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Nestling diet, secondary sexual traits and fitness in the zebra finch

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We examined the effect of nestling diet quality on a suite of physiological, morphological and life-history traits in adult male zebra finches, *Taeniopygia guttata*. Compared with birds reared on a supplemented diet, nestlings reared on a seed-only diet showed a reduced rate of growth and reduced cell-mediated immune function as measured by an *in vivo* response to a T lymphocyte-dependent mitogen. There were no differences between birds reared on the two diets in any of the following adult traits: body size, primary sexual traits (testes mass, numbers of stored sperm, sperm function, velocity and morphology), secondary sexual traits (beak colour and song rate), serological traits or immunological traits. The only differences we detected were a lower body mass and a greater proportion of individuals with plumage abnormalities among those reared on a seed-only diet (this latter effect was transient). The fact that male zebra finches reared on a seed-only diet were, as adults, virtually indistinguishable from those reared on a supplemented diet, despite having reduced growth and immune function as nestlings, demonstrates that they subsequently compensated through the differential allocation of resources. Our results indicate that differential allocation is costly in terms of fitness since birds reared on a seed-only diet experienced a significantly greater mortality rate than those reared on a supplemented diet. This in turn suggests the existence of a trade-off between the development of traits important for reproduction, such as primary and secondary sexual traits and longevity.

Keywords: differential allocation; *Taeniopygia guttata*; fitness; diet; catch-up growth; sexual selection

1. INTRODUCTION

The nutritional conditions an organism experiences during its development can have a profound effect on its performance as an adult (Elo & Preston 1992; Desai & Hales 1997). The nutritional levels experienced during development can be affected by a number of factors including environmental conditions (Ricklefs 1983; Arednt 1997) and variation in the parental trade-off between offspring number and quality (Stearns 1992). Among birds, a reduction in either the quantity or quality of food received by nestlings has been shown to influence a variety of adult traits including body size, the probability of survival, the expression of secondary sexual traits and immune function (Gershwin *et al.* 1985; Newton 1989; Richner *et al.* 1989; Lochmiller *et al.* 1993; de Kogel 1997). In the present study, we determined the extent to which a reduction in the quality of nestling diet simultaneously influenced physiological, morphological and life-history traits in the zebra finch *Taeniopygia guttata*. The aim of this study was to establish the effect of the quality of nestling diet on the subsequent performance of adult male zebra finches in terms of their morphology, primary and secondary sexual traits, condition, immune function and survival.

2. METHODS

(a) *General*

The study was conducted using domesticated zebra finches from an out-bred colony which had been maintained at the University of Sheffield since 1985. Birds were maintained at $22 \pm 2\,^{\circ}\mathrm{C}$ and under a 14 L:10 D cycle. All birds had been reared on a supplemented diet (see below) and maintained as adults on a seed-only diet, i.e. *ad libitum* seed together with *ad libitum* grit, cuttle fish and water, with lettuce and Abidec® vitamin supplement once per week. The seed component of the diet comprised a mixture (by volume) of pearl white millet (27.5%), panicum millet (27.5%), Japanese millet (13.8%), canary seed (13.8%), red millet (6.9%), yellow millet (6.9%) and Niger seed (3.4%). The protein contents of these seeds (percentage dry mass) were 12.0, 11.0, 11.0, 12.9, 11.6, 12.0 and 24.9, respectively (Vriends 1992; J. E. Haith, personal communication). Thirty pairs of birds *ca.* 12 months old and all of which had bred at least once previously were selected at random and allocated at random to rear offspring on either a seed-only diet or a supplemented diet, i.e. a seed-only diet (as above) plus 10 g of minced hard-boiled egg each day. The main difference between the two diets was that the seed-only diet comprised 12.1% protein, whereas the supplemented diet comprised 42–46% protein (based on a calculation in Etches (1996)). Pairs were housed individually in cages measuring 45 cm × 45 cm × 45 cm. After rearing one brood the chick diet treatment was reversed. Ten pairs reared at least one male offspring on each diet and 34 other pairs reared broods on only one of the two diets. After independence all offspring were maintained on the seed-only diet (see above) and

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those that were allowed to breed were provided with the supplemented diet when rearing nestlings. We selected a single male chick at random from each of the two broods reared by the same parents ($n = 10$) for a pairwise comparison of various traits (see below). From the other 34 pairs we selected 30 male offspring at random from each diet treatment and maintained them together in an aviary (1 m × 2.4 m × 2.1 m high) on the seed-only diet and monitored their survival until they were 500 days of age.

