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Male and Female Choice in Zebra Finches

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Females usually have a higher reproductive investment in their brood than males, so they should exercise more discrimination in choice of mate (Trivers 1972, Clutton-Brock and Vincent 1991). In monogamous birds, males provide substantial parental investment and they may also be expected to choose, or compete for, high-quality females (Trivers 1972, Burley 1977). The sex roles of Zebra Finches (*Taeniopygia guttata*) are weakly defined, with both sexes participating in incubation, feeding of the offspring, and nest defense (Burley and Coopersmith 1987). The male's contribution is roughly 40 to 45% of the total effort (Morris 1954, El-Wailly 1966, Delesalle 1986, Burley and Coopersmith 1987). Therefore, male choice might be expected and, indeed, there have been several studies demonstrating male choice in Zebra Finches (Burley et al. 1982, Burley and Coopersmith 1987). In this study we assess the relative strength of male and female choice in Zebra Finches by comparing such choice under controlled conditions.

Many cues are likely to be involved in mate assessment (Burley 1981, ten Cate 1985), including courtship behavior, song, and visual appearance. Recent sexual-selection studies have emphasized that these cues are often correlated with condition or general health of the prospective mate (Hill 1991, McComb 1991, Price et al. 1993). Individuals in good condition are expected to be favored as mates, either because these individuals are of high genetic quality (Hamilton and Zuk 1982, Iwasa et al. 1991), in which case the benefits of choice accrue in the fitness of offspring, or because they provide direct material benefits (Reynolds and Gross 1990, Price et al. 1993). In our experiments we first manipulated the condition of the finches in order to maximize the likelihood of demonstrating choice.

Methods.—We purchased or hand-raised 20 female and 20 male Zebra Finches. Birds of each sex were separated into two groups of 10 by mass. Mass has been shown to be correlated with nutrition during

TABLE 1. Statistics ($\bar{x} \pm$ SD) for feather-wear scores and mass of birds used in choice tests ($n = 10$ in each group). Birds scored and weighed on day of choice test.

	Condition of			
	Males[a]		Females[b]	
	Good	Poor	Good	Poor
Feather wear	3.6 ± 0.5	2.5 ± 1.1	3.6 ± 0.7	3.0 ± 1.1
Mass (g)	14.0 ± 0.7	12.5 ± 1.6	13.9 ± 0.7	12.8 ± 1.1

[a] Differences between good- and poor-condition males were significant for both feather wear (Mann-Whitney U-test; $P < 0.05$) and mass ($P < 0.01$).

[b] Differences between good- and poor-condition females were significant for mass only (Mann-Whitney U-test; $P < 0.05$).

growth (Boag 1987), although it is also affected by other factors such as genotype. The heaviest 10 individuals were maintained two to a cage on a diet of lettuce, egg, vitamins, olive oil, and seed. These are referred to throughout as good-condition birds. The lightest 10 individuals were maintained 5 to a cage on a diet of seed only. These are referred to as poor-condition birds.

All finches were adults (>four months old) when they were assigned to groups. The sexes were visually isolated from each other. Finches were maintained in these conditions for one month before any trials were run. We emphasize that any observed choice may be based on mass, condition, or some other cue. Knowledge of the basis of choice is not critical to evaluating the results, which are used to compare the relative intensities of male and female choice.

On the day of a given choice test, the finches to be used were weighed, examined visually, and scored on the following scale of 1 to 4 for overall appearance and feather wear: (1) unhealthy, feathers missing or very worn; (2) healthy, missing feathers; (3) healthy, feathers present but noticeably worn; and (4) healthy, feathers in good condition. Burley and Coopersmith (1987) found that beak color was used as a cue in mate choice. We attempted to score birds for beak color using a glossy Munsell color chart, and were unable to detect any differences.

