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Individual variation and repeatability of basal metabolism in the bank vole, *Clethrionomys glareolus*

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Basal metabolic rate (BMR) is a fundamental energetic trait and has been measured in hundreds of birds and mammals. Nevertheless, little is known about the consistency of the population-average BMR or its repeatability at the level of individual variation. Here, we report that average mass-independent BMR did not differ between two generations of bank voles or between two trials separated by one month. Individual differences in BMR were highly repeatable across the one month interval: the coefficient of intraclass correlation was 0.70 for absolute log-transformed values and 0.56 for mass-independent values. Thus, BMR can be a meaningful measure of an individual physiological characteristic and can be used to test hypotheses concerning relationships between BMR and other traits. On the other hand, mass-independent BMR did not differ significantly across families, and the coefficient of intraclass correlation for full sibs did not differ from zero, which suggests that heritability of BMR in voles is not high.

Keywords: endothermy; evolutionary physiology; heritability; mammals; oxygen consumption

1. INTRODUCTION

Basal metabolic rate (BMR) is a central aspect of the energetics of endotherms (McNab 2002). Estimates of BMR have been obtained in several hundred species of birds and mammals, and have been the basis of countless comparative studies. Initially, the issue of the slope of the relationship between BMR and body mass dominated the field, and the discussion continues (McNab 1988; Kozłowski & Weiner 1997; Garland & Ives 2000; Hochachka *et al.* 2003; White & Seymour 2003). Later, the focus shifted to interspecific variation and correlations with life history, environment, food habits and phylogenetic history (McNab 1980; Harvey *et al.* 1991; Koteja & Weiner 1993; Degen *et al.* 1998; Lovegrove 2003), and to the relationship between BMR and maximum or daily metabolic rate (Bennett & Ruben 1979; Koteja 1987, 2000; Hinds & Rice-Warner 1992; Sparti 1992; Hayes & Garland 1995; Ricklefs *et al.* 1996; Degen *et al.* 1998).

As the paradigm of evolutionary physiology has developed (Bennett 1987; Garland & Carter 1994; Feder *et al.* 2000), the research on ecological and evolutionary aspects of BMR has become more focused on variation across individuals (Hayes 1989; Hayes *et al.* 1992*a*; Chappell & Bachman 1995; Konarzewski & Diamond 1995; Koteja 1996*a*; Speakman & McQueenie 1996; Hayes & Jenkins 1997; Meerlo *et al.* 1997; Chappell *et al.* 1999; Dohm *et al.* 2001; Nespolo *et al.* 2003*a*,*b*). Natural selection does work primarily at the level of variation across individuals. However, if selection on a trait such as BMR is to be effective, the value of the trait must be consistent across at least some part of an individual's life, i.e. the trait must be repeatable. Repeatability alone is not a sufficient condition, however, as the trait will not evolve in response to selection if it is not heritable. Nevertheless, repeatability provides some information, albeit only approximate, about the upper limit for heritability (Lynch & Walsh 1998; Dohm 2002). If a trait is not repeatable, it is unlikely that it will change in response to selection; it may also be pointless to ask whether it is correlated with other traits.

Considering the great interest in BMR and the volume of the gathered data, it is surprising that rigorous estimates of the repeatability of BMR have been reported for only two species of bird (Bech *et al.* 1999; Horak *et al.* 2002); there are no estimates for non-domestic mammals. The only estimate for wild mammals is given in a study of the repeatability of resting metabolic rate in Merriam's kangaroo rats (*Dipodomys merriami*; Hayes *et al.* 1997). This scarcity of results for BMR contrasts with a more extensive dataset on the repeatabilities of maximum metabolic rates and daily energy expenditures (Hayes & Chappell 1990; Speakman *et al.* 1994; Chappell *et al.* 1995, 1996; Berteaux *et al.* 1996; Hayes *et al.* 1997; Koteja *et al.* 2000; Dohm *et al.* 2001).

In this study we compared BMR values obtained in two generations of bank voles (*Clethrionomys glareolus*), estimated the repeatability of BMR across a one month interval and estimated the correlations of BMR within full-sib families of voles.

