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Male phenotype and ejaculate quality in the zebra finch *Taeniopygia guttata*

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SUMMARY

We tested the idea that female preference for relatively attractive extra-pair males arises because the morphological and behavioural features that females find attractive covary with ejaculate features: Sheldon's (*Proc. R. Soc. Lond.* B **257** 25–30 (1994)) phenotype-linked fertility insurance hypothesis. Two phenotypic traits that female zebra finches find attractive in males are song rate and symmetry of chest band plumage, but we found neither of these to be significantly related to any of the following ejaculate features: number of sperm, percentage of live sperm, absolute number of sperm, sperm length or sperm swimming velocity. Furthermore, and surprisingly, we did not find the predicted negative relationship between male song rate and fluctuating asymmetry of chest band plumage. Because most ejaculate features (except sperm numbers in rested males) show low levels of repeatability, it is unlikely that female zebra finches could reliably obtain a better quality ejaculate by choosing to copulate with a more attractive male. There was thus no evidence for the phenotype-linked fertility insurance hypothesis. Nor did we obtain evidence for the more general fertility insurance hypothesis: we found that female zebra finches paired to a vasectomized male, and hence receiving no sperm, were no more likely to seek an extra-pair copulation than females paired to an intact male.

1. INTRODUCTION

In a large number of socially monogamous bird species females actively seek and engage in extra-pair copulations which result in extra-pair paternity (Birkhead & Møller 1992, 1995). The advantages of extra-pair fertilisations for males are obvious, but there is considerable debate over the benefits that females birds obtain from copulating with additional males (reviewed in Westneat *et al.* 1990; Birkhead & Møller 1992; Sheldon 1994). Two main types of potential benefit have been identified: (i) direct benefits, such as fertility insurance (e.g. Gibson & Jewell 1982; Wetton & Parkin 1991); and (ii) indirect or genetic benefits (Westneat *et al.* 1990). Because there is likely to be strong selection against male infertility (Alcock *et al.* 1978; Westneat *et al.* 1990) and because infertility appears to be rare in the wild (Birkhead & Møller 1992), some authors have assumed that female birds are unlikely to obtain direct fertility benefits from copulating outside their pair bond. Instead, the fact that females often engage in extra-pair copulations with males that are more attractive than their partner (for examples, see Smith 1988; Møller 1988; Kempenaers *et al.* 1992) has been interpreted as evidence for genetic benefits (see, for example, Møller 1992). By performing one or more extra-pair copulations with a male of genetically higher quality than their partner, females are thought to obtain genes which increase either the viability or attractiveness of their offspring. However, 'good genes' ideas are controversial because strong directional selection resulting from mate choice will deplete genetic variation in those male traits preferred by females and in populations at equilibrium, fitness should not be heritable (see, for example, Andersson 1994). Nonetheless, there is some evidence that females obtain genetic benefits from their choice of partner (Bakker 1993; Norris 1993; Petrie 1994; see also Pomiankowski & Møller 1995; Burt 1995).

Although many authors favour the idea of indirect benefits over direct benefits, Sheldon (1994) has argued that in terms of extra-pair copulation behaviour in birds, the evidence for the genetic benefits hypothesis is no better than that for the fertility insurance hypothesis. Specifically, Sheldon (1994) has pointed out that if functional fertility covaries with male phenotype, females are just as likely to obtain direct as indirect benefits by choosing to perform extra-pair copulations with an attractive male. This is a special case of the more general fertility insurance hypothesis (Gibson & Jewell 1982; see also Birkhead & Møller 1992), and we refer to it here as the phenotype-linked fertility hypothesis. The aim of this study was to test: (i) the phenotype-linked fertility insurance hypothesis, that male phenotypic characters covary with ejaculate features; and (ii) a prediction from the more general fertility insurance hypothesis, that females receiving no sperm from their partner are more likely to seek extra-pair copulations than those receiving normal numbers of sperm. This prediction assumes that females can determine whether they have been inseminated and hence assess male fertility directly, rather than indirectly through phenotypic traits. We show that there are no significant correlations between male phenotype and ejaculate quality and that females paired to vasectomized males are no more likely to seek extra-pair copulations.

