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Effects of early nutrition on growth rate and adult size in song sparrows *Melospiza melodia*

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We manipulated the quantity of food provided to hand-reared song sparrows *Melospiza melodia* from 3 to 18 days post-hatching, a period when young birds in the wild are especially likely to experience nutritional stress. A control group was given unlimited food, while an experimental group was limited to 60% of the intake of the controls. Both groups showed excellent survival. The controls had significantly higher growth rates than the experimentals and fledged significantly earlier. At the end of treatment, controls were significantly larger than experimentals in body mass, tarsus length, and length of the third primary. After treatment ended, when all birds were receiving the same diet, both groups showed a recession in body mass, but the amount of mass lost was significantly greater in the controls. Consequently the difference in body mass between the treatment groups was much reduced after the period of weight recession. As adults, the controls were significantly larger than experimentals in a principal component measure of size that combined six post-mortem bone measurements. Controls and experimentals did not differ in the number of fault bars in tail feathers grown in part during the period of nutritional manipulation, nor did they differ in the degree of asymmetry in bone measurements. We conclude that early nutrition affects growth rates in young song sparrows, with effects on skeletal size that carry over into adulthood. These results are consistent with the nutritional stress hypothesis, which posits that early nutrition affects adult phenotypic quality as well as display attributes.

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The nutritional stress hypothesis (Nowicki et al. 1998) proposes that young male songbirds face a tradeoff between investing in the brain structures that underlie song learning and production, which develop rapidly during the first few weeks after hatching, and investing in the many other aspects of growth and development that occur concurrently. During this early post-hatching period, young birds are particularly likely to experience nutritional stress, at first because of limitations on the ability of their parents to deliver food (Lack 1954), and later because of their own inexperience as foragers (Sullivan 1988, Weathers and Sullivan 1989). Only individuals that experience good levels of nutrition can afford to invest adequately in both song development and development of the overall phenotype. Song quality therefore becomes an honest indicator (Andersson 1994) of phenotypic quality. As predicted by this hypothesis, we have found that early nutritional stress has a negative effect on the development of song control nuclei in the brains of male swamp sparrows *Melospiza georgiana* (Nowicki et al. 2002a). We also have found that early nutritional stress negatively affects aspects of song learning in both swamp sparrows (Nowicki et al. 2002a) and song sparrows *Melospiza melodia* (Nowicki et al. unpubl. data), and that female song sparrows prefer well-learned over poorly-learned songs (Nowicki et al. 2002b). Here we test another important prediction of the hypothesis: that early nutritional stress negatively affects other aspects of phenotypic development, with effects that persist into adulthood. We conducted this test using song sparrows.

Growth rates of birds typically are extremely rapid early in life. Passerines, for example, often reach 80 to 110% of their adult mass in the space of 10 to 20 days after hatching (Ricklefs 1968a). A potential drawback of this developmental strategy is that any stress experienced during the period of rapid growth, stemming for example from fluctuations in food supply or weather, may have large, detrimental effects on an individual's adult phenotype and hence on its fitness. Such effects are not inevitable, however. One alternative is for a stressed bird to delay maturation, for example by delaying fledging, so as to prolong the period of growth (Emlen et al. 1991). Birds that can delay maturation may be able to avoid totally any effect of early nutritional stress on their adult phenotypes (Schew and Ricklefs 1998). A second strategy is for stressed individuals to undergo compensatory growth after a period of stress has ended. A strict definition of compensatory growth requires "accelerated growth relative to age or physiological state" (Schew and Ricklefs 1998), meaning that growth is faster than normal rather than simply extended in time. Compensatory growth is not necessarily cost-free, however, and may result in detrimental phenotypic effects that only appear later in life (Metcalfe and Monaghan 2001). A third alternative is for stressed individuals to shunt what resources they have from characters that are less important to fitness to ones that are more important, so that detrimental effects on overall fitness are minimized (Schew and Ricklefs 1998). Specifically, it has been suggested that "secondary sex traits... have low growth priorities compared to other organs" (Andersson 1986), presumably because secondary sex traits are not essential to survival while other organs are. Birds that are nutritionally stressed thus might sacrifice the development of display characters such as song while maintaining the development of other characters, such as bone sizes and body mass. This trade-off between investment in secondary sexual traits and other phenotypic characters provides one explanation for the evolutionary maintenance of honest signaling in mate choice (Andersson 1986).

