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EFFECTS OF NESTLING DIET ON GROWTH AND ADULT SIZE OF ZEBRA FINCHES (POEPHILA GUTTATA)

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ABSTRACT.—Manipulation of the diet of Zebra Finch (*Poephila guttata*) nestlings in the laboratory showed that a low-quality diet reduced growth rates of nine external morphological characters, while a high-quality diet increased growth rates. The growth of plumage characters was least affected by diet, while growth rates of tarsus and mass were most affected. The treatments also produced differences in the adult size of experimental birds, differences not evident in either their parents or their own offspring. Diet quality had the strongest impact on adult mass and tarsus length, while plumage and beak measurements were less affected. Analysis using principal components and character ratios showed that the shape of experimental birds was affected by the experimental diets, but to a minor extent compared with changes in overall size. Significant shape changes involved ratios between fast- and slow-growing characters. The ratios of characters that grow at similar, slow rates (e.g. beak shape) were not affected by the diets. Environmental sources of morphological variation should not be neglected in studies of phenotypic variation in birds. *Received 5 June 1986, accepted 30 October 1986.*

MORPHOLOGICAL differences between individual birds are often assigned functional significance, whether those individuals are of different species, different sexes, or different-size members of the same sex (Hamilton 1961, Selander 1966, Clark 1979, James 1982). In granivores such as Darwin's finches (*Geospiza* spp.), morphological differences have been related to variation in feeding efficiency at all three of these levels. Differences in feeding efficiency have in turn been correlated with variation in fitness due to spatial or temporal variation in seed availability (Boag and Grant 1981, Schluter and Grant 1984). Intraspecific morphological variation in several species, such as House Sparrows (*Passer domesticus*; Johnston and Selander 1971), Red-winged Blackbirds (*Agelaius phoeniceus*; Power 1969), Great Tits (*Parus major*; Hamilton 1961), and others (James 1970) has been correlated with clinal variation in climate. A classic example of the correlation between intraspecific morphological variation, between

fitness, and weather was seen in the nonrandom survival of House Sparrows collected by Hiram Bumpus following a winter storm (O'Donald 1973, Fleischer and Johnston 1982).

Recently, investigators have tried to demonstrate a genetic basis for intraspecific morphological variation in birds. Several studies have shown that variation in morphological traits of ecological interest is heritable (see review by Boag and van Noordwijk 1986). Although such analyses are difficult to perform and interpret, they have provided one of the few means available to test the plausibility of the hypothesis that natural selection is the primary determinant of the array of phenotypes maintained within avian populations.

One common misunderstanding of heritability studies is that even if variation in a trait *within* two different populations is highly heritable, this does not guarantee that the difference in the character *between* the populations has a genetic basis. For instance, regressions of

offspring bill size on parental bill size were identical and significant in two years of data collected for *Geospiza fortis* (Boag 1983). This indicated that the variation was highly heritable in both years. However, y-intercepts in these same regressions differed significantly (see Boag 1983: fig. 1). Boag (1983) hypothesized that different population densities and territory sizes in the two years led to differences in the quantity or quality of food fed to young, with the result that young grew to different adult sizes. Although it has been known for some time that nestling diets can alter growth rates (Bryant 1978), few authors have suggested that variation in growth rate contributes to adult morphological variation in wild birds (but see Smith and Zach 1979; James 1982, 1983; Boag 1983; Alatalo and Lundberg 1986). Laboratory data on birds (Allee and Lutherman 1940, Johnson 1971) and mammals (Harrison 1959, Lister and McCance 1965) suggest that diet in early life can affect adult size.

This possibility is supported by elegant experiments on Red-winged Blackbirds (James 1983). Reciprocal transplants of Red-wings between either end of two separate geographic clines in body size and shape showed that the transferred young grew to resemble their foster parents more than their biological parents. James concluded that Red-wing clines in morphology had a large nongenetic component, and that there probably existed complex covariation between genetic and environmental causes of individual differences in morphology.

The heritability studies discussed above, as well as the transplant experiments (James 1983), signal a growing need to consider the origins of phenotypic variation in avian populations. Such awareness came early to ecologists working with other taxa. For instance, the morphological plasticity of plants routinely forced botanists to dissect ecotypic variation in their study populations before invoking adaptive arguments concerning individual differences. This approach was epitomized by the classic ecotype transfers conducted by Clausen et al. (1940). Until recently, most avian ecologists have assumed implicitly that birds have essentially determinate growth, and that phenotypic differences between adults accurately reflect genetic differences, which are amenable to evolution by natural selection.

I report a simple experiment with laboratory-raised Zebra Finches (*Poephila guttata*). I show that qualitative differences in the diets fed by parents to their young produce substantial differences in the growth rates of several morphological characters. When these young are followed until adulthood, the different nestling diets produce adult birds with significantly different morphologies.