2. MATERIAL AND METHODS

(a) *Animals*

We used adult male bank voles (*C. glareolus*) from generations 1 and 2 of a colony established from 250 voles captured in Niepołomice Forest (southern Poland) in August and September 2000 (generation 0). Their offspring (generation 1) were weaned at day 21 and maintained individually in standard polypropylene mouse cages (26 cm × 20 cm × 16 cm). Voles from generation 1 were paired at the age of 4–6 months to produce generation 2 (some individuals in generation 2 were cousins or paternal half-sibs). The animals were maintained at constant temperature

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(20 ± 1 °C) and photoperiod (16 L : 8 D). Water and food (a standard mouse diet, GLM, Gan-rat, Kraków; 24% protein, 3% fat, 4% fibre) were provided *ad libitum*.

The voles were used in several experiments, as a part of a larger project. Briefly, we measured the ability of the voles to grow or maintain body mass when given a low-quality diet or a restricted amount of water, basal and maximum metabolic rates (at the age of 73–188 days and again 30 days later), food consumption, nesting behaviour and male dominance behaviour. Because of time constraints, BMR was measured only once in the first generation.

(b) *Measurements of basal metabolic rate*

Oxygen consumption (ml h^{-1}) was measured in a six-channel open-flow respirometric system based on the S-3A/II analyser (AMETEK, Pittsburgh, PA, USA). Animals were weighed at 08.30 and placed in plastic chambers without water or food at 30 °C (within thermal neutral zone; Petrusewicz 1983). Lights were left on. Air was passed through the chambers at *ca.* 360 ml min^{-1} (standard temperature, pressure, dry conditions; measured to ± 3 ml min^{-1} on each channel with individually calibrated LO 63/33 rotameters; Rota, Germany). Each vole was confined to the bottom of the chamber (with wire tops placed 5 cm above the bottom), so that it could not exhale near the air outlet (located 12 cm above the bottom).

Oxygen consumption was recorded between 14.00 and 18.00, i.e. 5.5–9.5 h after food deprivation. Dried samples of air were taken sequentially from the six measurement chambers and the reference every 10 min. In each cycle, each measurement chamber was active for 80 s, and oxygen deficit in the last 20 s was used for calculation of oxygen consumption. The measurement chambers (800 ml) were relatively large compared to the flow rate, so that the oxygen concentration in the effluent air depended on the metabolic rate during the previous few minutes. Thus, the short 20 s O_2 reading was equivalent to readings averaged over a few minutes recorded on a system with a fast turnover. The rate of steady-state oxygen consumption was calculated according to eqn (1b) in Koteja (1996*b*), assuming a respiratory exchange ratio of 0.75. If the actual respiratory exchange ratio was between 0.7 and 0.8 (i.e. between the values for fat and protein metabolism, as expected in post-absorptive animals), the error resulting from this assumption was below ± 1.5% (Koteja 1996*b*).

(c) *Data analyses*

For each animal we obtained 24 readings: one every 10 min over a 4 h trial. To determine the best estimate of BMR, we calculated repeatability from a number of readings of oxygen consumption as follows:

(i) the lowest, the second lowest, etc. reading (denoted B1–B24);
(ii) the lowest, the second lowest, etc. running average of two consecutive readings (denoted BB1–BB23);
(iii) averages of two low readings; and
(iv) averages of three low readings.

Repeatability (coefficient of intraclass correlation, ρ_i) was calculated for 64 individuals from generation 2, in which BMR was measured twice, based on variance components obtained in ANOVA (Lynch & Walsh 1998; Dohm 2002). Within-family correlation (ρ_f) was calculated for full-sib first-litter families with more than one individual (generation 1: 87 individuals from 33 families; generation 2, trial 1: 39 individuals from 19 families; trial 2: 35 individuals from 17 families). Because traditional ANOVAs are inefficient in random-effect models with unequal numbers of observations in the groups (Lynch & Walsh 1998), we obtained the variance components with a restricted maximum likelihood method (implemented in the SAS mixed-models procedure). We also calculated the coefficients for mass-independent values, i.e. residuals from a regression of BMR on body mass (after correcting variance components for decreased degrees of freedom). Finally, we tested models with both body mass and age as covariates.

ANOVA and ANCOVA were used to compare body mass and BMR in generation 1 with the equivalent values from the first trial in generation 2. Repeated-measures ANOVA/ANCOVA were used for comparisons between the two trials in generation 2. Because the relationship between BMR and body mass is allometric and because both the variables are usually right-skewed, log-transformed variables were used in all the analyses.