Previous studies that have manipulated the diet of nestling birds have produced mixed outcomes. A reduction in the quantity of food provided to nestlings generally reduces rates of growth in body mass during the nestling stage (Skagen 1988, Lacombe et al. 1994, Konarzewski et al. 1996). Effects on absolute mass may (Richner et al. 1989) or may not (Durant and Handrich 1998) extend beyond fledging. Effects on bone growth are even more mixed, perhaps because the skeleton is one of the systems in which growth is least likely to be sacrificed in avian development (Schew and Ricklefs 1998). Some studies have found that reducing the quantity of food depresses the growth rate of the tarsus (Schew 1995), but others have found no such effects (Richner et al. 1989, Lacombe et al. 1994). Similarly, reducing the quantity of food in the nestling stage sometimes does (Richner et al. 1989) and sometimes does not (Lacombe et al. 1994) affect adult tarsus size. Other studies have manipulated food quality rather than quantity, usually by manipulating protein content, with similarly mixed results on growth. Ohlsson and Smith (2001), for example, found that protein content in the early post-hatching diet affected adult tarsus length but not adult body mass in pheasants, whereas Birkhead et al. (1999) found that protein content in the nestling diet affected adult body mass but not tarsus length in zebra finches.

Inconsistent outcomes of diet manipulations are to be expected, given that no two studies have manipulated diet in exactly the same way. Moreover, it is in principle impossible to standardize diet manipulations across species, because of differences that exist between species in the quantity and composition of the natural diet and the timing and duration of different aspects of growth.

Early nutrition has been manipulated previously in our study species, the song sparrow, as part of the long term study of the population on Mandarte Island, off the coast of British Columbia (Smith and Arcese 1988, Hochachka and Smith 1991). The young of free-living pairs given supplemental food were significantly larger at 6 days post-hatching in body mass, wing length, and tarsus length (Smith and Arcese 1988). The condition of these supplemented young, as measured by the residuals of a cubic regression of mass on wing length, was no different from that of controls, suggesting that the extra resources were devoted to structural growth rather than to laying down additional fat (Hochachka and Smith 1991). When measured between 56 and 108 days, supplemented young were no longer significantly larger in any measurement (Smith and Arcese 1988). Smith and Arcese (1988) concluded that the control young most likely experienced compensatory growth that allowed them to catch up with the experimental young in size.

Here we examine the effects on nestling growth and adult morphology of restricting the quantity of food provided to hand-reared song sparrows during a period corresponding to the time when young birds are most likely to experience nutritional stress in the wild. Using this same experimental design, we also have shown that early nutritional stress affects brain growth and song learning abilities in swamp sparrows, a congener of the song sparrow (Nowicki et al. 2002a). Thus, if we find that this diet manipulation affects aspects of the adult phenotype such as body size and body mass, we can conclude that nutritional stress that is sufficient to affect song learning and production also is sufficient to affect these other adult traits.

Materials and methods

Collection and housing

Nestling song sparrows were collected in the vicinity of Hartstown, Crawford County, Pennsylvania, during the spring of 1999. The nestlings were taken at three to six days after hatching from nests found in the field. In some cases, we located nests in the egg stage and subsequently visited them periodically, so that day of hatching was known and the chicks could be aged exactly. In other cases, we located nests after hatching and estimated the age of the chicks from their developmental stage, following the descriptions of Nice (1943) and our own experience (Peters and Nowicki 1996, Nowicki et al. 1999) with known age young.

A total of 12 broods and 49 young were collected. Each brood was taken from the field in its own nest, and then transferred in the laboratory to another, natural song sparrow nest that had been sterilized. When collected, broods were assigned randomly to two treatment groups, experimental or control, with the restriction that we balanced the number of young in the two groups at all times as much as possible. Birds were sexed by laparotomy between 36 and 42 days of age. In the end, the control group consisted of six broods and 24 young, including 11 males and 13 females; the experimental group consisted of six broods and 25 young, including 16 males and 9 females.

Broods were kept separately in natural nests (changed periodically with fresh, sterilized nests for sanitation) until fledging, at which time they were housed in cages (30 × 30 × 46 cm) holding two broods each. At 18 days post-hatching, all subjects were transferred to smaller cages (23 × 23 × 46 cm) where they were housed singly. At all stages, both experimental and control birds were maintained in the same room under identical conditions, except for their feeding regimes.

Treatments

From the time of collection to 18 days post-hatching, the subjects were fed a standard hand-rearing diet, containing set proportions of ground beef, hardboiled eggs, tofu, Purina monkey chow, pureed carrots, avian vitamin powder (Avia, Nutra-Vet Research Corp.), and a calcium supplement (Osteo-form, Vet-A-Mix Corp.) blended in a food processor (detailed recipe available on request). This diet was provided to the chicks through syringes (Bectin-Dickinson, 1 cc Tuberculin), which allowed amounts to be controlled and measured to the nearest 0.1 ml. All chicks were fed at half hour intervals from dawn until dusk until nine days post-hatch, and thereafter at one hour intervals. The control birds were fed to satiation at each feeding interval. The average amount eaten by the controls was calculated for each feeding, and the experimental subjects were limited to 60% of that amount.