2. METHODS

The study was conducted on domesticated zebra finches *Taeniopygia guttata* from a colony established at the University of Sheffield since 1985, but with regular influxes of unrelated birds. The zebra finch is a small (12–15g) colonial estrildine finch, native to Australia and the Lesser Sunda Islands. It is sexually dimorphic: males possess four plumage features not found in females (black and white chest bands, black breast band, orange cheek patch, white-spotted chestnut flanks), and have a redder beak than females. Although socially monogamous, extra-pair behaviour is frequent and results in extra-pair paternity both in the wild and in captivity (Birkhead *et al.* 1988*a*, *b*, 1990). In addition, mate choice has been studied extensively in captive zebra finches (Burley *et al.* 1982; Burley & Coopersmith 1987; Burley *et al.* 1994; Ratcliffe & Boag 1987; Houtman 1992; Collins *et al.* 1994; Sullivan 1994; Swaddle & Cuthill 1994*a*, *b*,; Swaddle 1995) and among birds in the wild (Zann 1994). In the present study birds were maintained on a 14:10 light:dark cycle, with *ad libitum* food, water and grit, in cages measuring 50 cm long × 45 cm × 45 cm. All behavioural studies involved birds without colour rings: birds bore a single, metal numbered ring.

(*a*) *Phenotypic characters*

Several studies have found that in mate choice experiments female zebra finches prefer males with higher song rates (Immelmann 1959; Sonneman & Sjolander 1977; Ten Cate & Mug 1984; Ten Cate 1984; Ratcliffe & Boag 1987; Houtman 1992; Feil & Curio 1993; Collins *et al.* 1994), redder beaks (Burley & Coopersmith 1987; but see Collins *et al.* 1994, Burley *et al.* 1994; Price & Burley 1994), and more symmetrical chest band plumage (Swaddle & Cuthill 1994*a*). We measured each of these features for ten male zebra finches. Beak colour was scored subjectively on a scale of 1 (light orange) to 6 (dark red). We did not attempt any more sophisticated scoring of beak colour because Collins *et al.* (1994) have shown that the studies of Burley & Coopersmith (1987) and Burley & Price (1991) which reported that beak colour was important in mate choice, were confounded by song rate (see also Burley *et al.* 1994).

Song rate was scored by presenting each male with five different females, one on each day for five consecutive days, and recording the mean amount of time that the male sang during the first five minutes after the female was introduced. This is effectively the same method as that used by Houtman (1992), except that she used a 15 min period: we restricted our scoring to five minutes because 50% of the song activity occurred during this time. To minimize any effect of differences in the attractiveness of females, each male was presented with five different randomly chosen females. The mean percentage time spent singing by each male was used as a score of male song rate.

In assessing potential partners, female zebra finches are sensitive to fluctuating asymmetry (FA), small random deviations in morphological traits that would otherwise be bilaterally symmetrical (Swaddle & Cuthill 1994*a*, *b*). Female zebra finches prefer symmetrical males, both in terms of an artificial trait (colour rings) (Swaddle & Cuthill 1994*a*) and a natural trait, the fine black and white chest bands (Swaddle & Cuthill 1994*b*). The symmetry of chest band plumage was measured in exactly the same way as in Swaddle & Cuthill (1994*b*) because John Swaddle kindly undertook these measurements of the birds. This comprised measuring the relative amount of black and white plumage either side of the median line (see Swaddle & Cuthill 1994*b*): chest band FA was expressed as the absolute difference between the left and right sides. Since Burley & Price (1991) had previously found the prominent black breast band (which lies ventral to the fine chest bands) to affect mate choice, we also measured this trait: by video recording birds under standard conditions in a standard, upright posture and then tracing the area (mm^2) of the breast band.

