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# Long-term repeatability makes basal metabolic rate a likely heritable trait in the zebra finch *Taeniopygia guttata*

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## Summary

**Basal metabolic rate (BMR) is a physiological trait believed to show adaptational changes. Few studies have tested whether BMR shows stable between-individual variations. Repeatability indicates that the trait might be heritable and therefore a possible target for natural selection. We tested whether BMR was repeatable over a considerable time of the lifespan of a small passerine bird: the zebra finch *Taeniopygia guttata*. BMR was measured six times over a 2.5 year period in captive zebra finches. BMR residuals showed significant repeatabilities over a short (1.5 months) and a long (2.5 years) period for each sex as well as for both sexes pooled. In contrast to earlier studies on metabolism, our calculated repeatability (*R*) did not change significantly from the short to the long period in either males (*R* from 0.501 to 0.465), females (*R* from 0.413 to 0.522) or the pooled data (*R* from 0.571 to 0.567). Our results show that there are consistent between-individual variations in BMR on which natural selection can work, provided that this trait is heritable.**

Key words: basal metabolic rate, energetics, heritability, individual variation, natural selection, repeatability, zebra finch, *Taeniopygia guttata*.

## Introduction

Metabolism reflects the cost of living of an organism, and energy is therefore thought to play an important role in shaping behaviour, ecology and physiology in animals (Berteaux et al., 1996). Basal metabolic rate (BMR) is defined as the rate of energy transformation in an endothermic organism at rest in a postabsorptive state, measured within its thermoneutral zone (IUPS Thermal Commission, 2001). BMR is one of the most widely measured physiological traits in birds (e.g. Burness et al., 1998; Bech et al., 1999; Kvist and Lindström, 2001; Nilsson, 2002; Lindström and Klaassen, 2003), and shows great variation both between and within species. A similar variation is also found in the standard metabolic rate (SMR) of invertebrates (e.g. Terblanche et al., 2004). Differences in BMR between species seem to be closely linked to different habitats and way of life (McNab, 1994; Bryant and Furness, 1995), indicating that BMR has been, and probably still is, a subject for natural selection (Rezende et al., 2002; Furness, 2003).

Repeatability provides important information by setting the upper limit for heritability (Falconer and Mackay, 1996), although this may not always be the case (see Dohm, 2002). Because of this relationship with heritability, repeatability can give an indication of how effective natural selection will be in changing the trait. Studies on repeatability of metabolism in vertebrates have mainly been focused on maximum metabolic rate (Hayes and Chappell, 1990; Chappell et al., 1995, 1996; Hayes and O'Connor, 1999), although daily energy expenditure (Speakman et al., 1994; Potti et al., 1999), field metabolic rate (Berteaux et al., 1996) and resting metabolic rate (RMR; Vézina and Thomas, 2000) have also been studied. Despite the large abundance of data, we are aware of only very few studies reporting repeatability of BMR (Bech et al., 1999; Hõrak et al., 2002; Labocha et al., 2004; Vézina and Williams, 2005). Significant repeatabilities in those studies indicate permanent inter-individual differences in BMR. In addition to inter-individual variations (Rezende et al., 2004a), there also exist intra-individual variations in BMR during an animal's life cycle (Langseth et al., 2000; Lindström and Rosen, 2002; Lindström and Klaassen, 2003). This intra-individual phenotypic variance is mainly affected by the external environment that the animal experiences (Falconer and Mackay, 1996). Variations in BMR between individuals are affected by genetic differences in addition to the external environment. Because of this phenotypic flexibility the length of the measurement period could affect the repeatability of a physiological trait in such a way that repeatability decreases with the length of the measurement period (Chappell et al., 1996; Hõrak et al., 2002; Vèzina and Williams, 2005). A long period will normally involve larger environmental variation compared to a shorter period, and this may result in a greater variation of the trait, which in turn will decrease the repeatability. Several studies have reported flexibility in organ

size and metabolic physiology over short timescales depending on environmental conditions and physiological status (see Piersma and Lindström, 1997). Breeding is a life-cycle event that may lead to changes in organ mass and the metabolic machinery (Chappell et al., 1999; Langseth et al., 2000; Vézina and Williams, 2003).

For selection on a physiological trait to be effective the trait has to be consistent over a period that is long enough to make it possible for the trait to influence the fitness and/or survival of the individual. A very short interval between repeated measurements of a metabolic trait can fail to reveal any potential intra-individual variation in that trait because the 'metabolic machinery' has not had time to change. A changing environment might, over time, induce changes in metabolic traits, but in spite of a change in the absolute performance, the relative performance rankings of individuals can be unaltered and repeatability can still be high (Chappell et al., 1996). Even though the absolute maximal rate of oxygen consumption ($\dot{V}_{O2max}$) increased during 8 weeks of cold acclimation in deer mice *Peromyscus maniculatus*, the relative performance remained consistent and $\dot{V}_{O2max}$ was consequently highly repeatable over the period (Rezende et al., 2004b). A change in both absolute performance and ranking with time would result in low or zero repeatability, implying low heritability, and the effect of selection would be weak (Chappell et al., 1996). Friedman et al. (1992) found that $\dot{V}_{O2max}$ in a strain of mice was highly repeatable between 2 consecutive days, and Terblanche et al. (2004) found significant repeatabilities of SMR in tsetse flies *Glossina pallidipes* of different ages measured during an 84 min period. It may be argued that the time periods over which these repeatability measurements were obtained were not long enough to pick up any potential change in the trait and thus are less informative compared with longer measurement periods. It is therefore important to consider the length of the measurement period carefully according to which trait and species are being examined. This is especially important if the results are to be interpreted in light of heritability and natural selection.