At 18 days, when the birds were transferred to individual cages, both groups of subjects were provided with unlimited amounts of food (dry seed, seed that had been soaked in water, tofu, peas, corn, ground hardboiled eggs enriched with avian vitamins, and mealworms) which they could feed on themselves. Hand-feeding continued for another six days, but the amount of food taken by subjects quickly diminished. The nutritional manipulation thus effectively ended at 18 days post-hatching.

Survival was excellent in both treatment groups. One experimental bird (a female) died at 12 days and one control bird (also a female) died at 23 days; otherwise all subjects survived for the remainder of the experiment. Survival through the nestling and fledgling phases was thus 96% for both experimentals and controls. By comparison, Nice (1937) found that only 306 of 510 young, or 60%, survived from hatching to fledging (at a mean of 10 days) in a free-living population of song sparrows in Ohio.

Measurements

Subjects were weighed to the nearest 0.1 g (Ohaus LS200 electronic balance) either on the day of collection or on the day after, and then at two-day intervals until 42 days post-hatching. The birds were weighed at 11 am each time, just after being fed. We weighed each subject again on days 60, 84 and 350. We measured left and right tarsi and left and right third primary feathers to the nearest 0.1 mm (Fowler Ultra Cal III digital calipers) on day 18.

We collected two rectrices from each individual (taking the next-to-outermost feathers on the left and right sides) just prior to the first pre-basic molt and assayed them for fault bars under a low power dissection microscope. Fault bars are areas of a feather where barbs and barbules are reduced or absent (Riddle 1908), and which appear as translucent areas in the vane. Fault bars result, at least in part, from nutritional stress (Riddle 1908), and therefore have been used as evidence that individuals have experienced stress in the past (Newton 1968, Møller 1989). Because there is some subjectivity in deciding whether a translucent area is large enough to qualify as a fault bar, counts of fault bars were made by an observer blind to the treatment group from which each feather was taken. We use as our measure the total number of fault bars in the two feathers taken from a bird. We counted fault bars twice for a subset of 22 birds, and the correlation between the two counts was 0.936 ($P < 0.001$).

Subjects were euthanized at approximately one year (males) or two years (females) of age. Males were euthanized earlier than females in order to harvest their brains at the solstice of their first adult summer for a separate analysis not presented here. Song sparrows reach asymptotic size in most structural characters by two months (Smith and Zach 1979) and are usually thought to change little if at all thereafter (but see Smith et al. 1986). Bones were cleaned of flesh using a dermestid beetle colony. An observer blind to the treatment groups took six standard bone measurements, to the nearest 0.01 mm. These measurements were: (1) humerus length (cranial surface measured from top of humerus caput to bottom of ventral condyle), (2) ulna length (ventral surface measured from top of olecranon to groove between condyles), (3) femur length (cranial surface measured from edge of acetabularis to the intercondyle sulcus), (4) femur width (transverse mid-shaft diameter measured on the cranial surface), (5) tibiotarsus length (cranial surface measured from retro-patellar fossa to the groove between condyles), and (6) pelvis width (distance between left and right acetabula). All measurements were taken three times in sequence, with the median value recorded for analysis. If the range of the three values taken for a single measurement exceeded 0.05 mm, then another two measurements were made and the median of these five values was recorded. For all bilateral traits, we measured both left and right sides in each subject. In a small number of cases, a bone was damaged during processing on one side or the other of an individual, in which case only the undamaged bone was measured. For a subset of six birds, we followed the same procedure to make a second set of left and right measurements of the bilateral traits, several days after and blind to the first set of measurements, to use in analyzing fluctuating asymmetry.

Statistical analysis

In cases where we had left and right measurements of the same character, we averaged the two to produce individual means. SYSTAT© software was used to perform two-way nested ANOVAs on these individual means, through the General Linear Model procedure. Each model included treatment and sex as factors, with broods nested within treatment, and a sex by treatment interaction term. F-statistics were calculated for treatment and sex effects using the broods within treatments mean square as the error term.

Growth in body mass was analyzed by fitting logistic curves to the weight data using the method of Ricklefs (1967). The logistic growth model consistently provides a better fit to growth data in passerines than alternative models (Ricklefs 1968a). We estimated a curve for each individual, using all weights obtained for that individual between 3 and 24 days. The asymptote for each curve was estimated as the peak observed weight plus 0.2 grams.

Adult body size was measured as the first principal component (PC1) produced by a principal component analysis of the six post-mortem bone measurements. A principal component measure combining separate skeletal measurements is thought to provide the most meaningful estimate of adult body size in birds (Freeman and Jackson 1990).

