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Female zebra finches choose extra-pair copulations with genetically attractive males

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SUMMARY

One way that sexual selection for genetic benefits could operate in monogamous species is through female choice during extra-pair copulations (EPCs). EPCs are common in monogamous species, and field studies are consistent with the hypothesis of females choosing genetically attractive males for EPCs. Here I show that female zebra finches actively solicit and perform EPCs with males that are more attractive than their mates. Attractive males have higher song rates, have sons with higher song rates, and fledge heavier offspring. This provides a mechanism for sexual selection in monogamous species, and is consistent with 'good genes' models of sexual selection.

1. INTRODUCTION

When should females in monogamous species choose males for genetic rather than non-genetic benefits? As both males and females tend to care for offspring in monogamous species, a female is generally expected to choose her mate on the basis of resources important to reproduction (Alatalo *et al.* 1986; Kirkpatrick 1985), rather than solely on genetic traits which will affect her offspring's reproductive success or survival (Darwin 1871; Fisher 1958; Hamilton & Zuk 1982; Lande 1981). However, males in many monogamous species display elaborate secondary sexual characters, comparable with those found in polygynous species, which are assumed to have evolved through sexual selection. Such sexually selected characters could either be 'good genes' traits (Andersson 1986; Hamilton & Zuk 1982; Pomiankowski 1987), selected for associated viability genes all offspring would inherit, or 'Fisherian' traits (Fisher 1958; Lande 1981), selected for the mating advantage male offspring would gain by inheriting the trait. Darwin (1871) suggested that sexual selection for genetically based male traits could operate in a monogamous species through more 'attractive' or 'preferred' males pairing with more fecund females. This appears to be the case in the great tit (Norris 1990) and the swallow (Møller 1988).

Another way that sexual selection for genetic benefits could operate in a monogamous species is through extra-pair copulations (EPCs) if these were being achieved by a non-random subset of the male population. Some ways in which a non-random subset of males might achieve EPCs include more dominant males forcing EPCs on a female, or outcompeting her

mate for access to her, at which point she might passively accept an EPC. Alternatively, females might choose to have EPCs with attractive males. Genetic analyses of parentage in several avian species has shown that EPCs account for a high percentage of offspring in species previously thought to be monogamous (see review in Westneat *et al.* (1990)).

There is some evidence that a non-random subset of males achieve EPCs. Male swallows (Møller 1988) with experimentally lengthened tails had higher EPC rates than other males. Further, females whose mates had experimentally shortened tails performed EPCs at a higher rate than other females. In all observed EPCs in black-capped chickadees (Smith 1988), the dominance rank of the EPC male was higher than that of the female's mate.

The aim of this experiment was to determine the role of active female choice in EPCs, using the zebra finch as the study species. Zebra finches are monogamous, sexually dimorphic and breed in colonies, where the opportunities for EPCs should be high. EPCs are known to occur in the wild (Birkhead *et al.* 1988). The female actively solicits copulations in a distinctive and readily identified display, flattening out her body and shivering her tail sideways (Morris 1954).

2. METHODS

The experiments described here involved introducing breeding females to males to high and low attractiveness to determine whether they selectively have EPCs with more attractive males. Male attractiveness was measured as follows (see Houtman (1990, 1992) for more details on experimental design). Males (nine in group 1, eight in groups 2 and 3) were placed in small cages surrounding a larger central cage. Females were placed in the central cage, and the amount of time spent on a perch in front of each male's cage was monitored. The proportion of a female's total visiting time that she spent with each male (during repeated trials lasting

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1 h) was used as an indicator of her preference for him. Females significantly agreed on the relative attractiveness ranking of males (Kendall's test of concordance: group 1, $\chi^2 = 19.95$, $p < 0.05$, $n = 11$; group 2, $\chi^2 = 29.94$, $p < 0.001$, $n = 8$; group 3, $\chi^2 = 18.93$, $p < 0.05$, $n = 10$).

After their attractiveness was determined, males were randomly assigned partners from the females that had ranked them, and bred in individual cages for six months. To synchronize the breeding cycle of all pairs for the EPC trials, nestboxes were shut off and re-opened several weeks later. A female's EPC trials were started the day she laid her first egg upon re-opening the nestbox and completed within 3 d. This time period was chosen as it is within the female's fertile period (Birkhead *et al.* 1989) and can be accurately determined. The mates of the test males were also in the egg-laying stage of breeding. As most copulations occur during the early morning (Birkhead *et al.* 1989), EPC trials were run in the first 2.5 h after the aviary lights went on.