(b) *Effect of nestling diet on nestlings and juveniles*

We measured a cell-mediated immune response in nestlings when they were *ca.* 11–13 days of age. This assay, referred to as the wing web index (Goto *et al.* 1978; Lochmiller *et al.* 1993), was performed on all individuals because we were unable to sex nestlings at this age. The assay is a hypersensitivity response and comprises an injection of 20 μl of phytohaemagglutinin (PHA, 1 mg in 100 μl solution) into the wing web (patagium) of one wing and the same volume of sterile phosphate-buffered saline into the other wing. The thickness of the patagium was measured before injection and 24 h later using a spessimeter accurate to 0.01 mm. The wing web index was calculated as the mean difference in thickness of each patagium before and after the PHA injection minus the same difference on the control wing. The magnitude of the immune response is reflected by the size of the wing web swelling (Lochmiller *et al.* 1993). Our aim was to conduct this immunological assay when chicks were of similar size. However, since chicks on the seed-only diet grew more slowly than those on the supplemented diet, we were forced to adopt a compromise and, as a consequence, seed-only chicks were on average one day older and 2.5 g (20%) lighter than chicks on the supplemented diet when the assay was conducted. We used mass–age to calculate an index of growth rate when most chicks were 10–14 days old. We recorded the sex of all offspring at 40 days of age when adult plumage first becomes apparent (Zann 1996).

(c) *Effect of nestling diet on non-working adults*

When offspring were at least 100 days of age we measured their body mass using an Ohauss LS200 electronic balance to the nearest 0.1 g at the same time of day to avoid diurnal fluctuations (Metcalfe & Ure 1995). At the same time we measured fluctuating asymmetry in chest-band plumage between birds reared on the two diets since a previous study had shown that male zebra finches with more symmetrical plumage were more attractive (Swaddle & Cuthill 1994) and had higher reproductive success (Swaddle 1996) than asymmetrical birds. We therefore predicted that males reared on the seed-only diet would have more asymmetrical plumage than those reared on the supplemented diet. However, in a double-blind test we found no significant repeatability in chest-band plumage asymmetry for 16 birds measured twice on the same day ($F_{1,31} = 2.46$ and $p = 0.127$; repeatability 8.4%), so we did not pursue this further.

When males were 100 days of age we recorded beak colour, which is a condition-dependent secondary sexual trait (Burley & Coopersmith 1987; Zann 1996), subjectively on a scale of 1 (light orange) to 6 (dark red) using Munsell colour chips and verified the results using objectively spectroradiometric analyses (see Birkhead *et al.* 1998). Birds in better condition have redder beaks (Burley *et al.* 1992; Birkhead *et al.* 1998). Song rate is another condition-dependent secondary sexual trait (Zann 1996), but it does not always covary with beak colour (Birkhead *et al.* 1998): we measured song rate as in our previous studies by presenting each male with a different female on five consecutive days behind a wire mesh screen and recording the mean amount of time spent singing in the first 5 min. Both secondary sexual traits show high measurement repeatability (Birkhead *et al.* 1998). After song rate measurements were complete we took a sample of 75 μl of blood in order to obtain two indices of condition: haematocrit and granulocyte:lymphocyte (G:L) ratio. Haematocrit provides an index of condition since sustained exercise results in a reduction in packed cell volume (M. H. Harrison 1985; Riera *et al.* 1993; see also Birkhead *et al.* 1998) and, in another study of zebra finches, we found that birds in poor condition had relatively low haematocrit values (Birkhead *et al.* 1998). A reduction in the number of circulating lymphocytes and an increase in the number of neutrophilic or heterophilic granulocytes, i.e. an increase in the G:L ratio is a general avian stress response (Davison *et al.* 1983; Gross & Siegel 1983). After mixing 10 μl of blood with 100 μl of Natt and Herrick's stain we counted the total number of lymphocytes and granulocytes in 0.1 μl in a haemocytometer (Davison *et al.* 1983).