In the present study, rates of BMR were obtained over a 2.5 year period in zebra finches *Taeniopygia guttata* Vieillot in order to obtain short- as well as long-term repeatabilities of BMR. We are not aware of any previous study of repeatability of any metabolic trait over such a long time period. The present study, which involves repeated individual measurements over a considerable part of the zebra finches reproductive lifespan (2.5–4.5 years), should consequently be adequate to reveal any long-term repeatability of BMR within individuals.

## Materials and methods

### *Study species*

The zebra finch *Taeniopygia guttata* Vieillot is a small finch native to the Australasia. We kept zebra finches in large (10 $m^3$) walk-in aviaries. The ambient temperature in the room was kept at 22.5°C, and the relative humidity at 40%. A constant 12 h:12 h light:dark cycle was kept throughout the experimental period, with light on at 07:00 h. A mixed seed diet ('Life Care'; protein content 10.8% of dry mass; water content 9.8%) and drinking water were provided *ad libitum*. All birds used in the present study were raised in our laboratory and could be classified as adult at the start of the experimental period.

All birds had been kept in sex-specific holding aviaries since 6 weeks of age and had consequently not been breeding. The birds did breed in smaller breeding cages in a period from the start of September to the end of December, 2002. When the breeding experiment concluded at the end of December 2002 the birds were moved back into their sex-specific holding aviaries.

### *Metabolic measurements*

For each bird four measurements of BMR were obtained during the period March to May, 2002. The birds were measured in random order, but with a minimum of 5 days between each measurement. In 2004, BMR was again measured twice in each bird, once in April/May and once in October/November. Hence, a total of six BMR measurements were obtained from each bird during the period March 2002 to November 2004.

Basal metabolic rate was measured as $O_2$-consumption rates using an open flow system. Dry air was pumped through four metabolic chambers made from 1.5 l metal boxes. For each metabolic chamber a calibrated Bronkhorst High-Tech mass flowmeter (Ruurlo, The Netherlands) was used to adjust the flow to 400 ml $min^{-1}$. Both influent and effluent air was dried with Drierite® (Krugersdorp, South Africa). A Serwomex Xentra, type 4100, two-channel oxygen analyser (Crowborough, England) measured the oxygen concentration in the effluent air. Dry outside air (set to 20.95% oxygen) was used to calibrate the oxygen analyser and pure stock nitrogen was used for zero calibration. An automatic valve-system switched between the chambers, so that two chambers were measured simultaneously for 26 min, with fresh air being pumped through the system for 4 min between each switching. The birds were taken from their holding aviaries and placed individually in the metabolic chambers at about 19:00 h in the evening, i.e. at the time of the normal start of their resting phase. Measurements of oxygen consumption were obtained throughout the night, and the birds were removed again around 08:00 h, 1 h after the time of light-on in the morning. The voltage outputs from the oxygen analyser and mass flowmeters were stored on a Grant Squirrel, type 1200 datalogger (Cambridge, England) at 30 s intervals. The data was later transferred to a computer for subsequent analyses. The rate of oxygen consumption ($\dot{V}_{O_2}$) was calculated using formula 3A given by Withers (1977). Since the birds were assumed to be postabsorptive during the measurement a respiratory quotient of 0.71 was used. The lowest $\dot{V}_{O_2}$, which was calculated as the lowest 10 min running average value during the night, was used to represent the BMR. This was usually attained during the latter part of the night or in the early morning, supporting our assumption

that the birds were postabsorptive. Body mass at the time of the lowest oxygen consumption was used when calculating the mass-specific BMR. Body mass was obtained just before birds were placed in the metabolic chamber and again when the birds were taken out. A linear body mass reduction was assumed for obtaining the body mass at the time of the lowest $\dot{V}_{O_2}$. The temperature in the room containing the metabolic chambers was 35°C, which is within the thermoneutral zone for the zebra finch (Calder, 1964; B.R., B.M. and C.B., personal observations).

Since BMR is an energetic measure it should actually be expressed in energetic units. Since in the present study we are focusing on the consistency of the BMR values and not the absolute values, we have chosen to present BMR as rates of oxygen consumption, which are the actual measurements obtained.