METHODS

Adult Zebra Finches were selected at random from an outbred laboratory colony and mated to produce 14 pairs. Each pair was placed in a 50 × 30 × 40 cm breeding cage, provided with a wicker nest cup, shredded burlap nesting material, cuttlebone, an oyster shell–grit mixture, and water. Cages were maintained indoors on a 14L:10D lighting schedule at constant temperature and humidity, visually but not acoustically isolated from each other. Cages were assigned at random to one of three experimental groups, which were treated identically except for the quality of food available from the end of incubation until the young were approximately 14 weeks old. Parents were removed when young were about 35 days of age. Breeding under all treatments commenced simultaneously.

Families in the "standard-quality diet" treatment group were fed finch seed mix (red and white millet, with canary, rape, and flax seed) and standard nestling food mixture (see Table 1) *ad libitum*. The seed mix contained about 14% crude protein, while the nestling mix had about 24% protein, based on Kjeldahl analyses (Skoog and West 1969). In addition, these families received minced, hard-boiled hen's egg with added multivitamin-mineral powder (Perveline®, 8 in 1 Products Inc., about 1 g/100 g of egg) once a week (about 1 g wet mass egg mixture for each adult or young in cage). Three days after the egg ration, each cage of birds received approximately 5 g wet mass of fresh lettuce or spinach. The four standard-diet pairs each produced one brood, with a total of 6 male and 5 female offspring surviving to 1 yr of age or more.

Families in the "high-quality diet" group were given the standard seed mixture, and a high-protein nestling mixture (approximately 38% protein; see Table 1) *ad libitum*. They received about 1 g per bird of the egg mixture every day and 5 g of fresh greens every other day. Five high-diet pairs each produced one brood, for a total of 10 male and 4 female offspring at 1 yr of age.

Families in the "low-quality diet" group were given the standard seed mixture, and a low-protein nestling mixture (about 7% protein; see Table 1) *ad libitum*. From the end of incubation on, they received

about 5 g of greens once a week, but no egg. Five low-diet pairs produced one brood each, with 8 male and 8 female offspring at 1 yr. All three nestling food mixtures had roughly equal energy content [about 3,000 kcal/kg or 12.6 × 10⁶ J/kg, based on published values for component ingredients; metabolizable energy content (Fisher 1972) was not measured].

Nine external morphological characters were measured on the original parents before the experiment, on the experimental birds as they grew (once a day from hatch until day 14, every 2 days until day 40, once a week until day 98, and at 1 yr of age), and on the fully grown offspring later produced by the experimental birds. Offspring of experimental birds were produced by mating individuals with nonsibs from the same treatment group.

The measurements taken included: mass (MAS) in grams on an electronic balance; wing chord (WNG) in millimeters using a ruler on the flattened right wing; retrix length (RET) in millimeters using a ruler from the tip of the pygostyle to the furthest extension of the tail feathers; tarsus length (TRS) in millimeters using dial calipers from the nuchal notch to the furthest extension of the leg with the foot flexed at a right angle; toe spread (TOE) in millimeters, measured by pressing the foot on a ruler and noting the distance between the rearmost extension of the hind toe and the foremost extension of the middle toe (excluding claws); bill length at nares (BLN) in millimeters from the tip to the anterior rim of the nares; bill depth at nares (BDN) in millimeters perpendicular to the commissure at the anterior edge of the nares; lower bill width (LBW) in millimeters at the widest expanse of the tomia; body length (BOD) in millimeters, measured from the tips of the longest retrices to the beak tip of a bird gently flattened along a ruler, with the previously measured RET and BLN later being subtracted. All measurements taken during growth were made by one technician, while I made all adult measurements.

Growth coefficients were calculated for each character in each experimental chick from the measurements from day 1 to 98 in nonlinear regressions based on a logistic model of growth (Ricklefs 1984). The SAS procedure NLIN (SAS Inst. 1982) was used to estimate K (relative growth rate, as proportion of asymptote/day) values, as well as A (asymptotic size) and t_i (age at inflection point, or maximum growth rate) values. The K values and adult measurements for each morphological character were then examined in detail, using two-way ANOVA to examine the independent effects of sex and diet on growth rates and adult size. The effect of diet on morphological shape was examined using both ratios of characters (Mosimann and James 1979) and principal component analyses (PCA). All variables were evaluated for normality before statistical analysis. Although virtually all analyses were carried out on both log-transformed and raw data, there were only trivial

TABLE 1. Composition (% dry mass) of nestling mixtures used in experimental diets.

	Diet quality		
	Low	Standard	High
Rolled oats		34.0	
Pablum (baby cereal)		24.0	
Wheat germ		10.0	
Skim milk powder		20.0	12.0
Gelatin powder		10.0	7.6
Vitamin-mineral powder[a]	1.0	1.0	1.0
Alfalfa, dried	1.0	1.0	1.0
Dry dog food	6.0		20.0
Tryptophan			0.1
Cystine			0.1
Methionine			0.2
Wheat germ			10.0
Soya flour			19.0
Dried lean beef powder			10.0
Casein			10.0
Brewer's yeast			7.0
Wheat bran	12.0		2.0
Corn starch	68.0		
Dextrose	12.0		

[a] Perveline®, 8 in 1 Pet Products, contains vitamin A palmitate, desiccated liver, brewer's yeast, wheat germ and alfalfa meals, soy flour, dried milk, thiamine hydrochloride, riboflavin, pyridoxine hydrochloride, vitamin B₁₂ supplement, choline dihydrogen citrate, vitamin E supplement, calcium pantothenate, monosodium glutamate, tribasic calcium phosphate, potassium biphosphate, sodium chloride, iron orthophosphate, manganese phosphate, magnesium phosphate, copper phosphate, zinc oxide, potassium iodide, cobalt phosphate.

differences between results in all cases. The raw data are emphasized here, except as indicated in the shape and environmental sensitivity analyses. Unless indicated otherwise, SAS (SAS Inst. 1982) was used for statistical procedures, with interpretations based on Sokal and Rohlf (1981).

