessment females as well as the competitive-assessment females, the results will indicate that the physiological effects associated with reduced flight capabilities alone provide females with sufficient information regarding reduced quality to enact a preference change. (See Experimental Design for further analysis of the implications of all potential experimental outcomes.) Because advanced social interactions play a major role in the biology of this species, I predict that only the competitive-assessment females, and not the self-assessment females, will demonstrate a shift in mate preference direction towards low-quality males following treatment, thereby also supporting the widespread applicability of the claim that low-quality females prefer low-quality males (Swaddle 1996).

## **Experimental Design:**

### ***(a) Rearing conditions and brood size manipulation:***

The first segment of this experiment will generate high- and low-quality males and females via foster brood size manipulations. Four-hundred domesticated zebra finches (200 male, 200 female) will be housed in standard laboratory cages and fed *ad libitum* throughout the experiment until the feather trimming treatment (for details see Holveck & Riebel 2010). Three days after hatching, birds will be cross-fostered so as to create small (two- or three-chick) and large (five- or six-chick) broods with equal sex-ratios within each foster brood. Depending on

the size of the foster broods, this will allow me to induce favorable and unfavorable phenotypic qualities in chicks which will persist throughout adulthood, as individuals reared in small broods have been shown to have greater immune responses, greater body mass, higher survival, better condition and lower metabolism than individuals reared in enlarged broods (Verhulst *et al.* 2006; Riebel 2009; Holveck & Riebel 2010). Barring chick mortality, this will create 100 high- and 100 low-quality females as well as 100 high- and 100 low-quality males. At 35 days of age, each chick will then be assigned to a song tutor group consisting of a high-quality male, a low-quality male, a high-quality female, and a low-quality female from four different foster groups. The tutor groups will be led by a pair of unfamiliar adults.

**(b) *Song-learning phase and male song recording:***

Both male and female zebra finches are particularly sensitive to song-learning and song preference-learning from adult conspecifics between roughly 35 to 65 days of age (Riebel *et al.* 2002). It has been shown that during this time-frame, low-quality individuals are less successful than high-quality individuals at accurately recognizing and copying certain song elements from song tutors and thus develop lower-quality songs and less acute song preferences (Holveck *et al.* 2008). Each tutor group, consisting of both high- and low-quality males and females, will be housed with a tutor pair during this sensitive stage so as to provide each ‘pair’ of high- and low-quality males with the same song-tutoring. At 70 days of age, individuals from tutor groups will be placed in standard cages with four or five same-sex birds of both high- and low-quality, out of earshot and separated from the opposite sex to ensure no premature sexual interactions nor male song-familiarity biases develop prior to the song preference tests (Holveck & Riebel 2010). After sexual maturity has been reached (120 days of age), both high- and low-quality males will be placed alone into sound attenuation chambers so that their songs may be recorded. These

recordings will later be edited-down into specific song stimuli for each male for the preference tests, thus creating high- and low-quality male songs for the ensuing preference tests.

**(c) *Female song preference tests, establishing ‘within-individual’ controls:***

Prior research has demonstrated that the results of operant song preference tests (in which females are trained to peck response keys which provide different song playback) correlate strongly to female mate selection in nature and can therefore be used as reliable indicators of female mate preference (Holveck & Riebel 2007). Following the male song recording process, the 100 high-quality females will be placed in solitary operant testing cages containing two red song-playback buttons (Riebel 2000). Pressing either button will play the song of either the high- or low-quality male of one ‘pair’ of males coming from the same tutor group. Females will not be presented with the songs of males from their own tutor groups, as preference for familiar songs has been shown to override male quality-judgment (Riebel 2009; Holveck & Riebel 2010). Each high-quality female will undergo three trials, between which the call playback associated with each button will switch to eliminate the possibility of confounding side-preferences. Because females will have not yet experienced mating events, their preferences will not be affected by any prior mating experiences such as mate rejection (Holveck & Riebel 2010). Both the number of button pecks and the percentage of total button pecks for the high-quality males’ songs will be recorded. The values recorded here for each high-quality female will serve as the ‘within-individual’ control values which will be compared to the results of her preference tests following the feather trimming treatment.