We analyzed left versus right side asymmetry in the post-mortem bone measurements. We first examined the subset of measurements that were made twice on the same individuals ($N = 6$ birds), in order to distinguish true asymmetry from measurement error (Palmer and Strobeck 1986, Swaddle et al. 1994). Following Swaddle et al. (1994), we used a mixed model ANOVA, with factors individual (I), side (S), and replicate (R). The ratio of the I-by-S mean square to the sum of the I-by-S-by-R and I-by-R mean squares gives an F-test for whether between individual variation in asymmetry is greater than accounted for by measurement error (Swaddle et al. 1994). For those bone measures that passed this test for true asymmetry, we next tested whether the mean of the left minus right measurements differed from 0, using a one-sample t test. This test is used to distinguish fluctuating asymmetry ($\text{mean} = 0$) from directional asymmetry ($\text{mean} \neq 0$). Finally, we compared the magnitude of asymmetry in controls versus experimentals using ANOVA.

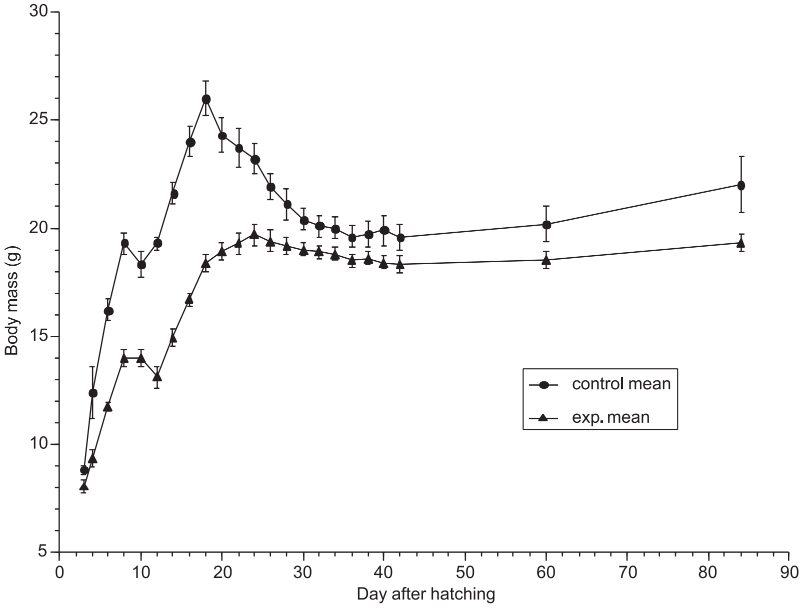
Results

Growth in body mass

Growth was rapid and continuous from the time of collection up to day 18 in the control group and day 24 in the experimental group, except for a small dip in mass that occurred in both treatment groups around the time of fledging (Fig. 1). In each brood, all individuals fledged on the same day, regardless of sex; consequently we treat each brood as a single data point in analyzing fledging date. Fledging occurred about a day earlier on average in the control group ($\text{mean} = 9.0$ days, ± 0.3 SE) than in the experimental group ($\text{mean} = 10.2$ days, ± 0.3); this difference was significant ($t = 2.91$, $df = 10$, $P = 0.016$).

Both treatment groups showed a recession in body mass between the peak mass attained and mass at 42 days (Fig. 1). All 23 of the control birds lost weight during this period, as did 22 of 24 experimental subjects. The least squares mean weight loss was 6.5 g (± 0.4) for control birds and 1.6 g (± 0.4) for experimental birds. The treatment difference was significant ($F = 24.37$, df 1,10, $P < 0.001$). There was no effect of sex ($F = 0.25$, $P > 0.10$) and no sex by treatment interaction ($F = 0.03$, $P > 0.10$). After day 42, both treatment groups showed a renewed but very gradual increase in mass.

Fig. 1. Growth in body mass from 3 to 84 days post-hatching. Mass is shown as the means of the brood means (±SE) for the controls and experimentals. The sexes are combined because there is little evidence of sexual dimorphism during this period.



Nutritional treatment had a strong and statistically significant effect on the peak mass reached during the first 30 days (F = 40.90, df = 1,10, P < 0.0001; Table 1). Within treatment groups, males tended to be slightly larger at their peak mass than females, but the effect of sex was not significant (F = 0.84, P > 0.10). There was no sex by treatment interaction (F = 0.07, P > 0.10). The well-fed controls reached their peak in mass four to five days earlier than did the nutritionally-restricted experimental group (Table 1), and this difference was significant (F = 45.37, df = 1,10, P < 0.0001). Sex had no effect on age at peak mass (F = 0.30, P > 0.10), nor was there a sex by treatment interaction (F = 0.002, P > 0.10).

Given that the controls reached a higher peak mass at an earlier age than the experimentals, it is not surprising that growth rates were higher in the controls (Table 1). K, the growth rate parameter in the logistic model, was significantly higher in the controls than in the experimental group (F = 18.26, df = 1,10 P = 0.0016). The sexes did not differ in growth rate (F = 0.20, P > 0.10), and there was no sex by treatment interaction (F = 0.05, P > 0.10).