RESULTS

Pairs on the low, standard, and high diets had respective averages of 3.2, 2.8, and 2.8 young surviving to at least one year of age, implying that the diets had no differential effect on breeding success. Young produced on the three diets appeared normal in terms of gross behavior and appearance, and individuals from each group went on to breed successfully themselves (e.g. Table 4). As is often the case in Zebra Finches, there was considerable variation between pairs within treatment groups in the extent to which they used the nestling mixtures for feeding their young. The high-protein mixture was less preferred by the parents than the standard mixture. Some parents given the low-protein nestling mixture
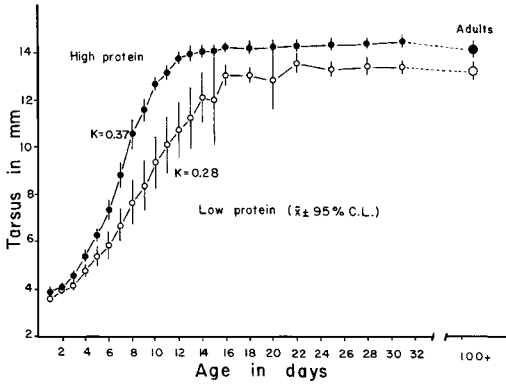
Fig. 1. Growth and adult size of TRS in Zebra Finches raised on low (O) vs. high (●) quality nestling diets. Standard-diet values were intermediate to low and high values, and are omitted for clarity. Points are means ± 95% confidence limits. K values are growth rates based on a logistic model of growth.

used it to a greater extent than did parents provided with the standard mix. Simultaneous choice tests with nonexperimental breeding birds confirmed that adults ranked the palatability of the mixtures as low > standard > high. The morphological effects reported below probably derive chiefly from the extra boiled egg ration in the high diet, vs. heavy use of the low-protein mix by parents feeding young in the low-diet group.

Diet and growth rate.—The diet composition had a clear effect on nestling growth rates, with the high diet causing young to grow significantly faster than young reared on the low diet (Fig. 1, Table 2). Two-way ANOVAs (SAS PROC GLM) on the growth coefficients (Table 2) showed a consistent, highly significant effect of diet on the mean growth rates of all characters except RET. There was essentially no sexual difference in growth rates, and no significant diet × sex interactions. A factorial multivariate analysis of variance (MANOVA; Norusis 1985) showed no interaction between diet and sex, no significant sexual difference in growth rates ($F = 1.10$, df = 10,21, $P = 0.41$), and a highly significant effect of diet ($F = 4.96$, df = 20,42, $P < 0.001$). As an approximate measure of the effect of diet on within-group variation in growth rates, I used a modified F_{max} test (Sokal and Rohlf 1981) on the ratio of the squared coefficients of variation (CV^2). Variation among low-diet young was consistently up to twice that seen among high-diet young, with the ratio significant in 5 of the 9 characters (Table 2; see also Fig. 2).

Diet and adult size.—The experimental diets had significant, permanent effects on adult size. The effect on TRS, a character for which there is no adult sexual size dimorphism in this species, is evident in Fig. 1. Similar results were seen for other characters when the measurements of 1-yr-old experimental birds were compared with two-way ANOVA (Table 3). As with growth coefficients, none of the diet × sex interactions were significant. There was evidence of sexual size dimorphism in RET and, to a lesser extent, in TOE. Of the 9 characters, 6 showed a significant effect of diet on adult size when sex was held constant. A factorial MANOVA showed no diet × sex interaction, a

TABLE 2. Effects of nestling diet on means ($\bar{x}$) and coefficients of variation (CV) of relative growth rates (K) from fitted logistic curves.

| | Diet | | | | | | Test | | |
| | Low ($n = 16$) | | Standard ($n = 13$) | | High ($n = 15$) | | | | |
Character	$\bar{x}$	CV	$\bar{x}$	CV	$\bar{x}$	CV	CV^2 ratio[a]	Diet[b]	Sex
MAS	0.190	29.8	0.255	23.4	0.299	10.4	**	***	NS
WNG	0.243	9.8	0.243	6.3	0.265	4.9	*	**	NS
RET	0.307	8.6	0.306	8.5	0.321	6.1	NS	NS	NS
TRS	0.276	15.0	0.316	12.3	0.370	8.1	NS	***	NS
TOE	0.281	18.6	0.336	15.6	0.373	12.4	NS	***	NS
BLN	0.124	18.7	0.150	7.1	0.148	9.6	*	***	NS
BDN	0.103	16.5	0.120	9.9	0.128	8.3	*	***	NS
LBW	0.112	18.2	0.142	12.6	0.139	20.3	NS	***	*
BOD	0.212	22.4	0.246	14.2	0.276	9.4	**	***	NS

[a] F test for larger of Low and High diet CV^2 divided by smaller, with significance indicated as *($P < 0.05$), **($P < 0.01$), and ***($P < 0.001$).
[b] Two-way ANOVAs with no significant interaction terms. Significance of diet and sex main effects indicated as above.