(d) *Effect of nestling diet on working adults*

The use of captive individuals allows control of many aspects of an experimental manipulation more easily than with wild individuals but the benign conditions of captivity may reduce the variance in traits and obscure any condition-dependent effects. We therefore arranged for ten pairs of brothers (same parents but different broods) which had been reared on the different diets to rear a supranormal brood of eight chicks. We paired each male to a female (previously reared on a supplemented diet) of similar age at random. Birds were allowed to rear their enlarged brood on a supplemented diet. Male zebra finches typically provide *ca.* 45% of nestling feeds (ten Cate 1982; Burley 1988). When their chicks were nine days old the adult males were inoculated with a novel antigen: 20 μl of standardized *Brucella abortus* agglutination concentrate (MAFF Laboratory, Weybridge, UK) administered via an intramuscular inoculation (Mosier & Subbarao 1982; Higgins 1996). Similarly, when their chicks were 10 and 11 days old we used the wing web assay again to measure cell-mediated immunity in the adult males (using the opposite wing to that used in these individuals as nestlings (see above)). Starting when chicks were 13 days old, males were removed from their partner and chicks for 10 min at the same time each day for five consecutive days to record their song rate. When chicks were 18 days old blood samples were taken from adult males to measure the antibody response to *Brucella*, i.e. nine days post-immunization during the peak antibody response (see Birkhead *et al.* 1998). We also used this blood sample to measure haematocrit and G:L ratio and we measured beak colour at this time.

(e) *Effect of nestling diet on primary sexual traits in non-working adults*

To determine whether there were any long-term effects of nestling diet on primary sexual traits in sexually rested males, we killed and dissected the ten pairs of males between three and six months after they had reared their enlarged brood and measured primary sexual traits. We record the combined mass of both testes and the total number of sperm in the seminal glomera. Using a subsample of sperm from the ejaculatory duct we recorded (i) sperm velocity ($n = 100$), (ii) the percentage of morphologically normal sperm ($n = 100$), (iii) the percentage of dead sperm ($n = 100$), and (iv) the total sperm length ($n = 30$; measured to the nearest 2 μm). The methods used in this part of

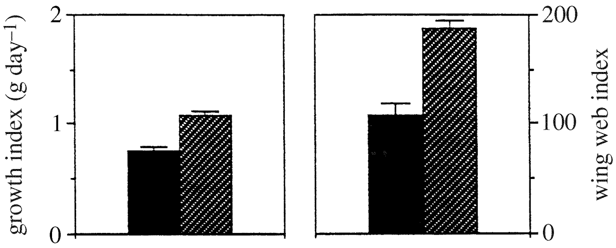

Figure 1. Growth (left) and cell-mediated immune function (right) of male zebra finch chicks reared on seed-only diet (black) and supplemented diet (hatched). Chick mass was recorded once when chicks were of a similar size (seed-only diet 13.09 ± 0.45 d s.e., mass 9.53 ± 0.16 g s.e. and $n = 34$; supplemented diet 11.56 ± 0.32 d s.e., mass 12.07 ± 0.20 g s.e. and $n = 37$) at the same time as the immune assay was conducted. The growth index is mass–age. The differences between the diets were significant: growth index $t_{69} = 6.93$ ($p < 0.001$) and wing web index $t_{69} = 5.94$ ($p < 0.001$).

the study were exactly the same as in our other studies (Birkhead *et al.* 1998).

3. RESULTS

(a) *Effect of nestling diet on nestlings and juveniles*

Male chicks reared on the seed-only diet grew more slowly and showed a significantly reduced cell-mediated immune response compared with those reared on the supplemented diet (figure 1). Because we were only able to sex birds retrospectively, we obtained the same data for females and found the same reduction in growth rate and immune function as for males (data not shown). At 40 days of age, when birds could be sexed by plumage characteristics, the sex ratio was male-biased among chicks reared on the seed-only diet (34 males and 17 females) compared to those reared on the supplemented diet (38 males and 39 females) ($\chi^2 = 3.73$, 1 d.f. and $p < 0.08$). This result suggests a sex difference in mortality among birds reared on the seed-only diet and is consistent with results obtained in other studies in which nestling zebra finches have been reared on different quality diets (Bradbury & Blakey 1998; Kilner 1998; see also de Kogel 1997).

At around 100 days of age, a significantly higher proportion of male birds reared on the seed-only diet had additional areas of black feathering in their plumage, around the black breast bar, throat and face (28%: 10 out of 36 males), than birds reared on the supplemented diet (3%; 1 out of 37 males; $\chi^2 = 8.96$ and $p < 0.01$). Interestingly, after the second body moult, which takes place at around 200–250 days (Zann 1996), no birds showed any sign of additional black plumage (figure 2). The association between poor quality diet and areas of 'melanistic' plumage in captive birds has been reported previously (C. J. O. Harrison 1985) but its causes and consequences have not been studied in detail.

(b) *Effect of nestling diet on non-working adult males*

We compared the body mass, two secondary sexual traits (beak colour and song rate) and two serological traits in the ten pairs of brothers reared on the two diet treatments. Only the mass differed significantly between the two treatments (table 1), a difference which persisted throughout the study (see table 2).