**(d) *Flight feather trimming and song preference tests for ‘self-assessment’ and ‘competitive-assessment’ females:***

After recording each of the 100 high-quality females’ preference data for male calls and

ensuring that all of these females prefer the calls of high-quality males, the females will be returned to the same unisexual cages in which they were previously housed. Several days later, 50 randomly chosen high-quality females will then undergo slight flight feather trimming: the ten outermost flight feathers on each wing will be slightly trimmed so as to maintain the normal wing shape phenotype and yet cause reduced flight ability (refer to Burley & Foster 2006 for specifics). Following treatment, the females will be randomly subjected to either solitary housing (these will be the self-assessment females) or, for the competitive-assessment females, to housing with other females meant to induce social interactions (namely competition). To eliminate confounding variables, the cage conditions will be identical between the self- and competitive-assessment females except for the presence of conspecifics. Each of the 25 competitive-assessment females will be placed into 3x10x3m flight cages with the same four or five untreated females they were previously housed with. To induce competition, the flight cages will contain only one feeding structure hanging one meter above the cage floor, as recently treated females have been shown to show difficulty ascending beyond this height, as well as sparse perches which females will likely squabble over (Burley & Foster 2006; Beauchamp 2000). The intent here is that given their greater flight difficulty, experimental females will face steeper competition than they did from their cage-mates prior to treatment and will, in some way, gain ‘knowledge’ of their reduced quality. The females will be kept in the flight cage for two weeks, as this was the time period shown to induce preference strength reduction, cause a 5% body mass reduction, and increase metabolic rate and overall flight cost in experimental females (Hambly *et al.* 2004; Burley & Foster 2006). Females will then be removed, fed *ad libitum* for three hours to control for the possible effects of reduced food consumption and hunger potentially caused by competition or increased energy expenditure, then subjected to the same

male song playback preference test procedure as previously described with the calls of an unfamiliar male pair.

If no shift in preference is observed, and therefore neither the physiological changes associated with feather trimming (decreased flight ability, increased metabolism and reduction in body mass) nor the results of competitive interaction following treatment affect the direction of female preference, little insight will be gained into whether competitive interactions are necessary for females to determine their quality (Hambly *et al.* 2004; Burley & Foster 2006). Furthermore, the claim that low-quality females prefer low-quality males will be proven to not be universally valid (Holveck & Riebel 2010). However, although this experiment specifically hopes to observe shifts in preference direction, less dramatic reductions in preference strength may still provide insight as to the processes underlying female determination of quality.

If competitive-assessment females exhibit a shift in the direction of their mate preference towards low-quality males, this shift can be attributed to the effects that feather trimming had on their intra-sexual competitive interactions, on their physiology, or some combination of the two. Clearly, this outcome alone will not indicate whether competitive interactions are necessary to provide females with some indication of their quality, although the outcome of the self-assessment female preference tests should. [The possibility that experimental females increase their preference for high-quality males following treatment would contradict previous results and seems so unlikely that it will not be further analyzed (Burley & Foster 2006).]

The 25 randomly selected high-quality self-assessment females will be subjected to identical treatment as the competitive assessment females, except that they will be housed solitarily between their feather trimming treatment and the following preference tests. If these females exhibit no shift in the direction of preference towards low-quality males, the results will

suggest that the physiological effects associated with reduced flight ability alone are not sufficient to provide females with the ‘knowledge’ of quality required to cause a shift in preference direction. This outcome will strengthen the claim that competitive social interactions are necessary for females to be provided with an indication of their quality (especially if the competitive-assessment females show a shift in preference direction). Conversely, if self-assessment females *do* show a shift in the direction of preference towards low-quality males, the results will support the hypothesis that the physiological effects associated with reduced flight ability alone may be sufficient to provide females some measure of their altered quality, as these females will not experience competitive interaction following treatment.

Assuming preference changes are shown, there is also a possibility that the experimental procedure itself rather than the physiological effects associated with the treatment or the effects of subsequent competitive interactions will account for the outcome. To investigate this, our previous results will be compared to those obtained from 25 self-assessment control females and 25 competitive-assessment control females. These females will be handled and exposed to the feather trimming materials and will undergo the same following social housing as were their respective experimental counterparts, but their feathers will not actually be trimmed.

**(e) *Statistical Analyses:***

The strength and direction of a female’s preference will be indicated by the percentage of button presses she allots to the high-quality male’s song. To test whether females’ preferences are statistically significant (non-random), P-values will be calculated. To determine whether a given female’s results are outliers, standard deviation and standard error will be calculated. Also, to determine whether a significant difference exists between ‘within-individual’ control and experimental preference results, paired T-tests will be performed.



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