TABLE 3. Effects of nestling diet on adult size.

| Character[a] | Diet | | | | | | Test[b] | | |
| | Low (n = 16) | | Standard (n = 11) | | High (n = 14) | | | | |
	$\bar{x}$	CV	$\bar{x}$	CV	$\bar{x}$	CV	CV^2	Diet	Sex
MAS	12.04	12.0	12.40	8.6	13.24	7.3	NS	*	NS
WNG	55.96	2.5	56.25	2.0	57.12	1.2	*	*	NS
RET	33.53	3.8	33.53	2.8	34.16	2.4	NS	NS	***
TRS	13.19	6.2	13.76	2.4	14.08	3.2	NS	**	NS
TOE	18.69	5.9	19.15	4.9	19.96	4.6	NS	**	*
BLN	7.85	6.2	7.71	2.0	7.90	2.9	**	NS	NS
BDN	7.11	4.9	7.12	3.7	7.43	2.8	NS	*	NS
LBW	6.71	4.5	6.75	3.1	6.91	4.3	NS	NS	NS
BOD	65.24	3.8	65.84	2.9	68.81	2.7	NS	***	NS

[a] MAS measured in grams, other characters in millimeters.
[b] See Table 2 for explanation of tests.

highly significant effect of sex ($F = 5.96$, df = 9,27, $P < 0.001$), and a significant effect of diet ($F = 2.01$, df = 18,54, $P = 0.02$). Relative variability of the measurements was compared in high- and low-diet birds as before; again, low-diet birds were more variable, though the increase was significant in only 2 of 9 characters (Table 3).

The morphological differences observed among the three groups of experimental birds at adulthood were not observed in any of the nine characters in either their parents or their own offspring (typical results shown in Table 4 for tarsus).

Diet and shape: principal components.—I examined the effect of the experimental diets on shape in two ways. First I extracted principal components from both the correlation matrix of growth coefficients and the correlation matrix of adult measurements. In most sets of avian morphometric data, PC I is highly positively correlated with all the univariate variables, and can be interpreted as "size" (Lemen 1983, Boag 1984). The second and subsequent components typically show character correlations of mixed signs; with much of the variation in size removed, such components define ratios of positively to negatively weighted characters, i.e. shape.

As expected, the PCA on the growth data showed a major PC I dominated by the overall trend for all characters to increase in size during growth (Table 5). The two-way ANOVA on PC I scores gave results similar to the univariate growth rates; no diet × sex interaction was evident, no sexual difference in PC I ($F = 0.05$, df = 1,30, $P = 0.82$) was seen, but a strong effect of diet on the growth rate PC I scores ($F = 12.61$, df = 2,30, $P < 0.0001$) existed. PC II represented a ratio between fast-growing leg measurements and slower-growing beak measurements, or measurements such as RET that were not affected by the experimental diets (Table 5). The two-way ANOVA on PC II showed no diet × sex interaction, a nonsignificant sex effect ($F = 3.10$, df = 1,30, $P = 0.09$), and a nonsignificant effect of diet ($F = 0.83$, df = 2,30, $P = 0.44$). Only PC III showed a significant diet effect ($F = 4.22$, df = 2,30, $P = 0.02$), with neither sex nor interaction terms significant. PC III is not included in Table 5 as it explained only 7% of the total variance in growth rates.

TABLE 4. Adult TRS size (in mm, $\bar{x} \pm$ SE) and ANOVA for Zebra Finches raised on 3 diets, with corresponding data for their parents and offspring. The other 8 characters showed similar patterns.

| | Diet | | | ANOVA |
	Low	Standard	High	
Parents	14.01 ± 0.13	14.23 ± 0.12	14.30 ± 0.17	$F_{2,25} = 1.16$ NS
Experimentals	13.19 ± 0.20	13.76 ± 0.10	14.08 ± 0.12	$F_{2,38} = 9.32$***[a]
Offspring	13.79 ± 0.21	13.80 ± 0.10	14.08 ± 0.27	$F_{2,23} = 0.68$ NS

[a] $P < 0.001$.

TABLE 5. PCAs on correlation matrices for growth rates ($n = 36$) and adult measurements ($n = 41$). Entries are correlations between PCs and univariate measures[a] (see also Fig. 2).