A comparison of the survival rates of males between fledging and 500 days of age showed that those reared on the seed-only diet had a lower rate of survival (mean survival time 352 days and 95% CI 294–411 days) than birds reared on the supplemented diet (mean survival time 461 days and 95% CI 427–494 days): this difference is significant (log rank 6.95, 1 d.f. and $p = 0.008$; see figure 3). The mechanism which resulted in the higher mortality among birds reared on the seed-only diet was not clear. Birds did not die as a result of any obvious disease, although among the males reared on the seed-only diet there was an almost significant positive correlation between the size of the nestling wing web swelling and life span ($r = +0.580$, $n = 11$ and $p = 0.061$), suggesting that immune function may have had some effect on longevity. Another possible explanation for the higher mortality among the birds reared on the seed-only diet is that they were subordinate to and/or less competitive than males with which they shared an aviary reared on the supplemented diet.

(c) *Effect of nestling diet on working adult males*

We compared a number of morphological, secondary sexual, serological and immunological traits in ten pairs of brothers each reared on the different diets while rearing an enlarged brood of eight chicks. However, apart from the difference in body mass reported earlier, none of these differences was significant (table 2). Similarly, we could detect no long-term consequences of nestling diet on primary sexual traits (table 2).

4. DISCUSSION

Our main results were that birds reared on a seed-only diet grew more slowly and, as nestlings, had a reduced cell-mediated immunological response compared with birds reared on a supplemented diet. A paired comparison between brothers reared on the two diets showed that, at sexual maturity, males reared on a seed-only diet had a lower mass, but showed no difference in two secondary sexual traits and two serological traits compared with birds reared on a supplemented diet. Even when rearing an enlarged brood of eight chicks there were no differences in any morphological, secondary sexual, serological or immunological traits between males reared on the two diets. Nor were there any long-term differences in primary sexual traits. Over the 500 days after hatching non-breeding males reared and maintained on the seed-only diet had a mortality rate over twice that of birds reared on the supplemented diet.

The fact that we found a clear effect of nestling diet on nestling growth and immune function but no effect, other than body mass, on subsequent attributes suggests that either (i) poor quality birds were eliminated relatively early (e.g. before fledging) and were therefore unavailable for comparison, and/or (ii) birds reared on the seed-only diet were able to compensate for their retarded early growth.

(i) Because we found no significant difference in the mortality of nestlings reared on different diets

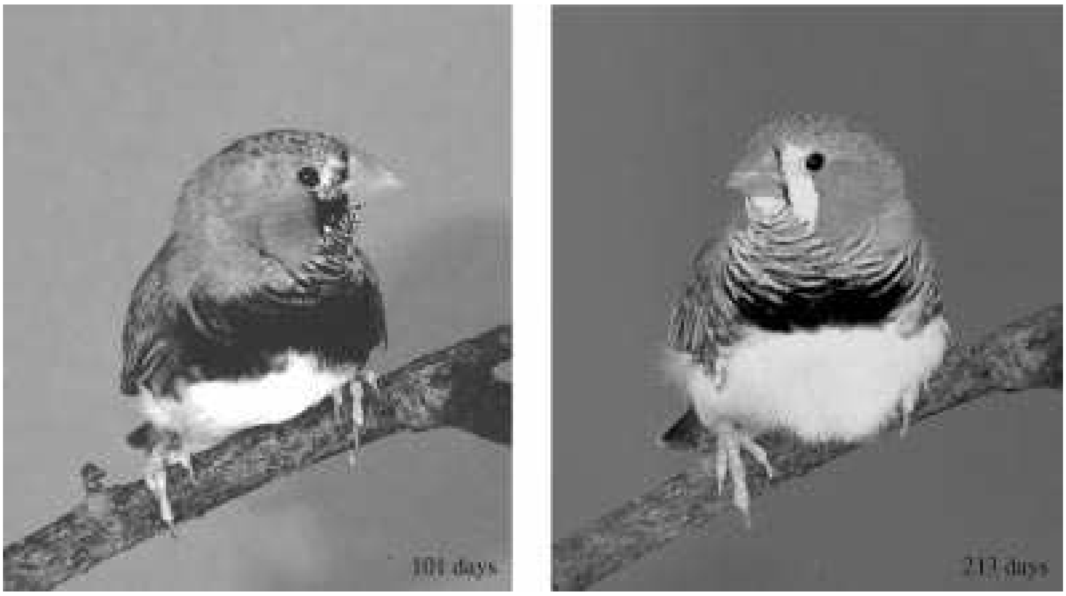

Figure 2. An example of a male zebra finch reared on a seed-only diet at 101 days of age showing abnormal areas of melanistic plumage (left) and the same individual after its second complete body moult aged 213 days (right).