An EPC trial began with a female being separated from her mate, by putting an opaque divider across their cage. The test male was then immediately introduced into the female's side of the cage for 30 min. The trial was videotaped and later analysed by an observer who had no knowledge of the males' attractiveness rankings.

Each female underwent two EPC trials, one with a male she had ranked of low attractiveness (≥ 4 of 8 or 9) and one with a male she had ranked highly attractive (≤ 3 of 8 or 9). The order of trials was randomly determined. All males were used, so each male was only introduced to two females. Each bird (both male and female) was used at most once per day. Out of the 25 pairs, only the 18 pairs which had bred successfully in the past were tested (successful breeding was not related to attractiveness: logistic regression, $\chi^2 = 0.28$, $n = 25$, d.f. = 1, $p > 0.5$).

3. RESULTS

Of the 36 trials, six resulted in an EPC. Only females with unattractive mates (rank ≥ 4 of 8 or 9) solicited EPCs. All EPCs were performed by females introduced to a male more attractive than their mate (one-tailed binomial test on copulation and more/less attractive, $n = 6$, $p < 0.02$; figure 1). To determine whether the probability of performing an EPC increased with an increasing difference in attractiveness between the female's mate and the introduced male, one trial for each female was randomly extracted from the data set (although the EPCs were formed by six different females and six different males, it might be argued that female behaviour in two trials is not independent). The probability of an EPC occurring correlated strongly with the difference in attractiveness between a female's mate and the introduced male (logistic regression, $\chi^2 = 5.38$, $n = 18$, d.f. = 1, $p < 0.01$, one-tailed test). Every successful copulation (with cloacal contact) was preceded by a female soliciting a copulation, showing that these were not forced EPCs. Further, there was no relation between the number of attempted copulations during a trial and an EPC occurring (logistic regression, $\chi^2 = 0.18$, $n = 36$, d.f. = 1, $p > 0.8$), suggesting that males did not wear down the resistance of unwilling females.

To uncover the traits that determined male attractiveness, males' mean attractiveness scores were regressed against a suite of morphological, plumage and behavioural characters (see Houtman (1990, 1992)

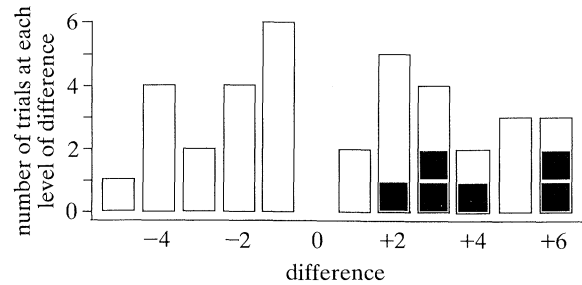


Figure 1. The number of EPCs (filled squares) in relation to the difference in attractiveness between a female's mate and the introduced male. Difference scores were calculated by subtracting the introduced male's attractiveness rank (e.g. attractive = rank 2 of 8) from the female's mate's attractiveness rank (e.g. unattractive = rank 8 of 8; difference score, $8 - 2 = 6$). Open boxes show all trials. The average attractiveness difference in trials without EPCs is 0 ± 0.58 ; in trials with EPCs it is 4 ± 0.68 .

Table 1. *Correlates of male attractiveness*

(Song rate is the amount of song (number of song phrases \times length of song phrase) a male sang in the first 15 min after being introduced to a female. Beak colour was compared with Munsell colour chips, which were then ranked from most to least bright by four people unfamiliar with the research. The average ranking of the chip corresponding most closely to a male's beak colour was used as a measure of beak brightness. Sample sizes were not large enough to allow multivariate analyses of all traits at once. Therefore, traits were initially regressed individually on preference scores. Traits that correlated significantly with preference scores were then combined in a multivariate analysis to determine their partial effects. Song rate data were not available for two males. See Houtman (1990, 1992) for more methodological detail.)

	<i>F</i>	<i>n</i>	<i>p</i>
linear regression			
song rate	21.3826	22	0.0002
beak brightness	10.9541	24	0.004
multiple regression			
song rate	24.29	22	0.0001
beak brightness	2.12	22	0.25

for more methodological detail). Song rate and beak brightness were significantly correlated with attractiveness (and each other: Pearson's $r = 0.4536$, $n = 22$, $p < 0.05$) (table 1). However, only song rate had a significant residual effect on attractiveness when song rate and beak brightness were included together in a multiple regression (table 1).