	Growth rates		Adult measurements	
Character	PC I	PC II	PC I	PC II
MAS	0.75	**−0.07**	0.64	−0.46
WNG	0.79	**0.04**	0.71	**−0.05**
RET	0.71	0.43	0.56	0.39
TRS	0.82	−0.52	0.83	**−0.17**
TOE	0.83	−0.46	0.76	**−0.05**
BLN	0.91	**0.30**	0.61	0.46
BDN	0.95	**0.21**	0.84	**0.15**
LBW	0.75	0.42	0.63	0.43
BOD	0.88	**−0.30**	0.60	−0.64
Eigenvalue	6.03	1.06	4.46	1.23
Percentage variation	67.00	11.80	49.60	13.60

[a] Boldface correlations are not significant; all others are significant at $P < 0.01$.

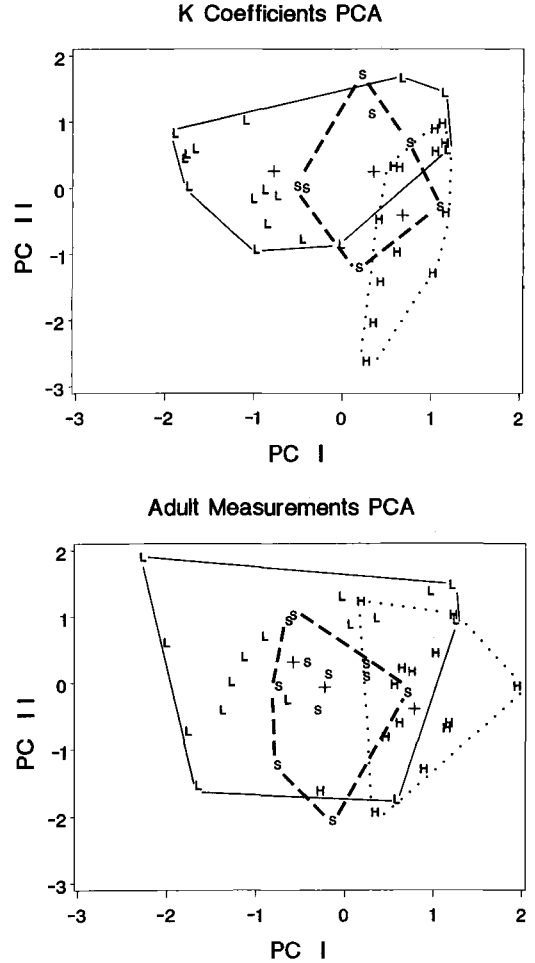K Coefficients PCA

Adult Measurements PCA

Fig. 2. Distribution of PCA scores based on growth-rate variables measured for Zebra Finches raised on low (solid line), standard (dashed line), and high (dotted line) diets (top). Bivariate means for each group are indicated (+). Bottom graph shows similar results, based on a PCA of adult size measurements. L = low, S = standard, H = high.

It represented positive correlations with WNG and RET, and negative correlations with the beak measures.

The PCA on adult measurements showed that PC I summarizes overall size variation among adults, with strong, positive correlations on all characters (Table 5). As for most of the adult univariate characters, PC I shows no significant sex or interaction terms, but a highly significant effect of diet on multivariate "size" (Table 6). In this and other analyses conducted on similar suites of characters for adult Zebra Finches, PC II consistently defines an axis of sexual shape dimorphism. It weighs MAS and BOD negatively, and RET and the beak measures positively; male Zebra Finches have a smaller body than females, but larger beaks and longer rectrices. PC II in adults had no interaction term, a highly significant effect of sex, and a significant effect of diet (Table 6). The means (Table 6) indicate that the high diet rendered the morphology of all birds, independent of sex, more "female-like," while the low diet tended to make all birds more "male-like," with smaller bodies in relation to beak measures and RET. PC III from adult measurements explained 9.8% of the total variation, and showed no significant variation among scores due to diet, sex, or interaction terms.

Plots of PC I vs. PC II provide a useful summary of the overall effects of the experimental diets on size, shape, and interindividual variability (Fig. 2). They account for over two-thirds of the total phenotypic variation in growth and adult data. The experimental diets primarily affected overall growth rate and adult size and had smaller effects on shape. The low-diet young had more variable growth rates and adult sizes (Fig. 2). Much of the variation in phenotypic response to the experimental diets actually was due to between-brood variation (Fig. 2). Young from the same brood tended to cluster together, with two pairs of breeding adults on the low diet producing young with growth

TABLE 6. Effects of diet on several indices of adult shape ($\bar{x} \pm SE$). All entries have been multiplied by 10 for display purposes.

Character	Diet			ANOVAs[a]	
	Low ($n = 16$)	Standard ($n = 14$)	High ($n = 11$)	Diet	Sex
PC I	-5.24 ± 2.94	-2.22 ± 1.42	7.73 ± 1.43	**	NS
PC II	3.65 ± 2.66	-1.08 ± 2.69	-3.32 ± 2.48	*	***
MASTRS[b]	-7.60 ± 0.05	-7.75 ± 0.04	-7.75 ± 0.05	NS	NS
WNGTRS	6.28 ± 0.05	6.11 ± 0.03	6.08 ± 0.04	**	NS
RETTRS	4.06 ± 0.07	3.87 ± 0.04	3.85 ± 0.04	**	*
TOETRS	1.52 ± 0.04	1.43 ± 0.07	1.51 ± 0.05	NS	**
BLNTRS	-2.25 ± 0.05	-2.52 ± 0.05	-2.51 ± 0.05	***	NS
BDNTRS	-2.68 ± 0.04	-2.87 ± 0.06	-2.78 ± 0.04	NS	NS
LBWTRS	-2.93 ± 0.07	-3.10 ± 0.06	-3.09 ± 0.06	*	NS
BODTRS	6.95 ± 0.07	6.80 ± 0.04	6.89 ± 0.04	NS	NS
BLNBDN	0.43 ± 0.06	0.35 ± 0.06	0.27 ± 0.03	NS	NS
BLNLBW	0.68 ± 0.06	0.58 ± 0.04	0.58 ± 0.04	NS	NS
BDNLBW	0.25 ± 0.04	0.23 ± 0.04	0.32 ± 0.04	NS	NS