Size at the end of treatment

We consider our treatment regime to have ended at day 18, when both groups began receiving unlimited food in their cages. Table 2 shows three measures of size taken at day 18: body mass, tarsus length, and length of the third primary. For all three characters, controls were larger than experimentals in both sexes. Treatment effects were significant for each character, sex effects were not significant, and there were no treatment by sex interactions.

Adult size

Our main measure of adult body size is the first principal component (PC1) from a principal component analysis of the six post-mortem bone measurements. All six bone measurements loaded positively onto PC1. The loadings were 0.935 for humerus length, 0.901 for ulna length, 0.919 for femur length, 0.358 for femur width, 0.909 for tibiotarsus length, and 0.757 for pelvis width. The eigenvalue for PC1 was 4.059, all other principal

Table 1. Growth in body mass for hand-reared song sparrows. Age at peak mass is the day between 3 and 24 post-hatching at which the body mass was greatest. K is the rate parameter from a logistic equation fitted to the mass data from days 3 –24. Sample sizes are numbers of broods.

	Peak mass (g)	Age at peak mass (days)	K
Female controls (N = 12)	25.7±0.7	18.0±0.4	0.27±0.006
Female experimentals (N = 8)	18.9±0.7	22.6±0.4	0.21±0.006
Male controls (N = 11)	26.4±0.6	18.5±0.3	0.26±0.005
Male experimentals (N = 16)	20.3±0.5	23.0±0.2	0.21±0.004

Table 2. Measurements of size at end of treatment (18 days). Values are least squares means and standard errors estimated from GLM ANOVA. No treatment x sex interactions were significant (P > 0.10 in all cases). Sample sizes are numbers of individuals. Degrees of freedom are 1,10 for each test.

Trait	Female controls (N = 12)	Female experimentals (N = 8)	Male controls (N = 11)	Male experimentals (N = 16)	Treatment effect	Sex effect
Mass (g)	25.5 ± 0.7	17.9 ± 0.7	26.4 ± 0.6	18.6 ± 0.4	F = 63.10 P < 0.0001	F = 0.56 P > 0.10
Tarsus (mm)	21.4 ± 0.2	20.1 ± 0.2	21.6 ± 0.1	20.2 ± 0.1	F = 43.56 P < 0.0001	F = 0.78 P > 0.10
Primary (mm)	48.1 ± 0.5	46.1 ± 0.5	50.5 ± 0.4	46.0 ± 0.3	F = 14.33 P = 0.0036	F = 1.54 P > 0.10

components had eigenvalues less than 1. PC1 explained 67.6% of the total variance in the bone measurements.

Within each sex, the mean PC1 scores were higher for the controls than for the experimentals, and within each treatment, the mean PC1 scores were higher for males than for females (Fig. 2). ANOVA indicated that sex had the stronger effect on adult size (F = 10.77, df = 1,10, P = 0.0083), but the effect of treatment was also significant (F = 7.31, df = 1,10, P = 0.022). There was no sex by treatment interaction (F = 0.33, P > 0.10).

The PC1 scores are normalized to give an overall mean of 0, and therefore do not convey a clear picture of the proportional effects of the nutritional treatment on size. Accordingly, we also present the separate bone measurements, calculated as the means of the family means for the two sexes separately (Table 3). For the four measures of lengths of bones, control males were larger than experimental males by 2.2% for humerus, 2.4% for ulna, 2.7% for femur, and 3.4% for tibiotarsus. For females, controls were larger by 2.3% for humerus, 1.6% for ulna, 3.0% for femur length, and 2.6% for tibiotarsus.

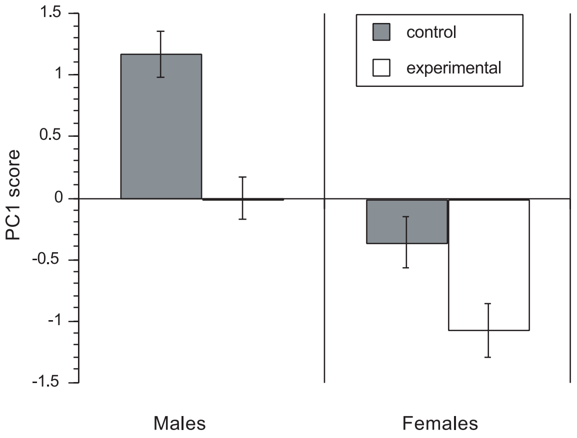


Fig. 2. Adult body size as measured by the PC1 scores combining six post-mortem skeletal measurements. The scores are shown as the means of the brood/sex means (±SE). Both treatment and sex effects are significant.

We weighed the males again, but not the females, at one year of age. The least squares mean mass at one year was 22.0 (±0.9) g for the controls (N = 11) and 20.3 (±0.7) for the experimentals (N = 16). This difference was not significant (F = 4.18, df = 1, 8, P = 0.075).