### *Data analyses*

Variance components derived from a one-way analysis of variance (ANOVA) were used to calculate the repeatability of BMR after the procedure described by Lessells and Boag (1987). Since whole-animal rate of $O_2$-consumption is highly dependent on mass, we removed body mass as a factor by using unstandardized residuals based on reduced major axes (RMA) regressions of $\log_{10}$ mass-dependent BMR on $\log_{10}$ body mass in the ANOVA. The residuals were calculated for each sex from all six measurement periods separately. The standard error of repeatabilities was calculated following Becker (1984). Short-term repeatabilites (over approximately 1.5 months) were calculated using the four measurements of BMR obtained in 2002. Despite the rather long measurement period (1.5 months) used as our shortest time period compared with many other studies on repeatability, we have decided to refer to this as the short period. Each individual bird was used for both the short-term and the long-term repeatability analyses. When calculating long-term repeatabilities, the two last BMR measurements from spring 2002 and the two measurements obtained in 2004 were used. This means that the two last measurements used in the short-term analyses are the same measurements used as the two first in the long-term analyses. A few birds died during the experimental period. Hence, the male group was reduced from 19 to 18 individuals and the female group from 20 to 18 individuals between the short- and long-term analyses.

Since ordinary least-square regressions might underestimate the true allometric exponent scaling BMR to body mass (Pagel and Harvey, 1988), a RMA-regression was used for calculating the allometric exponent and the residuals used in the calculation of repeatabilities. The allometric exponent in the RMA-regression was calculated as the ratio of the standard deviation (S.D.) of $y$ ($\log_{10}$ mass-dependent BMR) to the S.D. of $x$ ($\log_{10}$ body mass). The mixed linear model was performed using S-PLUS (Insight-ful Corp., Seattle, USA). All other analyses were performed using SPSS ver. 12.01 (SPSS inc., Chicago, USA). Values reported are means ± 1 S.E.M. The significance level was set at $P$=0.05.

Table 1. *Body mass, mass-dependent and mass-specific rate of oxygen consumption, and estimated marginal mean rate of oxygen consumption*

| Parameter | Males | Females | Both sexes |
|---|---|---|---|
| Body mass (g) | 14.0±0.30 | 14.4±0.31 | 14.2±0.21 |
| $\dot{V}_{O_2}$ (ml $O_2$ $h^{-1}$) | 37.5±0.52 | 41.2±0.68 | 39.3±0.52 |
| $\dot{V}_{O_2}$ (ml $O_2$ $g^{-1}$ $h^{-1}$) | 2.70±0.04 | 2.87±0.03 | 2.79±0.03 |
| Estimated marginal mean $\dot{V}_{O_2}$ (ml $O_2$ $h^{-1}$) | 37.8±0.42 | 40.8±0.42 | 39.3±0.30 |

Marginal mean $\dot{V}_{O_2}$ was estimated for body mass=14.19 g.
Values are the means of all six measurements.

## Results

### *Metabolic rate*

Mass-specific and mass-dependent BMR values as well as body mass for both the pooled data and the sexes separately are shown for comparison in Table 1. Both sex (GLM: $F_{1,33}$=25.4, $P$<0.001) and body mass (GLM: $F_{1,33}$=40.2, $P$<0.001) were significant determinants of the variation in BMR in a model with mass-dependent BMR as a dependent variable, sex as a fixed factor and body mass as a covariate. Mass-dependent BMR and body mass in this model were calculated as the average

Table 2. *Result of a mixed linear model investigating rate of oxygen consumption in relation to body mass, measurement (2002* vs *2004) and sex*

| Model | Parameter | $F_{1,34}$ | $P$ |
|---|---|---|---|
| | Body mass | 40.4 | <0.001 |
| | Measurement | 19.7 | <0.001 |
| | Sex | 17.9 | <0.001 |

| | Measurements | |
|---|---|---|
| Descriptives | 2002 | 2004 |
| Males | | |
| Body mass (g) | 13.6±1.0 | 14.4±1.9 |
| $\dot{V}_{O_2}$ (ml $O_2$ $h^{-1}$) | 37.5±2.8 | 37.1±2.9 |
| $\dot{V}_{O_2}$ (ml $O_2$ $g^{-1}$ $h^{-1}$) | 2.76±0.23 | 2.60±0.20 |
| Females | | |
| Body mass (g) | 14.3±1.4 | 14.3±1.3 |
| $\dot{V}_{O_2}$ (ml $O_2$ $h^{-1}$) | 41.4±3.5 | 39.8±3.3 |
| $\dot{V}_{O_2}$ (ml $O_2$ $g^{-1}$ $h^{-1}$) | 2.91±0.15 | 2.80±0.22 |

Individual identification was entered as a random factor to control for repeated measurements.

The 2002 values are the mean values of measurements 3 and 4 in April/May 2002, while the 2004 values are the mean values of both measurements in April/November 2004.

For comparison, we report the mean values of body mass and $\dot{V}_{O_2}$ (ml $O_2$ $h^{-1}$ as well as ml $O_2$ $g^{-1}$ $h^{-1}$) for each sex in 2002 and 2004.