(*b*) *Ejaculate features*

For each of the ten males we obtained between three and six entire ejaculates using a model female fitted with a false cloaca, a method which provides a reliable measure of natural ejaculate size (Pellatt & Birkhead 1994). Ejaculates were collected at least seven days apart, that is from rested males, since we have shown elsewhere (Birkhead *et al.* 1995) that this time period ensures that males have fully replenished sperm supplies. The number of sperm in each ejaculate was counted using an Improved Neubauer chamber, as described elsewhere (Birkhead *et al.* 1993). Using a subsample from each ejaculate we determined, first, the average path velocity (μm. s^{-1}) of 100 motile spermatozoa at 35 °C using computer-aided sperm analysis (Hobson Sperm Tracker). Although we have not directly tested for an association between sperm velocity and fertility in the zebra finch, extensive studies of poultry have shown that the numbers of sperm, the proportion of live sperm and their motility are all strongly and positively correlated with fertilising success (for examples, see Lake & Stewart 1978; Wishart & Palmer 1986). In addition, in humans sperm velocity is strongly correlated with fertilizing ability (Holt *et al.* 1989). Second we measured the proportion of live spermatozoa, using the nigrosin-eosin live-dead staining method described by Cooper & Rowell (1958), and used this to calculate the absolute number of live sperm per ejaculate. Finally, we measured the total length of sperm to the nearest μm using computer assisted image analysis (Videoplan).

We used repeatability analysis (Falconer 1960, 1981; Lessells & Boag 1987) to assess: (i) the reliability of our measurements of particular traits; and (ii) the consistency of traits within males. We attempted to obtain all variables for the same ten males but in some instances a male died before we could obtain all the information. To check whether our results were affected by samples sizes, we obtained data for 8–11 additional males for the two variables that have most convincingly been shown to affect female choice (male song rate and chest band FA: see above) and for ejaculate features based on a single (rested) ejaculate. Information derived from ten males is referred to as the restricted data set, and from up to 21 males, as the extended data set.

(*c*) *Behavioural observations*

The second prediction, that females which obtain no sperm from their partner should seek extra-pair copulations, was tested by using a different set of birds. Twenty females were each paired with a vasectomized male (Birkhead & Pellatt 1989) and allowed to initiate a normal breeding cycle. On the day the female laid the first egg the pair male was temporarily removed and the female presented with another (intact) male for five minutes with which she could potentially perform an extra-pair copulation. The experiment was then repeated with the same females using intact males as the male partner and an intact male as the potential extra-pair copulation partner. We recorded whether the female solicited or accepted an extra-pair copulation in both situations.

3. RESULTS

Mean values for all the variables are summarized in table 1. This table also presents estimates of the repeatability of these variables. In all cases measurement reliability was high. In terms of male consistency, song rate was repeatable, as was the number of sperm per ejaculate and the length of sperm. We did not measure the repeatability of chest band FA or black breast band because there is no *a priori* expectation that these features should be repeatable between moults.

The first prediction we tested was that phenotypic and behavioural characters and ejaculate features covary. However, comparing mean values of all parameters for ten males, only one of 26 comparisons was significant: area of black breast band and sperm numbers ($r_s = -0.733$, $p = 0.038$). Because this negative relation was not predicted we consider it to be a chance effect resulting from the high number of comparisons.

Few of either the phenotypic characters or the ejaculate features were correlated with each other (table 2). Unexpectedly, song rate and chest band FA, the two variables which have been shown to be features females use to discriminate between males (above), which we expected to be negatively correlated, were not, in either the restricted data set ($r_s = 0.433$, $n = 10$, $p = 0.203$; table 2) or the extended data set ($r_s = 0.053$, $n = 18$, $p = 0.818$).

Only one of the other relations examined using the extended data set was significant: chest band FA versus sperm length ($r_s = 0.554$, $n = 17$, $p = 0.027$). The other relations with chest band FA were as follows: sperm numbers, $r_s = 0.053$, $n = 18$, $p = 0.828$, sperm velocity, $r_s = 0.306$, $n = 16$, $p = 0.236$, percentage live sperm, $r_s = -0.158$, $n = 18$, $p = 0.514$. Song rate was not significantly correlated with any ejaculate feature,