[a] Two-way ANOVAs, with no significant interaction terms. Significance of diet and sex main effects indicated by *($P < 0.05$), **($P < 0.01$), and ***($P < 0.001$).

[b] MASTRS is an abbreviation for log(MAS) − log(TRS).

and adult PC I scores in the standard- to high-diet range. If a single character such as TRS was used to calculate average *within*-brood CVs, the growth rate means were 7.12, 4.31, and 4.93 for the low-, standard-, and high-diet young, respectively, while the corresponding values for adult TRS were 2.80, 2.00, and 1.81 (given the small number of broods, none of the ratios of CV² were significant in either case). This suggests that although much of the variation was between broods, the residual within-brood variation may remain higher among sibs reared on low compared with high diets. The heteroscedasticity among treatment groups was not severe enough to compromise the ANOVAs described earlier, as replicate analyses on log-transformed data as well as nonparametric

Kruskal-Wallis tests led to identical conclusions.

Diet and shape: character ratios in adults.—Mosimann and James (1979; see also James 1983) suggested that explicit definition of size and shape variables is preferable to multivariate measures that may not be readily comparable between studies. They recommended that differences between the logarithms of various characters and a single size measure (such as WNG or TRS) are appropriate indices of shape, insofar as they represent ratios on an arithmetic scale, but take into account the fact that morphological data tend to be log-normally distributed.

I chose TRS as a measure of size in Zebra Finches. TRS does not display sexual size di-

TABLE 7. Corrected experimental group deviations from grand means, in SD units. L+H is the sum of the absolute values of the low- and high-diet deviations, and provides a measure of environmental sensitivity (see text).

Character	Growth rates				Adult measurements			
	Low	Standard	High	L+H	Low	Standard	High	L+H
MAS	-0.81	0.38	0.79	1.60	-0.44	-0.13	0.60	1.04
WNG	-0.36	-0.20	0.55	0.91	-0.34	-0.13	0.49	0.83
RET	-0.23	-0.17	0.38	0.61	-0.11	-0.16	0.25	0.36
TRS	-0.69	0.00	0.85	1.54	-0.65	0.17	0.61	1.26
TOE	-0.58	0.24	0.58	1.16	-0.45	-0.06	0.56	1.01
BLN	-0.66	0.37	0.48	1.14	0.10	-0.34	0.15	0.25
BDN	-0.76	0.18	0.70	1.46	-0.31	-0.30	0.59	0.90
LBW	-0.71	0.58	0.41	1.12	-0.22	-0.12	0.35	0.57
BOD	-0.65	-0.05	0.72	1.37	-0.56	-0.31	0.88	1.44

morphism in this species, has been used by James (1983) for the same purpose, and, along with BDN, is the character most highly correlated with PC I for the adult measurement data (Table 5). The results of two-way ANOVAs on the ratios [actually differences between log-transformed values, e.g. the abbreviation MASTRS indicates log(MAS) − log(TRS)] between each character and TRS, as well as some ratios between the beak measures, are given in Table 6. Once again, none of the diet × sex interactions were significant, and only 2 of 11 ratios showed significant effects of sex. Four of 11 ratios showed significant effects of diet, all reflecting the fact that TRS is more sensitive to diet than any of the feather or beak measures. None of the beak shape measures gave any hint of diet group differences, indicating that subtle shape changes among similar, slow-growing characters were not taking place.

A measure of environmental sensitivity.—To compare the effects of the experimental diets on the nine characters for both growth rates and adult measurements, with sexual dimorphism statistically removed, a standardized measure of sensitivity to the dietary manipulation was created. First, all the growth coefficient and adult measurement data were converted to Z scores (mean of zero, standard deviation of one). Using the SPSS-X procedure ANOVA (Norusis 1985), two-way ANOVAs on diet and sex were performed with MCA (multiple classification analysis). Such an analysis gives the deviation from the grand mean of each experimental group, in standard deviation units, after adjusting for the other main effects. Thus, in the case of an adult measure such as TOE, diet explained 10% of the total phenotypic variation, with means for low = −0.45, standard = −0.06, and high = 0.56 (sex held constant), while sex explained 9% with means for males = 0.25 and females = −0.35 (effect of diet held constant). The measure of environmental sensitivity chosen was the sum of the absolute values of the corrected high- and low-diet deviations from the grand mean (L+H values in Table 7).