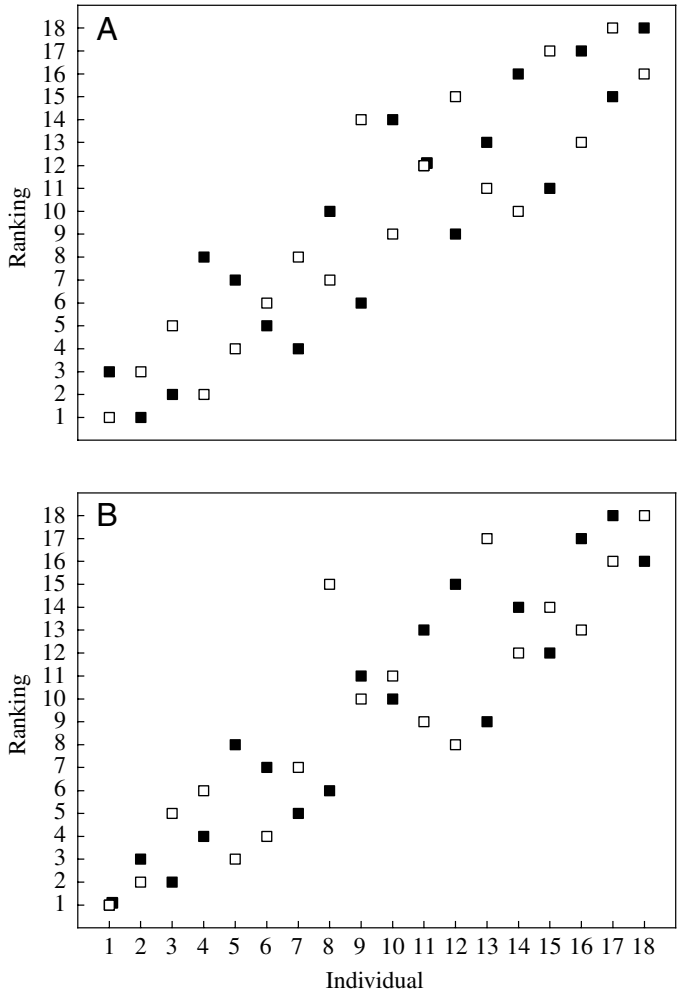


Fig. 1. Ranking of the BMR-residuals (based on RMA-regression of $\log_{10}$ mass-dependent BMR on $\log_{10}$ body mass) from 2002 (filled squares; average of last two measurements) and 2004 (open squares; average of both measurements) periods for males (A) and females (B) separately. For each period all individuals are ranked, with 1 indicating the individual with the highest BMR-residual.

of all six measurements. The partial coefficient of determination for sex and body mass was 0.435 and 0.549, respectively. The estimated marginal means of BMR (controlled for the effect of body mass) are shown in Table 1. The power function of BMR scaling using RMA-regression for males was: BMR (ml $O_2$ $h^{-1}$)=$6.55M_b^{0.662\pm0.082}$ and for females: BMR (ml $O_2$ $h^{-1}$)=$5.08M_b^{0.784\pm0.115}$. The slopes were not different between the sexes (d.f.=34, $t$=0.86, $P$>0.2).

A mixed linear model with repeated individual measurements showed that BMR was lower in 2004 compared to 2002 in both sexes (Table 2). In spite of this change in BMR in the period from 2002 to 2004, which contained a short breeding period, the ranking between the individuals remained rather unchanged (Fig. 1).

### *Repeatability*

The repeatability of BMR was highly significant ($P$<0.001) for both sexes for the short (male $R$=0.501; $F_{18,57}$=5.02 and female $R$=0.413; $F_{19,60}$=3.81) as well as the long period (male $R$=0.465; $F_{17,54}$=4.48 and female $R$=0.522; $F_{17,54}$=5.36; Table 3). Hence, a significant portion of the variation in the BMR can be attributed to permanent between-individual variations (Fig. 2). For both sexes pooled the repeatability was 0.571 ($F_{38,117}$=6.32; $P$<0.001) for the short period and 0.567 ($F_{35,108}$=6.24; $P$<0.001) for the long period. The 95% confidence intervals (i.e. 2 S.E.M.) substantially overlapped the means, and, consequently, the short- and long-term repeatability values were not significant different. This applied to the pooled sample as well as the sex-specific samples (Table 3).

## Discussion

### *Metabolic rate*

The mass-specific BMR found for the zebra finches in the present study (2.78 ml $O_2$ $g^{-1}$ $h^{-1}$) correspond well with an earlier study conducted on captive zebra finches (2.79 ml $O_2$ $g^{-1}$ $h^{-1}$; Lemon, 1993). The intraspecific scaling exponents (0.66 and 0.78) found for zebra finches in the present study are lower than the intraspecific scaling normally reported for birds, which exceeds 1.0 (see Kvist and Lindström, 2001). There could be several reasons for this,

