



# Diet, maternal condition, and offspring sex ratio in the zebra finch, *Poephila guttata*

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Where maternal condition affects condition and reproductive potential of offspring differentially with respect to sex, mothers in relatively good condition should produce more of the sex whose fitness is more dependent on condition. We experimentally manipulated body-condition in unmated zebra finches by feeding them for three months on high- or low-quality diets. Birds were then allowed to breed, while keeping the same diets. Females on the lower quality diet were in better condition and hatched significantly more males than females. Poorer condition females hatched an equal sex ratio. Chicks fed on the low-quality diet, but not on the high-quality diet, showed female-biased mortality. These results show that facultative sex ratio manipulation and sex-biased mortality can act together to produce extreme sex ratios in this vertebrate.

**Keywords:** diet; condition; sex ratio; sex-biased mortality; zebra finch

## 1. INTRODUCTION

In sexually reproducing organisms, frequency-dependent selection generally leads to an evolutionarily stable strategy of equal expenditure by parents on offspring of both sexes (Fisher 1930). Where one sex costs more to produce than the other, equal expenditure on the sexes will produce a sex ratio that is biased towards the cheaper sex. In birds, different costs of the sexes could be due to higher metabolic rates (Teather & Weatherhead 1988) or faster growth rates (Teather 1987) of one sex. However, if the fitness returns from investment in sons and daughters differ from each other, then unequal investment in the two sexes will evolve, allowing for the possibility of adaptive manipulation of sex ratios by individuals (reviewed by Charnov 1982). Despite the constraints of chromosomal sex determination (Williams 1979), there is increasing evidence that vertebrates, including birds (Ellegren & Sheldon 1997), can adjust the sex ratios of their offspring in order to increase their fitness.

One situation in which the relative reproductive values of sons and daughters may differ between individual females is where the fitness of offspring of one sex is more dependent on resources received from the parent than is the fitness of offspring of the other sex. Then, parents should produce more offspring of the sex with the greater requirements when resources are plentiful (Charnov 1982). Several studies of avian species have shown sex ratio skews in relation to resource availability (e.g. Patterson *et al.* 1980; Wiebe & Bortolotti 1992), and in some cases the apparent fitness consequences on the offspring have been identified (e.g. Appleby *et al.* 1997; Bradbury *et al.* 1997; Komdeur *et al.* 1997). Similarly, where maternal condition affects offspring condition differentially with respect to one sex such that their future reproductive success is also

affected, mothers in relatively good condition should produce more offspring of the sex whose fitness is more strongly dependent on condition (Trivers & Willard 1973). In American kestrels, *Falco sparverius*, for example, poor condition of either parent increased the likelihood of broods being male-biased (Wiebe & Bortolotti 1992).

The effect of nutrition on maternal condition and offspring sex ratios in birds has not been investigated experimentally (Gowaty 1991). We examined the relationship between sex ratio and parental condition by manipulating condition and resource availability in captive zebra finches, *Poephila guttata*. This species breeds easily in captivity, and previous studies have documented variable sex ratios (Burley 1981, 1982, 1986; Burley *et al.* 1989; but see Immelmann *et al.* 1982; Thissen & Martin 1982).

## 2. MATERIALS AND METHODS

### (a) *Bird husbandry and diet manipulation*

Thirty zebra finches of each sex, from an outbred laboratory colony, were housed in single-sex cages, five birds to a cage. Oyster shell-grit mixture, water and cuttlebone were supplied *ad libitum*, and all cages were kept in the same room, on a 14 h light : 10 h dark lighting schedule. Three cages of each sex were chosen at random and fed on a high-quality diet (HQ) of red and white millet with canary, rape, and flax seed, plus daily fresh lettuce and carotene-enriched rice *ad libitum*. The remainder of each sex were fed on a low-quality diet (LQ) of white millet (12.9% protein) *ad libitum*. After three months, when changes in body condition were assumed to have reached an asymptote, the following biometrics were taken from a random sample of ten birds of each sex from each treatment: (i) mass (to 0.1 g on a Pesola balance); (ii) wing length (maximum chord, in mm); (iii) tarsus length (mm) from the nuchal notch to the furthest extension of the leg when the foot was at a right angle; (iv) muscle score (0–2, in increments of 0.5) over the keel (Gosler 1991); and

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(v) tracheal-pit fat (score 0–5; Gosler 1996). To give a composite measure of body size, the first principal component of wing and tarsus was calculated. Brightness and intensity of bill colour (red) were scored using colour chips (Munsell system). Intensity of bill colour was measured on a scale from 0 to 10, representing a range of colour intensity with a normal distribution averaged at 5. Most intense colours occur at the centre of the range, with less intense colours at the periphery. Bill brightness was measured on a scale from 0 to 5.

