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Individual variation in the basal metabolism of Zebra finches *Taeniopygia guttata*: no effect of food quality during early development

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Abstract. We investigated the physiological background to individual variation in basal metabolic rate (BMR) in a laboratory population of a small passerine bird, the Zebra finch, *Taeniopygia guttata*. We especially explored whether food-quality during early development influenced the BMR later in life. Zebra finches were raised on two different food regimes; one ('low quality') involving only mixed seed diet, while the other ('high quality') in addition including a protein supplement and daily fresh hard-boiled eggs. The different diets were administrated to the birds only during the first 6 weeks of life. At an age of 1.5 to 2 years, and after a breeding period of their own, BMR was measured in all individuals. Food quality had a significant effect on body mass. Adult finches raised on high-quality protein-rich food were significantly heavier (2.2 g for males and 1.9 g for females) than their counterparts raised on low-quality food. Despite this, the BMR of the adult birds did not differ beyond that expected based on variation in body mass alone. Hence, the early feeding regimes, which induced a non-genetic phenotypic variability in body mass, did apparently not induce any long-term changes in body composition or in organ metabolic intensity. © 2004 Elsevier B.V. All rights reserved.

Keywords: Allometry; Basal metabolic rate; Diet quality; *Taeniopygia guttata*; Zebra finch

1. Introduction

The basal metabolic rate (BMR) represents the lowest sustainable aerobic metabolism of a resting, postabsorptive, endothermic organism at thermoneutral conditions [1]. The

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BMR differs greatly between endothermic organisms, both within and between species. The interspecific variation have been attributed to adaptations to either specific environmental conditions, or to certain behavioural traits of the species. In birds, for instance, a high BMR is characteristic of species living in colder climates and at higher latitudes [2–4], in species living in an aquatic environment [5] and in species with a high level of aerobic activity [6]. In contrast, low BMR is characteristic of birds living in the tropics [7,8], of birds living on islands [9], and of night-active birds [5].

Intraspecific variations in BMR may be of two types. Firstly, variation in BMR may occur between populations. Such variations usually correlate with different environments. In House finches (*Carpodacus mexicanus*), for example, those individuals living in Colorado and Michigan have a significantly higher winter-BMR compared to those individuals living in southern California, which experience much milder winters [10]. Secondly, BMR may also vary within populations. For instance, a significant repeatability of BMR, measured over two consecutive years, have been described within an arctic population of Black-legged kittiwakes (*Rissa tridactyla* [11]). Other studies have also shown BMR to be a repeatable parameter [12,13]. Hence, within populations, some individuals may be 'high-metabolic' while others may be 'low-metabolic'. The reasons to such differences in metabolic rate have hardly been studied. Some of the within-species BMR-variation may have a genetic component [14,15]. However, intraspecific variation in BMR within endothermic populations, may potentially also be attributed to variations in the physiology of the individuals caused by non-genetic factors. Such phenotypic flexibility is commonly found in living organisms [16], but it is not known whether this also would pertain to BMR. One factor which potentially could be involved in 'setting' the level of the basal metabolic rate, is the nutritional status during the early development. Both the amount and quality of food provided to avian nestlings have been shown to influence later adult body mass [17,18]. The amount of food may also influence body composition of nestlings [19,20]. Since both body mass and body composition are predictors of BMR, one could hypothesise that the level of BMR also would be influenced by early nutritional status.

In the present study, we test this possibility, by studying whether the BMR of adult Zebra finches will vary according to different nutritional status during their early growth.

2. Material and methods

The Zebra finch (*Taeniopygia guttata*) is a small finch native to the Australasia. The species will easily breed in captivity and is consequently often used in laboratory studies. We randomly assigned 15 pairs of finches to each of two large (10 m^3) walk-in aviaries. Twenty nest-boxes were placed in each aviary. These were accessible from the outside and were checked every day at around noon. All breeding birds were provided with a mixed seed diet ('Life Care'; protein-content: 10.8% of wet mass; water content: 11.7%). In one colony (low quality, LQ) this was the only food provided. In the other colony (high quality, HQ), the finches were in addition provided a commercial protein-supplement ('Eggfood Witte Molen'; protein-content: 11.3% of wet mass; water content: 9.8%) and daily fresh hard-boiled eggs (protein-content: 13.2% of wet mass; water-content: 76.4%). All types of food were provided ad libitum, as was drinking water. Ambient temperatures in the rooms with both breeding aviaries and ‘holding aviaries’ were kept at 24 °C and the relative humidity was kept at 40% RH. There was a light–dark regime of 12:12 h with light on at 07:00.