Fault bars

The nutritional treatment had no apparent effect on the number of fault bars in rectrices collected before the first pre-basic molt. Among females, the mean number of fault bars was somewhat higher among the controls (5.4 ± 1.0) than among the experimentals (3.6 ± 1.0), but the trend was opposite among males (2.0 ± 0.9 for controls; 2.9 ± 0.7 for experimentals). Overall there was no treatment effect (F = 0.06, df = 1,10, P > 0.10), no sex effect (F = 1.30, P > 0.10), and no sex by treatment interaction (F = 0.54, P > 0.10).

Asymmetry

For four of the five bilateral bone measurements, the level of left/right asymmetry that we measured was quite low, less than 0.5% (Table 4). The one exception was femur width, with a mean asymmetry of 1.82%. A mixed model ANOVA performed on the six individuals for which we had two measurements of each character showed that only for humerus and ulna lengths was the level of true asymmetry significant against the background of measurement error (F = 7.00, P = 0.0047 for humerus; F = 5.35, P = 0.012 for ulna; P > 0.10 for the other characters, df = 5, 10 for each test). Thus the higher apparent asymmetry in femur width is probably due to a higher level of measurement error, as a proportion of the mean values, in this character compared to the others, rather than to actual asymmetry.

For the two characters for which we had evidence of true asymmetry, humerus and ulna lengths, we tested whether the mean of the left minus right differences differed from 0. For this analysis, we used individuals as the sample points. For humerus lengths, the mean left

Table 3. Means (±SE) for the six post-mortem bone measurements. These are brood means for each sex and treatment. Sample size (in parentheses) are numbers of broods.

	Female controls (5)	Female experimentals (4)	Male controls (5)	Male experimentals (6)
Humerus length	17.24±0.11	16.86±0.13	17.80±0.14	17.42±0.09
Ulna length	17.98±0.09	17.69±0.13	18.95±0.13	18.51±0.13
Femur length	17.32±0.14	16.81±0.09	17.73±0.10	17.27±0.11
Tibiotarsus length	28.80±0.26	28.08±0.23	29.59±0.24	28.63±0.25
Femur width	1.38±0.02	1.36±0.02	1.40±0.02	1.35±0.02
Pelvis width	8.58±0.11	8.38±0.14	8.94±0.11	8.74±0.05

minus right difference was 0.036±0.016 (N = 40), which was significantly different from 0 (t = 2.32, P = 0.026). For ulna lengths, the mean left minus right difference was −0.042±0.009, which also was significantly different from 0 (t = −4.96, P < 0.0001). These results accord with directional asymmetry rather than fluctuating asymmetry.

The means of the absolute values of the left minus right differences were quite similar for the two treatment groups for both humerus and ulna (Table 5). No treatment effect on the magnitude of asymmetry was indicated by ANOVA.

Discussion

Our nutritional manipulation clearly affected the growth rates of young song sparrows, so that by the end of the treatment period the nutritionally-restricted birds were significantly smaller than the controls in mass, tarsus length, and the length of the third primary feather. Both nutritionally-restricted and control birds reached a peak weight early on and then lost mass after fledging to achieve their eventual adult weight (Fig. 1). Such a “weight recession” has been observed in other birds under natural conditions (Ricklefs 1968b, O’Connor 1978), but before rather than after fledging. At one year of age, control birds were no longer significantly heavier in mass than experimental birds, but they did retain their advantage in skeletal size, as shown by a principal component measure combining six skeletal traits.

Young birds have been described as using three mechanisms to counteract impairments in growth caused by nutritional stress: delayed maturation, compensatory growth, and the shunting of resources between developing structures. Compensatory growth may account for the convergence in size observed between control and supplemented young in an experiment with freeliving song sparrows (Smith and Arcese 1988). In our experiment with captive song sparrows, we found evidence of delayed maturation: the nutritionally-stressed experimental birds delayed fledging by one day and prolonged growth in mass by 4–5 days relative to controls. Although the prolongation of growth in the experimentals had some effect on closing their gap with the controls, more important was the reduced, post-treatment weight recession shown by the experimentals (Fig. 1). Control birds on average lost four times as much mass as experimental birds (6.5 vs 1.6 g). At the end of the period of weight loss (day 42), the treatment groups differed by only 8.9% in body mass, compared to 42% at day 18. These results thus suggest a fourth mechanism for counteracting early nutritional stress, a reduction of post-fledging mass recession. Whether this mechanism applies to song sparrows or other birds in nature is unknown.

Even though delayed maturation and reduced mass recession lowered the gap in size between controls and experiments, the controls maintained some size advantage into adulthood. The difference in mass between the treatment groups still was significant at day 42, after weight recession (F = 11.86, df = 1,10, P = 0.0063). At one year, the difference in the means between the treatment groups was nearly the same (8.4%) as at day 42, but the difference was no longer statistically significant because of an increase in within-treatment variance. The convergence of the treatment groups in mass thus was substantially completed by day 42. The controls retained their significant advantage in skeletal

Table 4. Estimates of left/right asymmetry in the five bilateral characters measured post-mortem. The magnitude of asymmetry is small (< 0.5%) for all characters except femur width. Sample sizes (in parentheses) are numbers of individuals.