Birds were released into two aviaries (16 m<sup>3</sup>), each equipped with 15 nest-boxes, forming breeding groups of either HQ or LQ pairs. The experimental diets continued unchanged throughout breeding, including during chick-rearing. The aviaries faced each other, enabling mate-quality assessment relative to all other individuals. Nests were inspected daily to check chick survival, and chicks were colour-ringed to enable identification. Chicks surviving to independence were unambiguously sexed at day 50 from plumage traits (Zann & Runciman 1994). Any nestlings that died before independence were collected and sexed from liver samples using a molecular method.

### (b) *Molecular sexing*

We used polymerase chain reaction (PCR) to amplify part of the W-linked avian *CHD* gene (*CHD-W*) in females, and its non-W-linked homologue (*CHD-Z*) in both sexes (Griffiths *et al.* 1998). Genomic DNA was extracted from macerated 0.1 g portions of liver with 10 M guanidine isothiocyanate, and isolated by binding onto silica (Boom *et al.* 1990). PCR reactions comprised 50–250 ng of genomic DNA, 200  $\mu$ M of dNTP, 1  $\mu$ M each of primers P2 (5'-TCTGTCATCGCTAAATCCTTT) and P8 (5'-CTCCCAAGGATGAGRAAYTG), 0.375 units *Taq* polymerase (Promega), 1.5 mM MgCl<sub>2</sub>, Promega *Taq* buffer (50 mM KCl, 10 mM tris-HCl, pH 9.0, 0.1% Triton X-100), in a total volume of 10  $\mu$ l. Reactions were performed with the following thermal profile: initial denaturation of 95 °C for 1 min 30 s; 30 cycles of 52 °C for 30 s, 72 °C for 30 s, 94 °C for 15 s; final annealing and extension of 52 °C for 30 s and 72 °C for 3 min, respectively. PCR products were separated on 3% agarose gels and visualized with ethidium bromide. Birds were sexed according to the presence of the PCR products of *CHD-Z* (350 bases; both sexes) and *CHD-W* (384 bases; females only).

### (c) *Statistical analyses*

Most analyses were performed using the GLIM (Generalised Linear Interactive Modelling) package v.4 (NAG 1993), including contingency tables and goodness-of-fit tests. For linear models with several predictor variables, the model simplification procedure of Crawley (1993) was followed. The effect of the interaction term was tested first, and then the effect of each of the predictor variables was tested while other variables were held constant. The statistical significance of including predictor variables in the model was assessed by the change in deviance ( $\Delta D$ ) on fitting each predictor variable, which is distributed approximately as  $\chi^2$ .

For brood sex ratios, the null model was specified with the number of males in a brood as the dependent variable and brood size as the binomial denominator, using a binomial error distribution and a logit link. This eliminates the problems of non-normal and non-constant variances inherent in proportional data (Crawley 1993). Brood sex ratios for each diet were also tested for departure from binomial expectations, using the deviance in the null model and a randomization procedure (supplied by K. Lessells as a GLIM macro routine). This

randomly reallocated sexed chicks across broods, given the original brood sizes, thus deriving binomial variation in sex ratio across broods. After each randomization, the deviance from the null model was compared to that observed in the original data; the proportion of randomizations (10 000 were performed) in which the deviance is greater than the null model equates with the probability of obtaining the observed deviance by chance.

## 3. RESULTS

### (a) *Hatching sex ratios*

The number of chicks of each sex produced on each diet are summarized in table 1. The results suggest that LQ females produced more male chicks than females, whereas HQ females produced an equal proportion of chicks of both sexes. Overall, more male chicks than female chicks were produced on the LQ diet (goodness-of-fit against the Mendelian expectation of equal number of both sexes:  $G_1=6.58$ ,  $p<0.05$ ) but not on the HQ diet ( $G_1=0.31$ , n.s.); the mean brood sex ratio (proportion of males) was significantly higher for the LQ diet compared to the HQ diet (HQ=0.756, LQ=0.473;  $t=2.71$ , 24 d.f.,  $p<0.05$ ; arcsin-transformed brood sex ratios); this was not due to any effect of diet on brood size, since mean brood size was not significantly different between diets (LQ=2.14, HQ=2.52;  $t=1.06$ , 41 d.f., n.s.). However, brood sex ratios within diets were not independent since some pairs had more than one brood, although the mean number of broods per pair did not differ between diets (HQ=1.50, LQ=1.56;  $t=0.24$ , 25 d.f., n.s.). Using data from first broods only (table 1), the overall sex ratio of chicks was still significantly male-biased for the LQ diet ( $G_1=4.28$ ,  $p<0.05$ ) but not for the HQ diet ( $G_1=0.00$ , n.s.). Since sibling sex may not be independent, pseudo-replication was avoided by analysis at the brood level. The distribution of brood sex ratios was significantly different from the binomial expectation of 50% sons for the LQ diet ( $p=0.044$ ; randomization test), but not for the HQ diet ( $p=0.341$ ).