Table 1. *Mass, size, secondary sexual traits, haematocrit and G:L ratios of non-working adult male zebra finches reared on different diets*

(Values are means ± s.e. and t-values are paired t-tests for ten pairs of brothers. The difference in mass remains significant after Bonferroni correction (Rice 1989).)

variable	supplemented diet	seed-only diet	t	p
mass (g)	19.60 ± 0.58	17.06 ± 1.03	3.13	0.01
beak score	3.43 ± 0.37	3.38 ± 0.42	0.16	0.88
song rate	7.78 ± 3.06	11.18 ± 5.31	0.67	0.52
haematocrit	51.25 ± 0.06	54.15 ± 1.98	1.48	0.17
G:L ratio	0.21 ± 0.06	0.19 ± 0.05	0.22	0.83

(proportion of chicks fledged from those hatched: seed-only 0.815 ± 0.049 s.e. ($n = 20$) and supplemented diet 0.892 ± 0.033 s.e ($n = 24$); Mann–Whitney U-test, $U = 197$ and $p = 0.26$) it seems unlikely that the early elimination of particularly poor quality birds could account for the lack of difference between adults on the two diets. Interestingly, in a similar study Boag (1987) did not observe any difference in nestling mortality of offspring reared on different quality diets, but did find a significant difference in adult body size.

(ii) The second explanation for our results is that birds reared on the seed-only diet eventually 'caught up' with those reared on the supplemented diet. Catch-up growth is a well-known phenomenon in both invertebrates and vertebrates and comprises a period of accelerated growth following a period of growth retardation (Wilson & Osbourn 1960; Sibly & Calow 1986). The ability to compensate for poor juvenile nutrition is particularly well developed in birds (Ricklefs 1983; Gebhardt-Henrich & Richner 1998; Schew & Ricklefs 1998). For example, chickens (*Gallus domesticus*) reared on a diet just sufficient for maintenance can be kept at a physiological age of *ca.* ten days for several weeks but quickly catch up following the return to an unrestricted diet and show 'little subsequent effect of adult body size or egg production' (Ricklefs 1983, p. 54; see also McRoberts 1965). In a study on the effect of brood size on morphology and sexually selected traits in adult zebra finches de Kogel (1997; see also de Kogel & Prijs 1996) found that birds reared in large broods (and, hence, under poor food conditions) had shorter tarsi as adults than those reared in small broods. On the other hand, there was no effect of brood size on wing length or beak redness in adults, suggesting that in terms of these traits birds from larger broods caught up with those reared in smaller broods. Skagen (1988) found no differences in several adult traits among zebra finches reared under conditions of different food abundance. In the present study, we found evidence for catch-up growth in tarsus length and beak size, but not body mass. Taken together these results suggest that zebra finches are often able to compensate to some extent for a poor start in life.

There were few detectable differences between birds reared on the different diets as adults, but the fact that individuals reared on the seed-only diet had a significantly higher mortality rate than those on the supplemented diet indicates that they incurred a long-term cost. Our results do not allow us to establish the cause of the higher rate of mortality in the birds reared on the seed-only diet. There are several possibilities: (i) mortality was a direct consequence of their poor initial diet, (ii) lower adult body mass may have resulted in their being less competitive even in the presence of *ad libitum* food or, more interestingly, (iii) it may have been a consequence of

Table 2. *Changes in mass and secondary sexual traits, serological traits and immunological assays for adult male zebra finches reared on different diets while rearing an enlarged brood, except for primary sexual traits which were measured later* (*see text*)

(Values are means ± s.e. and t-values are paired t-tests for ten pairs of brothers.)