Character	Mean±SE	|Left−Right|	Percent of mean
Humerus length	17.36±0.06 (46)	0.059±0.014 (40)	0.34%
Ulna length	18.33±0.08 (46)	0.053±0.007 (45)	0.29%
Femur length	17.32±0.06 (45)	0.081±0.01 (41)	0.47%
Femur width	1.370±0.008 (46)	0.025±0.004 (43)	1.82%
Tibiotarsus length	28.73±0.11 (47)	0.11±0.18 (41)	0.38%

Table 5. The mean absolute asymmetries in humerus and ulna lengths. These are brood means and the N's are the numbers of broods. There are no significant treatment or sex differences.

	Humerus asymmetry	Ulna asymmetry
Female controls (N = 5)	0.09 ± 0.05	0.06 ± 0.02
Female experimentals (N = 4)	0.05 ± 0.01	0.07 ± 0.01
Male controls (N = 5)	0.06 ± 0.02	0.08 ± 0.04
Male experimentals (N = 6)	0.07 ± 0.04	0.05 ± 0.01

size at one year, presumably because bone sizes were relatively fixed by the end of the treatment period.

Fitness consequences

Although early nutrition definitely affected growth and size in our experiment, we still need to ask whether the effects we observed were large enough to have any appreciable impact on fitness. One effect that we found that might well have fitness consequences is the one day delay in fledging that we observed in the experimental birds. Presumably, the delay occurred because the experimental young took longer to reach a stage of skeletal and feather development that would support flight. A similar effect of growth rate on time to fledge has been reported for great tits *Parus major* (Keller and van Noordwijk 1994). The high rates of nest predation experienced by passerines, especially open-nesting species, are thought to select for rapid growth so that the length of time spent in the nest can be curtailed as much as possible (Lack 1968, Bosque and Bosque 1995). Song sparrows are typical of open-nesters in experiencing intense nest predation (Nice 1937), and therefore might well pay an appreciable survival cost under natural conditions for a one day delay in fledging.

Another trait affected by our experimental manipulation that is likely to have fitness consequences in nature is size at fledging. Post-fledging survival has been found to be positively associated with body mass and tarsus length at the time of fledging in a number of passerine species (e.g. Perrins 1965, Krementz et al. 1989, Gebhardt-Heinrich and Richner 1998). In our experiment, the control birds at day 10 were about 30% larger in mass than the experimentals (Fig. 1), and at day 18 they were 42% larger in mass and 7% larger in tarsus length (Table 2). These size differences are as great or greater than those shown to be associated with differences in post-fledging survival in great tits (Smith et al. 1989, Tinbergen and Boerlijst 1990) and European blackbirds *Turdus merula* (Magrath 1991). Moreover, in free-living song sparrows, Smith and Arcese (1988) found that nutritionally-supplemented young, which at day 6 were just 8% larger in mass and 4% larger in tarsus length, had significantly higher survival to day 56 than did controls. We conclude that our nutritional manipulation probably would have affected post-fledging survival under natural conditions.

Nice (1943) found that the mean age at fledging in free-living song sparrows in Ohio was 9.9 days, a value intermediate between the 9.0 days we found for our control group and the 10.2 days we found for the experimentals. Similarly, the mean mass of free-living adult male song sparrows in Pennsylvania is 21.0 g (Dunning 1993), intermediate between the mean of 22.0 g we found in our adult male controls and the 20.3 g we found in our adult male experimentals. These comparisons suggest that our controls experienced better growth than free-living birds on some measures, so that they might better be considered a "supplemented" group, rather than a baseline group. In nature, other stresses such as parasitism might act synergistically to compound the effects of nutritional restriction on measures such as fledging date and adult mass, but at the same time hatching asynchrony and brood reduction might act under natural conditions to reduce such effects.

Nutritional stress and male quality

One goal in performing this experiment was to ask whether early nutrition affects aspects of male phenotypic quality that might be important to females during mate choice. A female chooses a mate from among available adult males, that is, from among those birds that have survived to adulthood, so effects of early nutrition on the survival of males as nestlings and fledglings are not directly relevant to answering this question. Instead, what should be relevant are effects of early nutrition on adult characteristics that potentially correlate with benefits a female might receive by mating with a particular male. We found a significant effect of nutrition on adult skeletal size, with some evidence also of an effect on adult body mass, although that effect was not significant ($P = 0.075$).