### (b) *Diet and adult body condition*

Adult biometrics and body condition were examined in a linear model, including both sex and diet as two-level factors. There was no significant relationship between sex, diet, or their interaction, and measures of body size (wing chord, tarsus; results not shown). This is to be expected as birds were allocated to their experimental diets after these characters were fully developed. There were also no significant relationships between sex ( $F_{1,37}=0.469$ , n.s.), diet ( $F_{1,37}=0.268$ , n.s.), or their interaction ( $F_{1,36}=2.351$ , n.s.) and body mass, after controlling for body size.

The effect of diet on body condition was examined by logistic regression, using the condition scores as binary dependent variables. Condition scores were grouped into two classes; fat (0=fat score  $\leq 3$ , 1=fat score  $> 3$ ) or pectoral muscle score (0=muscle score  $\leq 1.5$ , 1=muscle score  $> 1.5$ ). The results are summarized in table 2. There was a significant relationship between sex and fat score, males being fatter than females. The sex–diet interaction was also significant; males fed on the HQ diet were slightly fatter than those fed on the LQ diet, whereas females on the HQ diet were significantly leaner than

Table 1. Numbers of zebra finch chicks of each sex at (a) hatching, and (b) fledging, for the low-quality (LQ) and high-quality (HQ) diets

(Sex ratio = males/(males+females). The numbers in brackets are for first broods only.)

	(a) at hatching			(b) at fledging	
	no. of broods	no. of males/ females	sex ratio	no. of males/females	sex ratio
LQ diet	22 (14)	31/13 (20/9)	0.71 (0.69)	15/2	0.88
HQ diet	21 (14)	28/24 (18/18)	0.54 (0.50)	17/13	0.57

Table 2. Logistic regression of (a) tracheal-pit fat score, and (b) pectoral muscle score, for adult zebra finches on low- and high-quality diets

(The interaction term was tested first, and then each predictor variable was tested, while the other was held constant, after removal of the interaction from the model. The change in deviance,  $\Delta D$ , on fitting a predictor variable is distributed approximately as  $\chi^2$ .)

predictor	deviance	d.f.	$\Delta D$	$\Delta$ d.f.	$p$
(a) diet $\times$ sex	46.435	37	6.893	1	<0.01
(a) diet	46.937	38	0.502	1	n.s.
(a) sex	53.423	38	6.989	1	<0.01
(b) diet $\times$ sex	50.019	37	4.380	1	<0.05
(b) diet	50.019	38	0.000	1	n.s.
(b) sex	51.796	38	1.777	1	n.s.

those fed on the LQ diet ( $p=0.043$ , Fisher's exact test). There was also a significant relationship between muscle score and the sex-diet interaction. Males fed on the HQ diet had higher muscle scores than those fed on the LQ diet, whilst LQ females had higher muscle scores than HQ females.

Variation in bill colour brightness and intensity was examined by logistic regression: in each case, the binary dependent variable was created by grouping the colour scores into two classes (colour intensity, low = score of 1.5 or 10, high =  $1.5 < \text{score} < 10$ ; colour brightness, dull = score of 4, bright = score of 5). The results are summarized in table 3. When diet was held constant, there was a significant relationship between sex and both colour intensity and brightness. When sex was held constant, there was a significant relationship between diet and bill colour intensity but not bill brightness. Hence, males had brighter and more colourful bills than females, and birds fed on the HQ diet had brighter bills than those fed on the LQ diet.

**(c) Chick mortality**

The sex ratio of chicks that died before fledging was not different from equality for either diet (data in table 1; LQ,  $G_1=0.62$ , n.s.; HQ,  $G_1=0.00$ , n.s.). However, since significantly more male chicks than females fledged on the LQ diet, a higher proportion of females must have died on the LQ diet than on the HQ diet ( $G_1=5.69$ ,  $p<0.05$ ). This was not true for males ( $G_1=0.90$ , n.s.). To confirm this, analysis by brood was performed with separate linear models for each sex, specifying the number of males (or females) surviving to fledging as the dependent variable and the number of males (or females) in the brood as the

Table 3. Logistic regression of (a) bill colour intensity, and (b) bill brightness, for adult zebra finches on low- and high-quality diets

(The interaction term was tested first, and then each predictor variable was tested, while the other was held constant, after removal of the interaction from the model. The change in deviance,  $\Delta D$ , on fitting a predictor variable is distributed approximately as  $\chi^2$ .)