Table 1. *Mean values for phenotypic characters and ejaculate features, and repeatability estimates for ten male zebra finches*

			repeatability[a] (r_r) measurement reliability				repeatability (r_c) male consistency			
character	mean	s.d.	F	d.f.	p	r_r	F	d.f.	p	r_m
chest band FA	0.06	0.06	5.89	9, 36	< 0.001	high	—	—	—	—[b]
black breast band (mm^2)	149.64	42.77	19.56	8, 9	< 0.001	64.34	—	—	—	—[b]
song rate	12.55	7.02	524.50	9, 10	< 0.001	99.62	7.17	9, 40	< 0.0001	38.15
beak colour	4.10	1.20	14.11	24, 25	< 0.001	86.79	3.17	6, 7	0.079	51.26
number of sperm ($\times 10^6$)	9.47	4.14	91.86	9, 40	< 0.001	94.78	3.88	9, 33	< 0.002	40.38
sperm length (µm)[c]	70.21	5.50	47.76	49, 50	< 0.001	95.90	69.43	9, 190	< 0.001	87.25
percent live sperm	79.61	10.54	30.33	9, 30	< 0.001	88.00	1.65	9, 37	> 0.1	17.86
absolute number live sperm ($\times 10^6$)	7.72	3.75	—	—	—	—[d]	2.08	9, 37	0.0675	22.15
sperm velocity (µm s^{-1})[e]	29.16	6.19	13.21	9, 40	< 0.001	70.94	0.56	9, 27	> 0.8	-17.12

[a] Repeatability was calculated using ANOVA as described by Lessells & Boag (1987), except for chest band FA which was calculated using a mixed model ANOVA (described by Swaddle *et al.* 1994), which does not allow us to calculate a repeatability value. Nevertheless, the p value indicates that repeatability for this variable is very high.

[b] We did not calculate r_c for chest band FA or black breast band size because there is no *a priori* reason for these to be consistent between moults.

[c] Sperm length r_r was estimated by measuring 50 sperm twice from within a single ejaculate.

[d] We did not calculate r_r for absolute number of live sperm because this is calculated from the number of sperm and percent live sperm, both of which are highly repeatable.

[e] Sperm velocity r_r was estimated by using mean values from five groups of 100 sperm each from a single ejaculate for ten different males. Sample sizes (d.f.) vary for two reasons: (i) measurements of r_r for song rate and beak colour were made using preliminary data; and (ii) because some birds died during the study period (e.g. beak colour measured twice six months apart).

Table 2. *Spearman Rank correlation matrix showing correlation coefficients for morphological, behavioural and ejaculate features for 10 male zebra finches*

	black breast band	song rate	beak colour	no. of sperm	sperm length	percent live sperm	absolute live sperm	sperm velocity
chest band FA	0.190	0.433	−0.067	−0.450	0.567	−0.267	−0.250	0.617
black breast band		−0.550	0.533	-0.733^{a}	0.067	−0.233	−0.517	0.233
song rate			0.045	0.212	0.612	0.176	0.273	−0.067
beak colour				−0.221	0.312	−0.003	−0.197	0.003
no. of sperm					−0.297	0.309	0.842^{b}	−0.139
sperm length						−0.176	−0.248	0.297
percent live sperm							0.200	-0.673^{a}
absolute live sperm								−0.079

$^{a} = p < 0.05$ $^{b} = p < 0.02$ (two-tailed tests)

although the relation with sperm length approached significance ($r_s = 0.442$, $n = 20$, $p = 0.054$), the other relations were: sperm velocity, $r_s = 0.298$, $n = 19$, $p = 0.206$, percentage live sperm, $r_s = -0.031$, $n = 21$, $p = 0.890$.

The second prediction was that females receiving no sperm from their partner would be more likely to engage in extra-pair copulation. However, there was no evidence for this. Of twenty females paired to vasectomized males, only one engaged in an extra-pair copulation when presented with an intact male. When the females were paired to intact males, again only one female (a different one) performed an extra-pair copulation when presented with another male. Obviously, this difference is not significant, and shows that those females paired to vasectomized males and receiving no sperm are no more likely to seek an extra-pair copulation than those females obtaining sperm from their intact partner.