There was a significant correlation between the L+H values based on the growth data and the adult data (Spearman rank correlation, $n = 9$, $r_s = 0.73$, $P < 0.05$). Characters such as MAS and TRS showed consistently large effects, while LBW and RET showed small effects. In the growth data, the mean deviations for low and high diets were −0.61 and 0.61, respectively, while the comparable means for the adult data were −0.33 and 0.85. This suggests that the two diets elevated and depressed growth rates by about the same amount, while the high diet increased final adult size more than the low diet diminished it.

DISCUSSION

The quality of food available for rearing Zebra Finch nestlings not only affects growth rates, but also has permanent effects on adult size. Low-quality diets increase the variation in growth rate and adult size both among and within broods. The possibility that environmental effects such as the protein level in a diet might contribute to spatial or temporal morphological differences in birds has been considered by only a few workers to date (Smith and Zach 1979; James 1982, 1983; Boag 1983; Alatalo and Lundberg 1986). To interpret the results of my experiment, it is important to consider first if the small differences created here could be of ecological significance, and, second, whether such differences are likely to be produced under natural conditions.

To evaluate whether the morphological differences produced here could be of ecological importance, consider the difference between high- and low-diet means in Table 3 as a percentage of the low-diet means. The effect of the high diet is to increase the low-diet adult means 1–2% for BLN or WNG, or 7–10% for characters such as TRS or MAS. Changes in means of less than 2% are difficult to detect in nature without large sample sizes, and to detect their functional impact on activities such as foraging (Schluter and Grant 1984) would be equally difficult. Effects in the 3–10% range could be detected in the wild, and are more likely to be of functional significance. Indeed, many avian studies have assumed that intraspecific morphological differences in this range are important.

For instance, many monogamous passerines display sexual size differences of less than 10%. The significant differences between survivors and nonsurvivors in the Bumpus House Sparrow data (O'Donald 1973) and Isla Daphne Major *Geospiza fortis* data (Boag and Grant 1981) lie in the 2–8% range. In examples of ecotypic variation in avian morphology, Fretwell (1972)

noted significant between-habitat variation in tarsus length for Savannah Sparrows (*Passerculus sandwichensis*, 10%), Song Sparrows (*Melospiza melodia*, 4%), and Field Sparrows (*Spizella pusilla*, 2%). Grant et al. (1976) found significant between-habitat differences in *Geospiza fortis* morphology of well under 10%, while morphological differences of a similar magnitude have been noted for titmice (*Parus* spp.) living in coniferous and hardwood forests (Perrins 1979). Authors studying clinal variation in avian morphology (James 1970) or making island-mainland comparisons (e.g. island subspecies of the wren *Troglodytes troglodytes*; see Williamson 1981: 139) also commonly discuss the adaptive significance of differences between populations of well under 10%. In a recent summary of temporal and geographical morphologial variation in the Fox Sparrow (*Passerella iliaca*), Zink (1983) sought evolutionary interpretations of results for which the largest average percentage difference was 3.28%, with a range of 0.55–8.47%. Adaptive explanations for significant morphological changes of 3–5% in House Finches (*Carpodacus mexicanus*) in their new eastern populations compared with their ancestral western populations were proposed by Aldrich (1982). Dhondt et al. (1979) found that Great Tits gradually became 3–7% smaller over 14 years. Several mechanisms for the shift involving natural selection were suggested, revolving around the fact that the addition of nest boxes had doubled or tripled *Parus* breeding densities during this period.

In citing these studies, I am not suggesting that all such examples involve morphological differences attributable to nonadaptive, environmental effects such as nestling diet quality. I merely point out that avian ecologists regularly seek adaptive explanations for differences of a magnitude that I have produced by way of nonpathological variation in diet quality (by nonpathological I mean diets not producing nestling death or infertile adults). In some cases, e.g. the trend seen by Dhondt et al. (1979) in *Parus* size over time, I see parallels with the breeding-density-associated annual variation in offspring size noted by Boag (1983) for *Geospiza fortis.*

The second question raised above was whether variation in diet or other aspects of the nestling environment sufficient to produce significant morphological changes are common

under natural conditions. In general, we do not have adequate data to answer this question confidently. A few field studies have reported seasonal or annual variation in morphology (Perrins 1979, Smith and Zach 1979, Boag 1983), and Alatalo and Lundberg (1986) found significant differences in tarsus length of Pied Flycatcher (*Ficedula hypoleuca*) offspring reared by primary vs. secondary females of polygynous males. The differences (about 2%) were attributed to differences in paternal feeding rate. Alatalo and Lundberg (1986) also found significant effects of breeding density on tarsus length, with nests in high-density areas producing smaller offspring. Several other long-term studies probably have similar data, although often birds have not been measured as adults, or different workers have been involved in different areas or years, complicating comparisons.