In preliminary tests we included chamber number as a categorical predictor, to check for possible systematic biases resulting from using a multi-channel system. The effect was not significant ($p > 0.35$ in all series of measurements), and the variable was not included in the final models.

The analyses were performed with Systat v. 10 and SAS v. 8.2 for Windows.

3. RESULTS

The voles in generation 1 were, on average, younger and smaller than in generation 2 at the time of the first trial (table 1). In generation 2, body mass increased between the first trial and the second trial performed 30 days later. The repeatability of body mass was very high ($\rho_i = 0.87$). In both generations body mass varied significantly across families and was highly correlated within families (generation 1: $p = 0.001$, $\rho_f = 0.35$; generation 2, first trial: $p = 0.001$, $\rho_f = 0.63$; second trial: $p = 0.012$, $\rho_f = 0.50$).

Single readings of oxygen consumption during the 4 h trials ranged from 37 to 140 ml h^{-1}, with an average of *ca.* 60–66 ml h^{-1} (figure 1*a*). In the first generation there was no significant trend across the 4 h ($p = 0.74$), but in the second generation the mean metabolic rate decreased slightly over time, both in the first trial ($p = 0.03$) and in the second trial ($p = 0.001$). However, for particular individuals, minimum readings could be observed at any time during the trial including the first records.

Low readings of oxygen consumption were highly repeatable ($p < 0.001$), but the two lowest readings (B1 and B2) had a lower repeatability than B3 to B6 readings (figure 1*b*). Repeatability was also lower for still higher readings. Repeatabilities of the running means of two readings were lower than those of single readings, except for intervals with high metabolic rates (figure 1*b*). A substantial part of the interindividual variation could be attributed to differences in body mass (R^2 from 0.31 to 0.49; figure 2), but repeatabilities of mass-independent values were also highly significant (figures 1*b* and 3*b*). In further analysis we used the average of B3, B4 and B5 as an estimator of BMR (table 1), although the repeatability of such an average (absolute values: $\rho_i = 0.70$; mass independent: $\rho_i = 0.56$; $p < 0.001$; figure 3) was not markedly higher than that of single readings.

Table 1. Age, body mass and BMR in bank voles from two generations.
(Significances of differences between generations were tested with ANOVA or ANCOVA, and between trials with repeated-measures ANOVA or ANCOVA. CV, coefficient of variation.)

	generation 1 ($n = 118$)			generation 2 ($n = 64$)						significance of differences (p)	
				trial 1			trial 2				
variable	mean	s.d.	CV	mean	s.d.	CV	mean	s.d.	CV	generation	trial
age (days)	97	14	14.0	124	37	29.6	154	37	23.8	< 0.001	
body mass (g)	20.9	2.4	11.4	21.9	2.7	12.5	22.9	2.7	11.9	0.010	< 0.001
BMR (ml O_2 h^{-1})	52.5	5.4	10.4	54.0	6.5	12.1	55.9	7.3	13.0	0.105	0.006
mass-independent BMR (ANCOVA)										0.961	0.708