Parent-offspring and sib-sib heritability estimates were calculated (Falconer 1981) to determine whether the sons of males with high song rates also display high song rates. Both estimates were highly significant (table 2). To exclude the possibility that males learned their song rate from their fathers, 11 hatch-day chicks were swapped with same-age chicks in eight nests. The six male offspring resemble their true father, not their adopted father, in song rate (table 2). Although the sample size is small, the results are significant and support the results of the larger breeding experiment.

Table 2. Heritability estimates (h^2) of song rate

(Parent-offspring heritability estimates equal twice the slope of the regression of offspring song rate on father's song rate. Standard errors are also doubled. Sib-sib heritability estimates are obtained by doubling the intra-class correlation coefficient calculated from the variance components obtained in a one-way ANOVA.)

	h^2	s.e.	F	parents	offspring	p
parent-offspring estimate	0.67	0.20	11.11	11	24	0.01
sib-sib estimate	0.80	—	2.99	11	24	0.05
swap experiment						
true parent-offspring estimate	1.02	0.10	25.11	6	6	0.005
adoptive parent-offspring estimate	-0.15	2.60	0.003	6	6	0.96

'Good genes' traits (Hamilton & Zuk 1982; Andersson 1986; Pomiankowski 1987) should be correlated with measures of male and offspring viability, whereas no such correlations are expected with 'Fisherian' traits (Fisher 1958; Kirkpatrick 1982; Lande 1981). In zebra finches, song rate is correlated with clavicular fat level (0-5 scale (Gosler 1987), Pearson's $r = 0.3784$, $n = 23$, $p < 0.04$, one-tailed test), a measure of male condition that is not confounded by general body size. Song rate is also correlated with average offspring mass at independence (multiple regression: $F = 7.65$, $n = 14$, $p < 0.005$, one-tailed test; see Houtman (1990) for more methodological detail). Mass at fledging is correlated with survival in other species (Perrins 1965; Garnett 1981), suggesting that it may be an important component of offspring viability in zebra finches.

4. DISCUSSION

Of all females tested, 33% (six of 18) chose to have an EPC when presented with only two possibilities of doing so. It might be argued that, as these birds were assigned partners, they would be more likely to have EPCs than birds in more natural circumstances, or might even simply be trying to abandon their mate and pair with the introduced male. This does not appear to be the case. Birds assigned mates in this experiment had similar breeding success (32% did not breed) to those in an aviary study allowing birds to choose their own mates (33% of paired birds did not breed (Birkhead *et al.* 1989)). Further, the birds used in this experiment were from the subset of successfully breeding birds, so females whose mates were unacceptable were not included in the experiment. Finally, the rate of EPCs observed in this experiment, 33% of all females, is well within the range of naturally occurring EPC rates identified through genetic analyses of parentage (several recent studies estimate up to 20-40% of offspring are due to EPCs (review in Westneat *et al.* 1990)). These lines in evidence suggest that the observed EPCs are not artefacts of the experimental design.

There are at least four potential benefits of an EPC to a female: increased fertility (Buitron 1983), parental care (Davies 1985), genetic variability (Gavin & Bollinger 1985), or genetic benefits (Andersson 1986;

Fisher 1958; Hamilton & Zuk 1982; Lande 1981). Increased fertility seems unlikely, as all of the females had successfully raised several broods with their mate. Increased parental care cannot explain why female zebra finches solicit EPCs, as zebra finches actively defend nests against conspecific intruders (R. Zann, personal communication). If a male who had achieved an EPC attempted to feed a female's nestlings, the resident male would drive him off. This is supported by recent studies of EPCs (Frederick 1987; Westneat 1988) which found that only the putative father, and not the true father, fed offspring. Finally, if females were attempting to increase the genetic variability of their offspring, all females would be predicted to solicit EPCs. However, only females with unattractive mates solicited EPCs, and they only solicited males of higher attractiveness than their mates. Thus, only female choice for genetic benefits can fully explain the pattern of EPCs observed.

Whatever other factors may be influencing the distribution of EPCs (Frederick 1987; Walker 1980; Westneat 1988; Westneat *et al.* 1990), EPCs are biased towards males with high song rates. Clayton & Pröve (1989) also found that female zebra finches prefer high song rates when male song is played to them. As song rate appears to be heritable, and correlates with offspring viability, the result will be the increasing representation of genes coding for high song rates in the following generations. Therefore, choice by female zebra finches for EPCs with males more attractive than their mates provides evidence of female choice for genetic benefits, and is consistent with 'good genes' models of sexual selection.

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