Table 3. *Repeatability-values of* $\dot{V}_{O_2}$*-residuals calculated from variance components derived from a one-way ANOVA*

| | | | Repeatability | | Statistics | |
|---|---|---|---|---|---|---|
| Sex | Period (days) | $N$ | $R$ | S.E.M. | $F$ | $P$ |
| Males | 46±14 | 19 | 0.501 | 0.119 | 5.018 | <0.001 |
| | 917±11 | 18 | 0.465 | 0.126 | 4.482 | <0.001 |
| Females | 49±15 | 20 | 0.413 | 0.122 | 3.811 | <0.001 |
| | 914±10 | 18 | 0.522 | 0.121 | 5.363 | <0.001 |
| Both sexes | 48±15 | 39 | 0.571 | 0.077 | 6.324 | <0.001 |
| | 915±11 | 36 | 0.567 | 0.080 | 6.239 | <0.001 |

The table shows values of repeatability ($R$) and standard error (S.E.M.) from the short and long measurement period for females and males separately and for both sexes pooled. $N$=number of individuals.

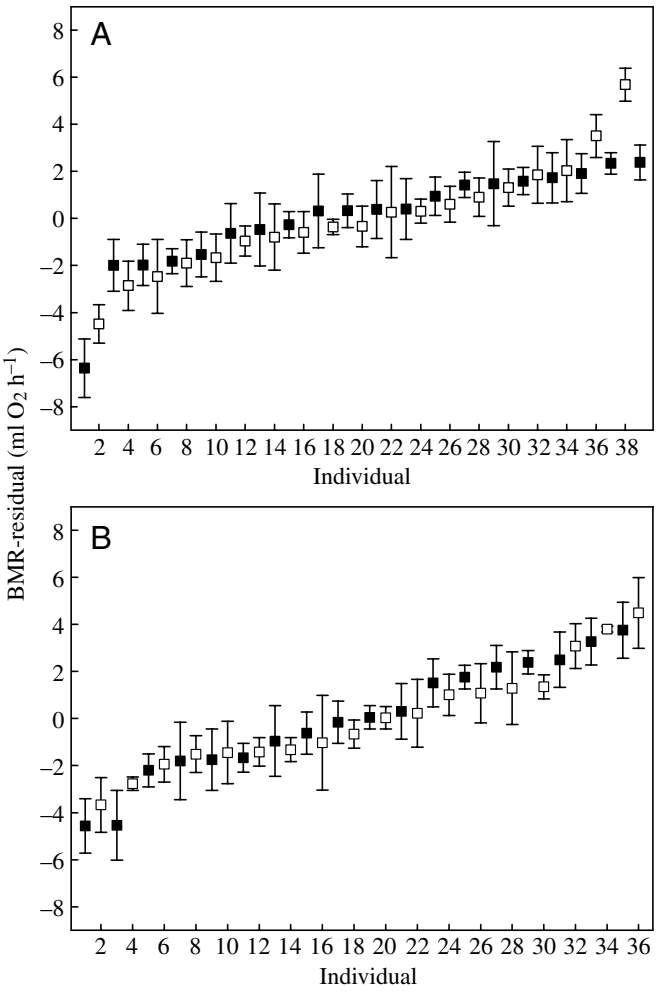


Fig. 2. Residual values (± 1 S.E.M.) of BMR (from a RMA-regression) in male (open squares) and female (filled squares) zebra finches, during the short (A; 20 females and 19 males) and the long (B; 18 females and 18 males) measurement periods. For each period all individuals are ranked after increasing value of residual BMR.

including disproportional changes in internal organs (see Bech et al., 2004).

Metabolism in wild living birds appears to exhibit considerable flexibility (Langseth et al., 2000). In laboratory studies we are able to control environmental factors such as temperature, photoperiod, humidity, food availability and breeding activity, which all influence the metabolic rate in the wild. Different activity patterns can influence the RMR of zebra finches (Nudds and Bryant, 2001). Our birds were kept in uniform large cages during the experimental period, and any intraspecific differences in BMR are therefore unlikely to be explained by differences in activity patterns.

### *Repeatability*

Body mass is shown to be a highly repeatable trait in birds and mammals (Hayes and Chappell, 1990; Hõrak et al., 2002). Since there is a strong linkage between body mass and BMR, the repeatability of mass-dependent BMR values and, to some extent, also mass-specific BMR, could be influenced by repeatability of body mass. In the present study, however, this was controlled for by using residual values of BMR.

In the present study we found a highly significant repeatability of BMR for both sexes of zebra finches over a 1.5 month as well as a 2.5 year period. To our knowledge no other study has examined the repeatability of BMR over such a long time period, so it is difficult to find results for direct comparison. A field study of black-legged kittiwakes *Rissa tridactyla* showed a significant repeatability of BMR over 1 month ($R$=0.642) and 1 year ($R$=0.347; Bech et al., 1999). BMR in captive greenfinches *Carduelis chloris* showed significant repeatability over both short periods of 4 and 8 days ($R$=0.89 and 0.84, respectively) and a time period of 4 months ($R$=0.65; Hõrak et al., 2002). In both of these studies, the repeatability decreased from the short to the long measurement interval, but was still high and significant during the longest time period. Hence, the present data on the zebra finches differ in that the repeatability was of the same magnitude even when measured during the long (2.5 year) period. In a recent study, Vézina and Williams (2005) reported a decline in the repeatability of RMR over time for non-breeding captive male zebra finches. Their short measurement period was 8 days (with $R$=0.626), and their long measurement periods were 127–249 days ($R$=0.445) and 135–257 days ($R$=0.287). The two longest time periods were thus of approximately the same length, but gave quite different repeatability values. Their short period was much shorter than our short period of 1.5 months, and they used two measurements when calculating the repeatabilities while we used four. Except for those differences between their and our study we can offer no explanation as to why the results differ.