4. DISCUSSION

Our results show that none of several phenotypic characters, such as song rate or fluctuating asymmetry of chest bands, which on their own have been shown to attract female zebra finches, covary with ejaculate features. These results indicate that female zebra finches could not predict ejaculate quality from these aspects of a male's appearance or behaviour. Furthermore, the repeatability of ejaculate features was generally low, making it less likely that females could reliably obtain a better ejaculate from another male. In addition, the fact that female zebra finches paired to vasectomised males are no more likely to initiate extra-pair copulations than females paired to intact males, indicates that female zebra finches do not perform extra-pair copulations as insurance against infertility. There are several implications of these results.

One potential reason for a lack association between phenotypic, behavioural and ejaculate features is that they exhibit little or no individual consistency. Although song rate was moderately repeatable (table 1), with the exception of sperm numbers and length (see table 2), ejaculate features were not significantly repeatable (table 1). The variability in ejaculate features we recorded in the zebra finch is not unusual: it is also well known in other animals (Amann 1981; see also Birkhead & Petrie 1995). Moreover, the variability in ejaculate features between and within males in nature is likely to be even greater than reported here. In the present study we attempted to minimise variability by using ejaculates from only rested males, but elsewhere we have shown that zebra finch ejaculate features are even more variable in sexually active males (Birkhead *et al.*, 1995): all ejaculate features vary with time since last ejaculation within males, with several variables (sperm numbers, percent live, percent morphologically normal and velocity) declining by 50–70% in two successive ejaculates (Birkhead *et al.* 1995). This means that female zebra finches could rarely if ever predict the quality of ejaculate they would obtain from any particular male, and thus could not predict the quality of ejaculate from a male's phenotypic traits. However, it remains true that by performing extra-pair copulations females reduce the risk of infertility, regardless of whether they can determine which male is most fertile. On the other hand, if general fertility insurance was the main explanation for why female birds engage in extra-pair copulations, we predict that most females should perform extra-pair copulations (Birkhead & Møller 1992): this is not the case in the zebra finch (Birkhead *et al.* 1988*a*, 1990).

Another possible explanation for the lack of association between phenotype characteristics and ejaculate features is that zebra finches outside their native Australia and Lesser Sunda Islands are effectively domesticated (Sossinka 1982). Captive breeding, coupled with artificial selection for traits such as large body size (Sossinka 1982; Zann 1996), may have unintentionally reduced the variance in certain traits and hence made it difficult to detect an association between phenotypic and ejaculate features. It would therefore be worth repeating this study with wild zebra finches.

Assuming that our results accurately reflect what happens among zebra finches in nature, they provide no evidence for Sheldon's phenotype-linked fertility insurance hypothesis. Because there appear to be few other direct benefits that female birds obtain from extra-pair copulations (see Birkhead & Møller 1992), this implies that the main benefit females obtain from extra-pair copulations are genetic. Without critically assessing the alternatives, this is also the implicit conclusion reached by other workers who have examined choice of extra-pair copulation partners in captive zebra finches. Both Houtman (1992) and Burley *et al.* (1994) found that female zebra finches preferentially solicit or accept extra-pair copulations from males that were more attractive in some way than their partner. Houtman (1992) showed that females preferred males with high song rates and because song rate appears to be heritable and correlates with offspring viability, implied that females obtain viability genes for their offspring by seeking extra-pair copulations. Burley *et al.* (1994) on the other hand, showed that females preferred males with red colour rings, and stated that females behave towards males as though these traits were heritable, which if they were, these males would then produce attractive sons. At present there have been no experimental tests in any species to distinguish between viability and attractiveness genetic benefits.

One other aspect of our results was unexpected: we predicted that different phenotypic characters would covary. Specifically, we expected the two characters which have most clearly been shown to be important in female choice, song rate and fluctuating asymmetry of chest bands, to be negatively correlated, yet this was not the case. This indicates that another trait (or traits) may be correlated with female preference, and possibly with ejaculate quality, although the variability in ejaculate quality makes this unlikely. Our results suggest that it would be informative to conduct a study using a large number of birds in which several phenotypic traits are considered in a multivariate analysis in order to assess the relation between them and their relative importance (see, for example, Warner & Shultz 1992).

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