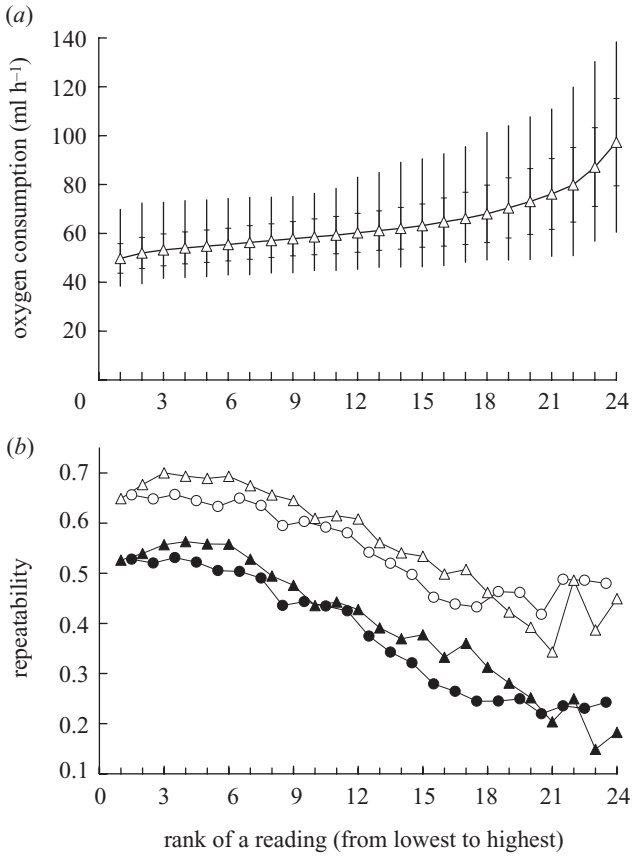

Figure 1. (*a*) Average ± s.d. and range of readings of oxygen consumption ranked within each individual from lowest to highest, and (*b*) repeatability (coefficient of intraclass correlation) of the absolute and mass-independent O_2 readings, in the bank voles from generation 2 (see § 2c for further explanation). Open triangles, single readings—absolute; open circles, running means—absolute; filled triangles, single readings—mass independent; filled circles, running means—mass independent.

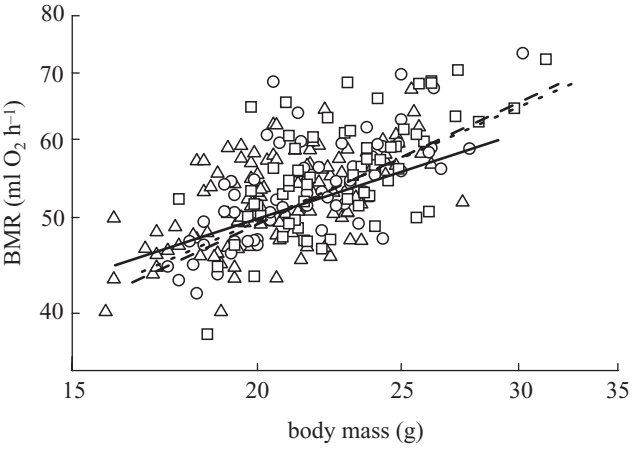

Figure 2. Relation between BMR and body mass in bank voles from generations 1 and 2 of a laboratory colony (in generation 2, trial 2 was performed 30 days after trial 1; note the logarithmic scale). Open triangles, generation 1; open circles, generation 2, trial 1; open squares, generation 2, trial 2. Regression lines: solid, generation 1; dotted, generation 2, trial 1; dashed, generation 2, trial 2.

Absolute values of BMR did not differ significantly between generation 1 and generation 2, but BMR was higher in the second trial of generation 2 than in the first trial (table 1; note, however, that the difference between trials in generation 2 was tested with a repeated-measures test, which may have a higher power than the independent-sample test used to compare the generations). Coefficients of phenotypic variance (CV = 100 × *s.d./mean*) were similar in all three datasets (10.5–13.1%). BMR clearly increased with body mass ($p < 0.001$; figure 2). The least-square model I regression slopes of the allometric relations between BMR and body mass did not differ between the two trials in generation 2 (± s.e.: $b = 0.68 \pm 0.09$ and 0.70 ± 0.11; $p = 0.88$; figure 2). The slope tended to be lower in generation 1 ($b = 0.51 \pm 0.07$) but the difference was not significant ($p = 0.15$). The slopes of reduced major axes (model II regression) were close to 1.0 in all three datasets (generation 1: 0.91; generation 2, first trial: 0.97; second trial: 1.12).

With the effect of body mass included in the ANCOVA models, mass-independent BMR did not differ between the two generations ($p = 0.96$) or the two trials in generation 2 ($p = 0.71$) (table 1, figure 2).

Variation across families in absolute values of BMR was not significant in generation 1 ($p = 0.16$, $\rho_f = 0.13$), but it was significant in generation 2 (first trial: $p < 0.001$, $\rho_f = 0.68$; second trial: $p = 0.01$; $\rho_f = 0.51$). However, mass-independent BMR did not differ across families in any of the three datasets (generation 1: $p = 0.27$,