Depending on the flexibility of a particular trait, the repeatability would generally be expected to decrease with an increase in the time period over which it is measured. In the present study there were only small and non-significant differences in the repeatability values of BMR between the short and long measurement period, both in the pooled sample as well as the sex-specific samples. Hence, the repeatability of BMR for the zebra finches was unaffected by the length of the measurement period. There might be several reasons why BMR for the zebra finches in our study shows high stability over such a long time period compared with other metabolic traits in other species ($\dot{V}_{O2max}$ in Belding's ground squirrels *Spermophilus beldingi*, Chappell et al., 1995; field metabolic rate in meadow voles *Microtus pennsylvanicus*, Berteaux et al., 1996). It should be kept in mind that the zebra finches in this present study, although going through a breeding period, were being kept under laboratory conditions when the BMR measurements were conducted. Such an environment does not generate phenotypic adjustments to the same extent as in the wild. However, this cannot be the only explanation since the BMR of the greenfinches in the study by Hõrak et al. (2002) showed a marked decrease in repeatability with time despite being held in laboratory conditions, as did those measured by

Vèzina and Williams (2005) in laboratory-held zebra finches. It is possible that BMR has higher potential stability, compared with metabolic traits like $\dot{V}_{O2max}$ and field metabolic rate, because BMR mainly represents the anatomical and physiological characteristics of an animal (Daan et al., 1990; Burness et al., 1998), and hence is not so influenced by behavioural variation.

The BMR measurements used for the repeatability estimation from the long time period were not evenly distributed. The two first measurements used were obtained in spring 2002 and only separated by a few days, while the last two were obtained in 2004 and separated by approximately 7 months. During the 2 year period, when no measurements of BMR were obtained, all the finches underwent a breeding period, which is known to induce large changes in BMR (Bech et al., 1999; Langseth et al., 2000; Nilsson, 2002; Vézina and Williams, 2005). As mentioned above, an increase in the population mean value does not necessary lead to a change in the variance between the individuals. There is no way of knowing for certain if the repeatability estimates would have been different if the BMR-measurements were evenly distributed through the long period. Breeding is a stressful challenge and may evoke individual adjustments in metabolism that can lead to lower repeatability in BMR. In the present study BMR still showed a high repeatability even when measurements, conducted after these potential adjustments made during breeding, were incorporated in the analyses. In a study of zebra finches, Vézina and Williams (2005) found a significant repeatability of RMR between two breeding periods. Our results are noteworthy because we report that repeatability persists when comparing periods before and after a breeding event.

### *Natural selection*

The significant repeatability of BMR over 2.5 years, which constitutes a substantial part of the reproductive lifetime in free-living zebra finches (maximum lifespan 2.5–4.5 years; Zann and Runciman, 1994), clearly shows that there is significant between individual variation in this particular trait, upon which natural selection can work, provided that the trait is heritable. However, it should be mentioned that it also could be the capacity to change BMR rapidly in response to changing ecological conditions that is the selective trait. An important question to ask is: over what timescale does the trait have to be repeatable to consider the possibility that natural selection is working upon it? Huey and Dunham (1987) concluded that in the lizard *Sceloporus merriami*, which has a maximum lifespan of 6 years and a cohort generation time of 1.5 years, repeatability in running speed over a 1 year period is sufficient to render it convenient for studies of natural selection. It seems likely that the required length of the measurement period of a trait to test if it is sufficiently repeatable to be a possible target for natural selection varies with the lifespan and generation time. In other words: to detect selection in a trait, it has to be repeatable over the timescale during which selection occurs; it is obvious that this timescale is longer for long-lived species with long generation times than for short-lived animals with short generation times.

In addition to having a significant repeatability to be affected by natural selection, the trait also has to be heritable and have a consequence for fitness (Falconer and Mackay, 1996). The repeatability provides little information about the actual value of heritability, and a trait with high repeatability might have a heritability of zero (Merilä and Sheldon, 2001). The few studies on heritability of BMR indicate that the heritability of BMR might be very low (Dohm et al., 2001; Nespolo et al., 2003). However, a recent study by Sadowska et al. (2005) reports a relative high narrow-sense heritability of BMR in the bank vole *Clethrionomys glareolus*. One of the important advantages of a laboratory study like ours is that genealogy is easy to record, and this simplifies heritability estimates compared to a field study.