For choice tests, we modified the design of ten Cate and Mug (1984). Individual finches were placed in a central cage. This cage was flanked by two cages; each contained one of the two finches whose attractiveness was to be compared. The two flanking cages were 0.5 m wide and the central cage was 2 m wide. We put four perches across the central cage. There was a perch 10 cm from each flanking cage and two others in the middle of the cage. We always placed the finches in their respective cages at least 1 h prior to starting observations. Trials lasted 40 min. The flanking cages were exchanged after 20 min to ensure that there was no bias toward a given side. We recorded the total amount of time spent by the focal finch on a perch next to each of the stimulus finches. In female-choice tests where a female was presented with two males, we counted the number of times each male sang his

courtship song. In male-choice tests, where a male was presented with two females, we counted the number of times the male sang to each female.

For the first series of tests, which were run over a two-week period, a good-condition male was paired with a poor-condition male for a total of 10 stimulus-pairs. Two 40-min trials were run with each stimulus pair of males. In one trial, a good-condition female was tested for choice, and in the other trial a poor-condition female was employed. We alternated the order in which the good-condition and poor-condition females were tested from one stimulus pair to the next. Each of the 20 females was used once. After completing these trials, we conducted a series of trials in which we examined male choice of females, following the same procedures.

Results.—Diet and crowding had no obvious affect on adult mass, which remained approximately unchanged across the 70 days of the experiment (with the exception of one male in the poor-condition group whose mass increased). Males maintained in the crowded conditions on the low-nutrition diet showed greater feather wear than those maintained in the better environment (Table 1). Since the initial assignment of birds was made on the basis of size and not feather wear, it is probable (but not certain) that wear was a result of subsequent crowding. Males, in particular, fought a great deal in the crowded conditions.

The focal females chose to spend more time with the good-condition male (Fig. 1). In order to compare choice among the two groups of males, we used a repeated-measures ANOVA where the replicates are the two females per male pair. There was a significant difference in the time females chose to spend near the good-condition male ($\bar{x} = 1{,}041 \pm$ SE of 156 for good-conditioned males, 581 ± 72 for poor-condition males; $F_{1,10} = 14.8$, $P < 0.01$). This difference actually underestimates the strength of female choice because one poor-condition male weighed more than his counterpart from the good-condition group and the heavier male was preferred (Fig. 1). The song rate of the good-condition males was lower than that of the poor-condition males ($\bar{x} = 40.4 \pm$ SD of 36.9 songs in the 40 min of a single test vs. 75.6 ± 121.7 songs), but these values are not significantly different (Mann-

Whitney U-tests, $P > 0.1$) and there was considerable intermale variability. Some males sang continuously, while others did not sing at all.

Male choice of females followed the same trend as female choice of males (Fig. 1). Given a choice between two females, one from each group, the focal male spent more time with the good-condition female ($\bar{x} = 1,293 \pm$ SE of 394 for good-condition females, 612 ± 281 for poor-condition females; $F_{1,10} = 10.5$, $P < 0.01$). The number of songs uttered to the good-condition females was higher than the number uttered to the poor-condition females ($\bar{x} = 34.8 \pm$ SD of 52.9 vs. 192. ± 27.8 songs), but this difference was not significant (Mann-Whitney U-tests, $P > 0.1$).

We compared the strength of the choice of poor-condition and good-condition birds (Fig. 1). Choice was largely attributable to the poor-condition birds. Good-condition females showed no obvious preference (paired t-test comparing proportion of time spent near good-condition male with that near poor-condition male; $t = 1.2$, df $= 9$, $P > 0.1$), whereas poor-condition females showed a strong preference ($t = 4.2$, $P < 0.01$). Similarly good-condition males showed no clear preference for either kind of female ($t = 0.7$, $P > 0.1$), but preference among the poor-condition males was close to significance ($t = 1.9$, $0.05 < P < 0.1$). We have no good explanation for these findings. It is possible that the choice we measured may not reflect mating decisions, but instead measures a tendency of birds to preferentially associate with healthier individuals, and this may be more to the advantage of poor-condition birds.