Size has been shown to correlate with female choice in some passerine species, with females preferring larger males (e.g. Weatherhead and Boag 1995, Kempenaers et al. 1997), although there is no evidence for this effect in song sparrows (Schluter and Smith 1986). A female might prefer larger males if male size correlates with increased ability to provide direct benefits to her or her offspring. Larger birds may have a survival advantage during adverse weather (Bumpus 1899, Boag and Grant 1981, Pugesek and Tomer 1996, Brown and Brown 1998), and survival of her mate must be important to a female song sparrow because she depends heavily on him for help with parental care and for territory defense (Nice 1937, 1943). It is not clear, however, whether such a survival advantage would be realized in song sparrows within a breeding season, given that year to year survival was shown not to be associated with size among male song sparrows on Mandarte Island in British Columbia (Schluter and Smith 1986). Females also might benefit by mating with a larger male if size confers an advantage in aggressive interactions that translates into superior territory defense. A relationship between size and dominance is particularly likely to be present in organisms with indeterminate growth (Censky 1995, Nakano 1995, Schuett 1997), but also has been observed in birds (Searcy 1979, Hagelin 2002). In song sparrows, however, size was found not be to be associated with dominance, again in the Mandarte Island population (Arcese and Smith 1985).

Another reason females might be interested in large males is that, if heritable factors affect size, females mating with large males might benefit indirectly through producing genetically superior offspring. Many studies have demonstrated considerable genetic variation for growth rate and body size in birds (reviewed by van Noordwijk and Mark 1998), suggesting that a female's offspring will generally be larger, and thus more viable, if she mates with a larger male. Our experimental data do not address the question of how different genotypes respond to nutritional stress. In a natural population, however, both variation in the amount of stress experienced and variation in how well an individual's genotype responds to a given level of stress are likely to contribute to growth rate and adult body size. To the extent that response to developmental stress is revealing of genotypic quality, females would be expected to prefer large males even if they receive no direct benefits from that preference.

Developmental stress may affect many other aspects of male phenotype that are less apparent than size, but which might equally well affect a male's ability to feed young, defend a territory, and so forth (Lindström 1999, Buchanan 2000). The degree of asymmetry between the left and right sides of bilateral traits has been widely used to measure developmental response to stress, with the assumption that the degree of asymmetry observed is a measure of development stability that correlates with other physiological and anatomical outcomes affecting viability (Parsons 1992, Watson and Thornhill 1994). Attention has focused in particular on fluctuating asymmetry, defined as left/right differences that are normally-distributed with a mean of zero (Palmer and Strobeck 1986). The degree of fluctuating asymmetry exhibited by an individual has been claimed to increase with increasing stress (Møller and Swaddle 1997), though this claim remains controversial (Bjorksten et al. 2000, Lens et al. 2002).

We found no evidence of fluctuating asymmetry in the five skeletal traits that we analyzed (Table 4 and 5). In only two of these traits was there evidence of significant asymmetry, and in both of these asymmetry was directional rather than fluctuating. Although fluctuating asymmetry has been the form of asymmetry most typically used to measure developmental instability, some authors have argued that directional asymmetry can be used for the same purpose (Graham et al. 1993, 1998). In any case, we found very low levels of asymmetry in most of the bilateral skeletal elements that we measured, and no evidence that nutritional stress affected the level of asymmetry.

Another measure that has been used as a proxy for the quality of development in birds is the number of fault bars observed on flight feathers (e.g. Newton 1968, Møller 1989). We found no difference between experimental birds and controls in the numbers of fault bars observed in rectrices that developed in part during the period of diet manipulation. Riddle (1908) induced fault bars in captive, juvenile ring doves through food deprivation, but, judging from the higher mortality observed in Riddle's study compared to ours, the level of food deprivation that he imposed must have been much more severe. Negro et al. (1994) found that more moderate food restriction had no effect on the formation of fault bars in hand-reared American kestrels *Falco sparverius*. Other stresses, such as handling (Machmer et al. 1992, Negro et al. 1994), also are known to affect the formation of fault bars. The tail feathers in many of our young birds suffered excess wear, especially from brushing against the sides of cages, and these effects may have been sufficiently large to obscure any effect of nutrition we might have observed.

Conclusion

Nutritional restriction early in life, during the period when young birds would normally be dependent on parental care, had a strong effect on the growth of song sparrows. The nutritionally restricted birds were able to compensate to some extent for impaired early growth by delaying maturation and by limiting their post-fledging weight recession relative to controls. Despite these efforts at compensation, the nutritionally-restricted birds remained significantly smaller in skeletal size as adults. The effects of nutritional stress we observed include ones that would likely affect survival in the nestling and post-fledging stages under natural conditions, but it is less clear whether these effects would be important to females in mate choice. Also unclear is the degree to which our manipulation affected other aspects of the phenotype that are less apparent than body size but that may also affect fitness later in life. Possible examples include immunocompetence, physiological and muscular efficiencies, and brain function. Such effects, if they occur, would provide additional pathways by which early stress influences the quality of adults and their desirability as mates.

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