In summary, we have found a significant repeatability of BMR in zebra finches over a considerable time period. Hence, one of the prerequisites for natural selection to act upon this trait is fulfilled. It remains to be seen if these differences in metabolism will have consequences on fitness. Whether BMR is heritable and if natural selection is acting on the inter-individual variation in this particular trait remains to be fully answered.

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## References

**Bech, C., Langseth, I. and Gabrielsen, G. W.** (1999). Repeatability of basal metabolism in breeding kittiwakes *Rissa tridactyla*. *Proc. R. Soc. Lond. B* **266**, 2161-2167.

**Bech, C., Rønning, B. and Moe, B.** (2004). Individual variation in the basal metabolism of Zebra finches *Taeniopygia guttata*: no effect of food quality during early development. *Int. Congr. Ser.* **1275**, 306-312.

**Becker, W. A.** (1984). *Manual of Quantitative Genetics*, 4th edn. Washington: Pullman Academic Enterprises.

**Berteaux, D., Thomas, D. W., Bergeron, J.-M. and Lapierre, H.** (1996). Repeatability of daily field metabolic rate in female Meadow Voles (*Microtus pennsylvanicus*). *Funct. Ecol.* **10**, 751-759.

**Bryant, K. L. and Furness, R. W.** (1995). Basal metabolic rate of North Atlantic seabirds. *Ibis* **127**, 219-226.

**Burness, G. P., Ydenberg, R. C. and Hochachka, P. W.** (1998). Interindividual variability in body composition and resting oxygen consumption rate in breeding tree swallows, *Tachycineta bicolour*. *Physiol. Zool.* **71**, 247-256.

**Calder, W. A.** (1964). Gaseous metabolism and water relations of the zebra finch, *Taeniopygia castanotis*. *Physiol. Zool.* **37**, 400-413.

**Chappell, M. A., Bachman, G. C. and Odell, J. P.** (1995). Repeatability of maximal performance in Belding's Ground Squirrels, *Spermophilius beldingi*. *Funct. Ecol.* **9**, 498-504.

**Chappell, M. A., Zuk, M. and Johnsen, T. S.** (1996). Repeatability of aerobic performance in Red Junglefowl: effects of ontogeny and nematode infection. *Funct. Ecol.* **10**, 578-585.

**Chappell, M. A., Bech, C. and Buttemer, W. A.** (1999). The relationship of central and peripheral organ masses to aerobic performance variation in house sparrows. *J. Exp. Biol.* **202**, 2269-2279.

**Daan, S., Masman, D. and Groenvold, A.** (1990). Avian basal metabolic rates: their association with body composition and energy expenditure in nature. *Am. J. Physiol.* **259**, R333-R340.

**Dohm, M. R.** (2002). Repeatability estimates do not always set an upper limit to heritability. *Funct. Ecol.* **16**, 273-280.

**Dohm, M. R., Hayes, J. P. and Garland, T., Jr** (2001). The quantitative

genetics of maximal and basal rates of oxygen consumption in mice. *Genetics* **159**, 267-277.

**Falconer, D. S. and Mackay, T. F. C.** (1996). *Introduction to Quantitative Genetics*, 4th edn. Harlow: Longman Group.

**Friedman, W. A., Garland, T., Jr and Dohm, R.** (1992). Individual variation in locomotor behaviour and maximal oxygen consumption in mice. *Physiol. Behav.* **55**, 97-104.

**Furness, R. W.** (2003). It's in the genes. *Nature* **425**, 779-780.

**Hayes, J. P. and Chappell, M. A.** (1990). Individual consistency of maximal oxygen consumption in deer mice. *Funct. Ecol.* **4**, 495-503.

**Hayes, J. P. and O'Connor, C. S.** (1999). Natural selection on thermogenic capacity of high-altitude deer mice. *Evolution* **53**, 1280-1287.

**Hõrak, P., Saks, L., Ots, I. and Kollist, H.** (2002). Repeatability of condition indices in captive greenfinches (*Carduelis chloris*). *Can. J. Zool.* **80**, 636-643.

**Huey, R. B. and Dunham, A. E.** (1987). Repeatability of locomotor performance in natural populations of the lizard *Sceloporus merriami*. *Evolution* **41**, 1116-1120.

**IUPS Thermal Commission** (2001). Glossary of terms for physiology. *Jpn. J. Physiol.* **51**, 245-280.

**Kvist, A. and Lindström, Å.** (2001). Basal metabolic rate in migratory waders: intra-individual, intraspecific, interspecific and seasonal variation. *Funct. Ecol.* **15**, 465-473.

**Labocha, M. K., Sadowska, E. T., Baliga, K., Semer, A. K. and Koteja, P.** (2004). Individual variation and repeatability of basal metabolism in the bank vole, *Clethrionomys glareolus. Proc. R. Soc. Lond. B* **271**, 367-372.

**Langseth, I., Moe, B., Fyhn, M., Gabrielsen, G. W. and Bech, C.** (2000). Flexibility of basal metabolic rate in Artic breeding Kittiwakes (*Rissa tridactyla*). In *Life in the Cold* (ed. G. Heldmaier and M. Klingenspor), pp. 471-477. Berlin: Springer-Verlag.