Discussion.—Even if choice of mate is not directly being measured, both males and females exercise choice, and there is no reason to think that this should not apply in mate decisions. The main result is that both males and females spent more time with the prospective mate from the good-condition group, with no obvious differences between the sexes in the strength of their choice. Male choice has been emphasized in species where the male takes the dominant role in raising the offspring, as in many species of fish (e.g. cichlids and sticklebacks; Ferno and Sjolander 1976, Weber and Weber 1976, Barlow et al. 1977), but it should also be expected whenever males invest in offspring and the number of matings are limited. Males have been observed to mate selectively in a number of different taxa, including mammals, isopods, insects, and amphibians (for reviews, see Dewsbury 1982, Clutton-Brock and Vincent 1991).

In monogamy, there is no direct correspondence expected between strength of mate discrimination and the intensity of associated sexual selection (Kirkpatrick et al. 1990). Our results suggest that male choice of mate can be as strong as female choice in Zebra Finches, but this apparently translates into stronger sexual selection on males, because males are brighter than females. Both further laboratory and field studies
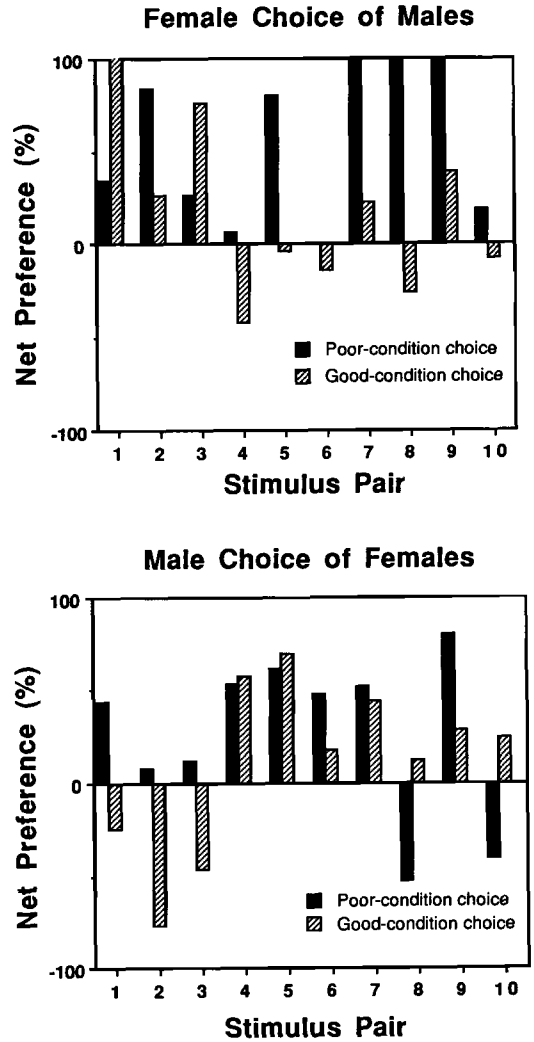

Fig. 1. Results of choice tests. Each set of two bars refers to two trials with one pair of stimulus birds. In one trial a finch from poor conditions (first bar) was tested for choice, and in the other a finch from good conditions (second bar) was used. Net preference calculated as percentage of time spent associating with good-condition finch minus percentage of time spent with poor-condition finch (all time spent in center of cage was excluded in calculating proportions). Above: Female choice of males. In stimulus pair 4, poor-condition male was heavier than good-condition male. The former was preferred by one female. Below: Male choice of females.

are needed to determine the relationships among male choice, female choice, and sexual selection.

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Turnover of ^{13}C in Cellular and Plasma Fractions of Blood: Implications for Nondestructive Sampling in Avian Dietary Studies

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The assay of naturally-occurring stable isotopes of carbon and nitrogen in avian tissues to infer diet offers a number of advantages over conventional dietary investigations (Hobson and Sealy 1991, Hobson and Clark 1992a, b). For example, because stable-isotopic compositions of a consumer's tissues can be related ultimately to those in its diet (reviewed by Peterson and Fry 1987), this technique provides a