predictor	deviance	d.f.	$\Delta D$	$\Delta$ d.f.	$p$
(a) diet $\times$ sex	16.510	37	0.000	1	n.s.
(a) diet	20.944	38	4.434	1	<0.05
(a) sex	54.446	38	37.940	1	<0.01
(b) diet $\times$ sex	6.502	37	0.000	1	n.s.
(b) diet	7.941	38	1.439	1	n.s.
(b) sex	55.251	38	48.750	1	<0.001

binomial denominator, and using a binomial error distribution and a logit link. Diet significantly increased the fit of the model for females ( $\Delta D_1=6.395$ , 24 d.f.,  $p<0.05$ ) but not for males ( $\Delta D_1=0.904$ , 32 d.f., n.s.). Hence, brood sex ratios at fledging had a similar male-biased skew on the LQ diet as at hatching (table 1, all fledglings: HQ,  $G_1=0.53$ , n.s.; LQ,  $G_1=11.25$ ,  $p<0.001$ ), but of a greater magnitude due to additional female mortality.

**4. DISCUSSION****(a) Diet and adult body condition**

Pre-breeding diet has previously been shown to affect reproductive output in zebra finches (Selman & Houston 1996). Then, zebra finches were maintained on pre-breeding diets for just two weeks, and females on better diets were in better condition. The opposite result was observed in this experiment, in which the pre-breeding period on the experimental diets was much longer (three months). We suggest that the LQ females had higher muscle scores than the HQ females prior to egg-laying (which was contrary to expectation), because the long-term exposure to a low-quality diet led to the formation of stores, while birds exposed to a high-quality diet did not lay down reserves. Bird muscle and certain other tissues may act in a storage capacity, enabling a female to mobilize limiting amino acids later for egg production (Houston *et al.* 1995a-c). Stores may be essential, as egg proteins are richer in sulphur amino acids than dietary protein or most tissue proteins (Houston *et al.* 1995a). A similar storage strategy is shown by great tits, *Parus major*, in which the amount of fat that is stored for overnight

survival is greater in birds with more limited access to food resources (Gosler 1996).

### (b) *Body condition and offspring sex ratio*

Our results suggest that females in better physical condition skewed their hatching sex ratio towards males. This may be adaptive since male zebra finches are slightly larger than females (Zann 1996), and should, therefore, be more costly to raise. Hence, production of males may be relatively less costly to females in relatively good condition, and our result may be an example of the effect proposed by Trivers & Willard (1973).

Variation in environmental quality, as well as parental condition, may be a selective force on offspring sex ratio (Appleby *et al.* 1997). Poor food availability would favour production of females, which are less costly to raise and, therefore, less risky to produce. In this experiment, female condition and environmental quality are predicted to favour sex ratio biases in different directions. Hence, the sex ratio skew observed is contrary to that predicted if females were reacting to the 'condition' of their environment.

Our results failed to show a relationship between sex ratio and male attractiveness, as observed by Burley (1981, 1982). Although the HQ males were both in a better condition and had brighter bills than the LQ males, as would be expected as their diets were carotene-enriched, there was no skewing of the sex ratio by the HQ pairs.

### (i) *Chick mortality*

In addition to the male-biased sex ratio at hatching, female chicks are more likely to die on the LQ diet. It has been argued that differential mortality of the sexes may occur because parents selectively kill (Burley 1986) or differentially provision chicks (Clotfelter 1996) in order to adjust their offspring sex ratio. Sex-biased mortality may also be non-adaptive. First, one sex, usually the larger, may be more susceptible to starvation (e.g. Griffiths 1992). Second, one sex, usually the smaller, may be out-competed for food by the other (e.g. Teather 1992).

In captive zebra finches, Boag (1987) noted no sexual difference in growth or survival in chicks fed on high- or low-quality diets. However, other evidence suggests that female chicks are more vulnerable to nutritional stress than males. Zann & Runciman (1994) noted a higher proportion of male young in a wild colony when food was relatively scarce or of low quality, and Burley *et al.* (1989) found that the sex ratio of young at a colony was correlated with rainfall in the previous season. When rainfall was low, there was little plant growth and little seed in the subsequent year. Male chicks then out-competed females for food, leading to male-biased fledgling sex ratios. Our results, too, suggest that females are more vulnerable on low-quality diets. However, we have not been able to directly test whether the sex-biased mortality is due to females being more susceptible to starvation or to their being out-competed by males. Further experiments could target the quantification of the effects on sex ratio of competition between nestlings.

These results illustrate the potential of both facultative sex ratio manipulation and non-adaptive sex-biased mortality to play a role in determination of avian fledging

sex ratios. With an increasing body of evidence for facultative sex ratio manipulation by birds, and several possible mechanisms (Krackow 1995), an experimental study is urgently required to investigate these possibilities.

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