trait	supplemented diet	seed-only diet	t	p
morphological traits				
mass (g)	15.47 ± 0.53	14.29 ± 0.57	2.57	0.03
change in mass	4.13 ± 0.61	2.77 ± 0.65	1.94	0.08
tarsus length (mm)	16.73 ± 0.21	16.57 ± 0.14	0.16	0.88
beak height (mm)	7.01 ± 0.10	6.89 ± 0.12	0.56	0.59
secondary sex traits				
change in beak colour	0.47 ± 0.41	0.28 ± 0.38	0.46	0.65
change in song rate	7.18 ± 2.82	9.58 ± 5.56	0.64	0.64
serological assays				
haematocrit	45.31 ± 1.07	48.35 ± 1.61	1.35	0.21
change in haematocrit	5.94 ± 1.81	5.80 ± 1.51	0.05	0.96
G:L ratio	0.24 ± 0.10	0.24 ± 0.08	0.03	0.98
change in G:L ratio	0.04 ± 0.08	0.05 ± 0.08	0.16	0.88
immunological assays				
wing web index	103.68 ± 6.39	118.22 ± 11.18	1.43	0.19
Brucella antibody titre	5.90 ± 0.59	6.30 ± 1.03	0.41	0.69
primary sex traits				
testes mass (g)	0.06 ± 0.1	0.06 ± 0.01	0.99	0.36
relative testis mass	0.40 ± 0.05	0.25 ± 0.09	1.49	0.18
number of sperm $(\times 10^6)$	5.74 ± 1.38	3.60 ± 1.55	1.37	0.21
sperm velocity (μm s^{-1})	20.68 ± 0.92	20.83 ± 0.86	1.39	0.21
per cent abnormal sperm	10.36 ± 2.50	9.89 ± 2.54	0.27	0.79
per cent dead sperm	26.28 ± 2.93	24.03 ± 7.36	1.20	0.27
sperm length (μm)	70.50 ± 0.80	67.97 ± 1.28	2.14	0.06

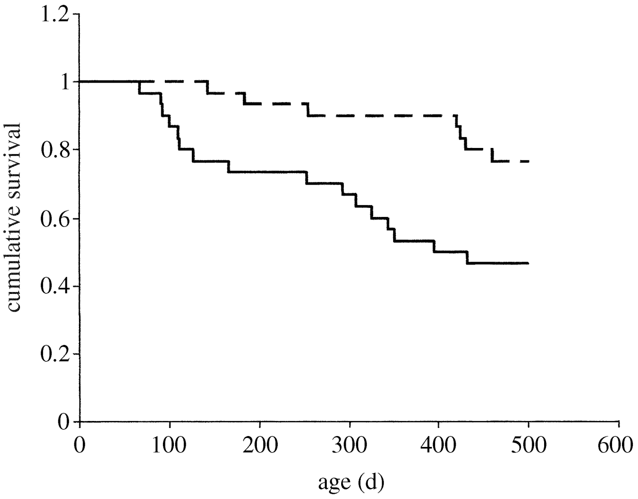

Figure 3. Kaplan–Meier survivorship plots for two groups of male zebra finches reared on two different diets. The initial cohort in both cases was 30 males followed for 500 days. The birds reared on a supplemented diet (upper, broken line) had a significantly lower mortality rate than those reared on a seed-only diet (solid line) (log rank 6.95, 1 d.f. and $p = 0.008$).

the differential allocation of resources to maintain immune function and primary and secondary sexual traits. There is abundant evidence in mammals that foetal malnutrition results in changes in organ development which in turn appear to result in increased susceptibility to disease and a reduction in life span among adults (Desai & Hales 1997). In rats, disease and reduced life span appear to be consequences of catch-up growth, particularly among males (Hales *et al.* 1996), an effect which appears to be mediated by the switch from poor to better nutrition rather than a direct consequence of foetal malnutrition (Desai & Hales 1997). The differential allocation of resources among rats which experience foetal malnutrition is thought to be adaptive, which it would be if individuals experiencing poor foetal nutrition also experience poor nutrition as adults. However, if they subsequently experience better levels of nutrition, longevity is actually reduced (Desai & Hales 1997). A similar phenomenon may have occurred in this study if, among the birds reared on the seed-only diet, protein levels were less than adequate during early development but more than adequate once the birds were independent. Whatever the mechanism, our results suggest that zebra finches trade-off various traits, including immune function and secondary sexual traits, against life span, although this idea needs to be tested directly.

It is generally assumed that the expression of condition-dependent secondary sexual (and other) traits honestly signals individual quality and co-varies with lifetime reproductive success (Andersson 1994). This was not true in the present study, since male zebra finches appeared to trade-off the expression of various traits, presumably for a short-term gain in reproductive success, against longevity. A similar pattern occurred in *Drosophila nigrospiracula*, where reduced life span, mediated by parasitism, resulted in an increase in male reproductive effort (Polak & Starmer 1998). Among birds, this trade-off may be more pronounced in very short-lived species such as the zebra finch (Zann 1996) than in longer-lived species.

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