Breeding was recorded in both colonies from August 2001 to June 2002. All chicks produced in the two colonies were removed at an age of 6 weeks, at which time they were fully independent of their parents. After removal from the breeding colonies, they were kept in sex-specific larger holding aviaries until September 2002, when they themselves were assigned to breeding aviaries. During the ‘holding period’ and the subsequent breeding period, which lasted until June 2003, they all received a diet of normal ‘medium’ quality (NQ), consisting of the mixed seed diet and the protein-supplement. After the breeding period (in June 2003), all birds were again assigned to separate sex-specific holding aviaries and received the NQ food until September 2003, when measurements of BMR were obtained. Hence, at the time of BMR-measurements the birds were 1.5–2 years of age and the only experimental difference were in the food-quality they received during the first 6 weeks of age.

The basal metabolic rate was measured using an open-flow system. Dry air was pumped through metabolic boxes made from 1.5-l metal boxes painted flat black on the inside. Each metabolic chamber received an air flow of approximately 400 ml/min; measured accurately by a calibrated mass flowmeter (Bronkhorts). The effluent air was dried using drierite before the oxygen concentration was measured by an oxygen analyser (Servomex, two-channel analyser, type 4200). The oxygen analyser was calibrated using dry outside air (set to 20.95% oxygen) and pure stock nitrogen. Rates of oxygen consumption (VO_2) were calculated using formula 3A given by Withers [21], assuming an RQ of 0.71, and corrected for wash-out delay in the system by the method described by Niimi [22]. In this way, we obtained the instantaneous oxygen consumption rates. Birds were placed in the metabolic chamber in the evening (at about 19:00) and stayed overnight in the metabolic chamber. They were taken back to their holding aviaries at about 08:00 the next morning. An experimental set-up was constructed so that we could measure up to four birds per night. An automated valve-system switched between the four metabolic chambers, so that two chambers simultaneously were measured at a time for 26 min, interspersed between shorter periods of 4 min, during which fresh air entered the oxygen analyser. Hence, each individual was measured 26 min every hour during the night. All voltage outputs from the oxygen analyser and the mass flowmeter were stored at 30-s intervals on a datalogger (Grant Squirrel, Type 1203) and later transferred to a computer for analysis.

The lowest night-time level of VO_2, which was taken as representative of BMR, was calculated as the lowest 10-min running average of instantaneous oxygen consumption. This was usually experienced during the latter half of the night. The body mass (M_b) was measured (with an accuracy of 0.01 g) immediately before and after the experiment and a linear decrease in body mass was assumed when assessing the body mass value at the time of BMR-measurements. All measurements of BMR were conducted at an ambient temperature of 35 °C, which is within the thermoneutral zone of the Zebra finch (own unpublished results).

Before performing linear analysis on the relationship between M_b and BMR all data were log10-transformed. Linear regressions between M_b and BMR are presented as both ordinary least squares regression (OLS) as well as reduced major axes (RMA). The latter method is used because OLS might underestimate the true allometric exponent (see Pagel and Harvey [23]). The RMA-values were calculated according to Sokal and Rohlf [24]. All statistics were performed using SigmaStat ver. 3.0 (SPSS). Results are shown as mean ± 1 S.D.

3. Results

Food quality during the first 6 weeks of life had a distinct effect on the resultant adult body mass of Zebra finches. Hence, those individuals which were fed only seeds during early growth had an adult body mass significantly smaller that of the individuals which received a protein-rich food during early development. This was the case for both females (13.6 ± 2.1 g for LQ-fed individuals vs. 15.5 ± 1.1 g for HQ-fed; $t_{2,42}$=3.967, P<0.001) and for males (12.3 ± 0.9 g for LQ-fed individuals vs. 14.5 ± 1.5 g for HQ-fed; $t_{2,40}$=4.898, P<0.001). Within both feeding regimes, the adult body mass of the females was significantly higher than that of the males (P<0.001 for both).

In order to test for the influence of experimental group (either low-quality or high-quality food during early life) in addition to body mass and sex, which could be presumed to influence BMR, we performed a multiple linear regression with BMR (expressed as mass dependent oxygen consumption; ml O_2 h^{-1}) as the independent parameter, and group, sex and body mass as dependent parameters. Both sex and body mass were significant determinants of the variation in BMR (both P<0.001). Experimental group, however, did not contribute in explaining the BMR-variation (P=0.738). Hence, whether birds experience low- or high-quality diet during early life, will not affect their BMR later in life, despite large variation in body mass. The combined regression lines (OLS) for adults males is BMR (ml O_2 h^{-1})=$10.12*M_b^{0.504}$ (n=42, r^2=0.452, P<0.001) and for females BMR (ml O_2 h^{-1})=$9.51*M_b^{0.548}$ (n=44, r^2= 0.452, P<0.001). By using the