Despite the paucity of data, there is no reason to believe such effects are rare in nature. The experimental regime I used does not involve a totally unrealistic or pathological range of diet qualities. Many estrildid finches routinely raise young on seed alone in the wild (Goodwin 1982, Morton and Davies 1983, Zann and Straw 1984), and many of them inhabit savannah habitats with concomitant seasonal and annual unpredictability in the timing, quantity, and quality of resources during the nesting season. This may result in occasional, opportunistic insect feeding or periodic food limitation, during which time nestlings and fledglings starve (Zann and Straw 1984). Granivores with faster development times than Zebra Finches require a high-protein diet for breeding to be successful. Such species often feed nestlings on insects (Jones and Ward 1976) or other protein-rich items such as the specialized use of *Spirogyra* algae by Sharp-tailed Munias (*Lonchura striata*; Avery 1980). Many birds dependent on insects for rearing young show considerable seasonal or annual variation in nestling growth rates, fledging success, and brood-reduction behavior (Bryant 1975, 1978; Perrins 1976; Howe 1977; Ricklefs and Peters 1979), implying that the potential exists for diet-induced morphological change. Dietary protein can have major effects on both growth and adult size of captive ducks (Johnson 1971) and domestic fowl (Fisher and Griminger 1963). Other environmental effects have also been in-

vestigated. For example, pullets raised at 6°C during 3–6 months of age were shorter, gained more weight, and had smaller tarsi and tails than former flock mates kept at about 23°C (Allee and Lutherman 1940). Similar studies reported the impact of environmental effects on morphology in mammals (Widdowson and McCance 1960, Lister and McCance 1965, Williams and Hughes 1975, Barnett and Dickson 1984), including humans (Hulse 1968). In one of the best longitudinal studies of associations between intraspecific morphological variation and fitness in mammals, Clutton-Brock et al. (1982) found that diet or density-related maternal effects can have profound effects on body size and the lifetime reproductive success of individuals or entire cohorts of red deer (Cervus elaphus).

Among the Zebra Finches used in this experiment, there was considerable variation in the response of different breeding pairs to the diet treatments; one pair was able to raise young to "high-diet size" on the low diet. Part of this variation may be an artifact of the multicomponent, qualitative diets used, which made it difficult to control the amounts of protein, energy, or other dietary components consumed by each young bird. Zebra Finches can raise young on seed alone, so it is unlikely any birds suffered from an energy shortfall. Similarly, all nestling and egg mixtures contained a vitamin-mineral supplement, making specific shortages in these components unlikely. The most obvious difference between the diets was in crude protein availability; however, in the absence of detailed data on assimilation efficiencies, amino acid balance, or micronutrient availability (Fisher 1972), it would be misleading to conclude that the morphological effects observed here are solely the result of dietary protein level. Some of these difficulties could be avoided if a single, synthetic food ration had been used (e.g. Murphy and King 1982). It is possible to switch Zebra Finches to a synthetic diet, but this can cause adult mortality and poor breeding success, at least initially (T. Scheuhammer pers. comm.). The complications described above are important in designing future experiments, but do not alter my principal finding that diet quality can affect adult size as well as growth rates in Zebra Finches.

Under natural conditions, differences in the quality of parental care might produce be-tween-brood morphological differences that are due to environmental effects. Some effect of diet on variation within Zebra Finch broods remained after accounting for between-brood variation, indicating that processes such as sibling competition might affect intraspecific morphological variation. Environmental effects that alter the distribution of variance within and between broods can have important consequences for heritability analyses (Falconer 1981). Although such effects are cited regularly in criticisms of heritability studies under field conditions, almost no data exist to support their existence or nonexistence. Van Noordwijk (1984) suggested that environmental effects resulting from naturally occurring poor breeding seasons or from manipulation of brood size can at least temporarily increase morphological variation among sibs, and hence decrease heritability estimates.

The Zebra Finch data suggest that the primary effect of variation in diet quality is on overall growth and adult size. There was not enough differential impact on characters to produce large changes in shape. The small shape changes observed were due primarily to differences between characters in their rate and timing of growth. Measurements such as MAS or TRS increase quickly and reach asymptotes at an early age; they are affected most by variation in diet. Beak characters grow more slowly, for a prolonged period. Beaks are less susceptible to dietary influences that have their major effect while young are dependent on their parents. Characters involving feather growth also are affected less seriously, despite rather high growth rates. This reflects the high developmental priority of passerine plumage development, which tends to proceed according to a fixed schedule even if a nestling is starving.

It remains to be seen if environmental effects induced by variation in the quality or quantity of nestling diets, or other aspects of the nest environment, regularly influence natural patterns of intraspecific morphological variation in birds. Considerable scope exists for long-term, longitudinal studies of the environmental correlates of morphological variation, as well as more natural experiments of the type I have conducted here (e.g. Berthold 1976, 1977; Smith and Arcese 1987). The primary data on variation in avian growth rates have not been sup-

ported by studies that followed young to adult-hood to check for permanent effects on morphology. Hence, we cannot discriminate which avian characters display compensatory, or "target-seeking," growth (Atchley 1984) once the period of parental dependence is past, and which do not. Judicious choice of characters may well minimize the likelihood of signifi-cant environmental effects in studies of avian morphometrics. Until additional data are avail-able, however, the possibility of environmen-tal effects should not be dismissed automati-cally in favor of selective explanations for morphological differences between bird pop-ulations.

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