**Lemon, W. C.** (1993). The energetics of lifetime reproductive success in zebra finch *Taeniopygia guttata*. *Physiol. Zool.* **66**, 946-963.

**Lessells, C. M. and Boag, P. T.** (1987). Unrepeatable repeatabilities: a common mistake. *Auk* **104**, 116-121.

**Lindström, Å. and Klaassen, M.** (2003). High basal metabolic rates of shorebirds while in the arctic: a circumpolar view. *Condor* **105**, 420-427.

**Lindström, Å. and Rosen, M.** (2002). The cost of avian winter stores: intra-individual variation in basal metabolic rate of a wintering passerine, the greenfinch *Carduelis chloris*. *Avian Sci.* **2**, 139-143.

**McNab, B. K.** (1994). Energy conservation and the evolution of flightlessness in birds. *Am. Nat.* **144**, 628-642.

**Merilä, J. and Sheldon, B. C.** (2001). Avian quantitative genetics. In *Current Ornithology*, Vol. 16 (ed. V. Nolan Jr and C. F. Thompson), pp. 179-255. New York: Kluwer Academic/Plenum Publishers.

**Nespolo, R. F., Bacigalupe, L. D. and Bozinovic, F.** (2003). Heritability of energetics in a wild mammal, the Leaf-eared mouse (*Phyllotis Darwini*). *Evolution* **57**, 1679-1688.

**Nilsson, J. Å.** (2002). Metabolic consequences of hard work. *Proc. R. Soc. Lond. B* **269**, 1735-1739.

**Nudds, R. L. and Bryant, D. M.** (2001). Exercise training lowers the resting metabolic rate of Zebra finches, *Taeniopygia guttata*. *Funct. Ecol.* **15**, 458-464.

**Pagel, M. D. and Harvey, P. H.** (1988). The taxon-level problem in the evolution of mammalian brain size: facts and artefacts. *Am. Nat.* **132**, 344-359.

**Piersma, T. and Lindström, Å.** (1997). Rapid reversible changes in organ size as a component of adaptive behaviour. *Trends Ecol. Evol.* **12**, 134-138.

**Potti, J., Moreno, J. and Merino, S.** (1999). Repeatability of parental effort in male and female Pied Flycatchers as measured with double labelled water. *Can. J. Zool.* **77**, 174-179.

**Rezende, E. L., Swanson, D. L., Novoa, F. F. and Bozinovic, F.** (2002). Passerines *versus* nonpasserines: so far, no statistical differences in scaling of avian energetics. *J. Exp. Biol.* **205**, 101-107.

**Rezende, E. L., Bozinovic, F. and Garland, T., Jr** (2004a). Climatic adaptation and the evolution of basal and maximum rates of metabolism in rodents. *Evolution* **58**, 1361-1374.

**Rezende, E. L., Chappell, M. A. and Hammond, K. A.** (2004b). Cold-acclimation in *Peromyscus*: temporal effects and individual variation in maximal metabolism and ventilatory traits. *J. Exp. Biol.* **207**, 295-305.

**Sadowska, E. T., Labocha, M. K., Baliga, K., Stanisz, A., Wróblewska, A. K., Jagusiak, W. and Koteja, P.** (2005). Genetic correlations between basal and maximum metabolic rates in a wild rodent: consequences for evolution of endothermy. *Evolution* **59**, 672-681.

**Speakman, J. R., Racey, P. A., Haim, A., Webb, P. I., Ellison, G. T. H. and Skinner, J. D.** (1994). Inter- and intraindividual variation in daily energy expenditure of the pouched mouse (*Saccostomus campestris*). *Funct. Ecol.* **8**, 336-342.

**Terblanche, J. S., Klok, C. J. and Chown, S. L.** (2004). Metabolic rate variation in *Glossina pallidipes* (Diptera: *Glossinidae*): gender, aging and repeatability. *J. Insect Physiol.* **50**, 419-428.

**Vézina, F. and Thomas, D. W.** (2000). Social status does not affect resting metabolic rate in wintering Dark-Eyed Juncos (*Junco hyemalis*). *Physiol. Biochem. Zool.* **73**, 231-236.

**Vézina, F. and Williams, T. D.** (2003). Plasticity in body composition in breeding birds: what drives the metabolic costs of egg production? *Physiol. Biochem. Zool.* **76**, 716-730.

**Vézina, F. and Williams, T. D.** (2005). The metabolic cost of egg production is repeatable. *J. Exp. Biol.* **208**, 2533-2538.

**Withers, P. C.** (1977). Measurements of $\dot{V}_{O_2}$, $\dot{V}_{CO_2}$ and evaporative water loss with a flowthrough mask. *J. Appl. Physiol.* **42**, 120-123.

**Zann, R. and Runciman, D.** (1994). Survivorship, dispersal and sex ratios of Zebra finches *Taeniopygia guttata* in southeast Australia. *Ibis* **136**, 136-146.