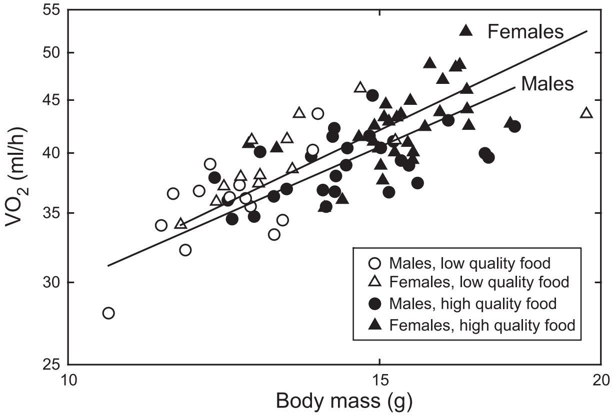

Fig. 1. Basal metabolic rate, expressed as oxygen consumption, in adult Zebra finches fed either low quality food (open symbols) or high-quality protein-rich food (filled symbols) during the first 6 weeks after hatching (circles=males, triangles=females). Regression lines (reduced major axes) are shown for males and females separately. See text for statistics.

reduced major axes method, we arrive at slightly larger exponents, the regression line being for males being BMR (ml O_2 h^{-1})= 5.34*$M_b^{0.749}$ and that for females BMR (ml O_2 h^{-1})=4.63*$M_b^{0.815}$ (Fig. 1).

4. Discussion

It is important to notice that the present study has not involved a food-deprivation experiment, since the birds in both experimental groups had free access to food at all time. Only the quality, through the protein content, were manipulated. Hence, our data are not directly comparable with the many studies showing that reduced food intake, will alter the adult morphology including body mass [18,25,26].

Our finding that food quality during early development significantly influences the adult body mass concur with the results of Boag [17] and Birkhead et al. [27] also on Zebra finches. Boag [17] likewise manipulated the protein-content of the diet given to Zebra finch nestlings and found that both the growth rate as well as the adult body mass was higher when chicks were fed high-protein food than when fed a low-protein diet. The body mass difference was found to be evident for up to one year of age. Hence, the present study supplements that of Boag [17] in that we found the diet-induced body mass difference to be present up to an age of 2 years. Other studies, in which manipulation of food quality have been performed have produced mixed results. Hochachka and Smith [28] supplemented the food of free-living Song Sparrows (*Melospiza melodia*), and in this way manipulated the food-quality of the nestlings. They also found an immediate positive effect on the growth rate in the food-supplemented nestlings. However, when measured at an age of between 56 to 108 days, there was no difference in body mass between the experimental groups. A similar lack of long-term effect on adult body mass was also reported by Ohlsson and Smith [29] after manipulation of the protein-content of the diet fed to chicks of the Ring-necked pheasants (*Phasianus colchicus*) (although in this species the tarsus length was affected). We can offer no explanation as to why food quality during early life has a strong effect on body mass in Zebra finches and apparently not in other species. It is, however, difficult to compare the results directly because they involve quite different food-manipulation techniques. Our results together with that of Boag [17] and Birkhead et al. [27] clearly show that drastic phenotypic variation can be induced by environmental effects, even in a physiological character such as body mass which generally is known to be highly heritable [30].

Since BMR is the sum of the metabolic rates of all organs and components of an organism, any change in body mass will in turn affect the BMR. Consequently, correlative relationships between body composition and BMR have been repeatably reported [19,20,31–34]. The relationship between body mass and BMR is generally described by exponential relationships, and if all organisms were built in proportionally the same way and the organs had similar metabolic intensity, the mass exponent of such relationships would be 1.0. Normally, however, mass exponents will be lower or higher than 1.0. Our finding of intraspecific allometric exponents for the Zebra finches (0.75–0.82 for RMA estimates and 0.50–0.55 for OLS estimates) is strikingly similar to what is normally found for interspecific relationships in birds [5]. In contrast, our exponents are below that normally reported for intraspecific BMR–body mass relationships in birds, where exponents well above 1.0 generally are reported (see Kvist and Lindström [35]). It is difficult to ascertain exactly why this is so, except that in contrast to most other bird species, high body mass in Zebra finches is apparently not paralleled by disproportionally larger organs having a high metabolic intensity, which have been the usual explanation for allometric exponents above 1.0. On the contrary, high body mass in Zebra finches must be paralleled by either disproportional smaller high-metabolic organs or their organs must have lower metabolic intensity. One explanation could be that heavier individuals are carrying larger amounts of fat, which has little metabolic activity compared to most other internal organs. Lindström and Rosén [36] recently showed that the accumulation of fat carried a high metabolic cost in Greenfinches (*Carduelis chloris*). However, their experiments were carried out over a very short time span (days) where such an immediate 'cost' would be eminent. Presumably, there are fewer metabolic costs involved when fat is permanently stored as in heavier vs. lighter individuals.

Irrespective of the reason for the low intraspecific allometric exponent in the Zebra finches, our study has demonstrated that despite the significant effect on body mass incurred by manipulation of the food-quality during the nestling stage, the BMR of the resultant adult birds did not differ beyond that expected based on variation in body mass alone. Hence, the early feeding regimes have apparently not induced any long-term changes in body composition or in organ metabolic intensity. Our results imply that the non-genetic phenotypic variability in body mass, which we have induced during nestling development by different feeding regimes, will not result in disproportional organ masses inducing different metabolic rates.

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