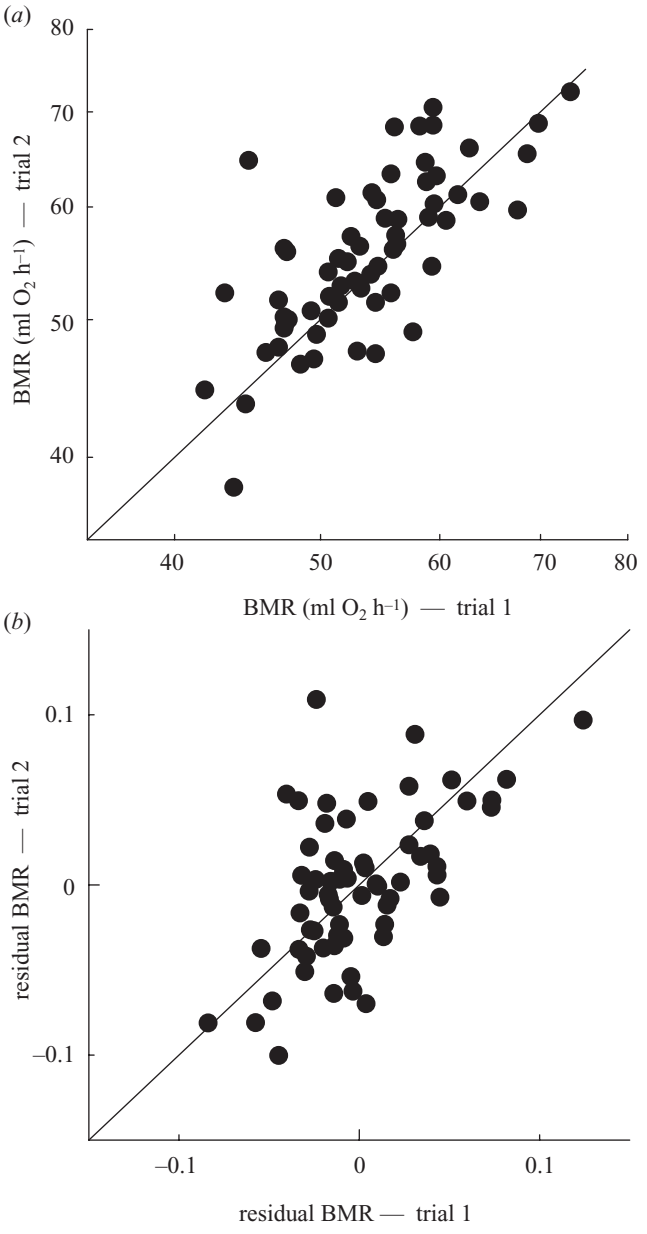

Figure 3. Correlation between the values of BMR measured in two trials (30 days apart) in 64 bank voles. (*a*) Absolute log-transformed values, Pearson's $r = 0.72$, $p < 0.001$; (*b*) mass-independent values, i.e. residuals from regression, partial $r = 0.57$, $p < 0.001$; identity lines are shown.

$\rho_f = 0.11$; generation 2, first trial: $p = 0.31$, $\rho_f = 0.09$; second trial: $p = 0.10$, $\rho_f = 0.28$).

The effect of age on BMR, tested in models including both age and body mass, was not significant (generation 1: a negative trend, $p = 0.21$; generation 2: a positive trend, first trial: $p = 0.065$, second trial: $p = 0.098$). Conclusions concerning differences between generations and the estimates of repeatability were nearly the same as those based on the models without age.

4. DISCUSSION

By definition, the BMR should represent a minimum sustainable level of aerobic metabolism of a resting, normothermic, post-absorptive and non-growing animal at thermal neutral conditions (McNab 2002). However, estimates of BMR are considerably affected by the length of the entire measurement and by the length of the time interval used for calculating BMR (Hayes *et al.* 1992*b*). A minimum from a short interval may underestimate BMR, owing to inevitable random errors in the measurements, but long intervals, or averages of several short intervals, may overestimate BMR by including intervals in which the animal is active or just alert. Therefore, we calculated 'BMR' in a few ways and checked the repeatability of the estimates over a one month interval.

Repeatabilities of the two minimum recorded values (B1 and B2) were lower than those of the B3–B6 readings (figure 1*b*). Thus, the lowest readings suffered from an additional source of random error (e.g. fluctuations of baseline owing to changes in air pressure). On the other hand, repeatabilities of B7 and of higher readings were also lower, perhaps because intervals with active animals were included in the analysis. Thus, it seems justifiable to use the average of the third to fifth readings as an estimate of BMR. It could be argued that it would be even better to record oxygen consumption for longer intervals in each cycle, rather than to rely on frequent but very short intervals. The trade-off is that with longer intervals a lower number of records would be taken for each individual. If an individual was not resting for a long time, none of the records would measure BMR. Interestingly, the repeatabilities of running means of two consecutive readings were markedly lower than those of single readings (figure 1), even though statistical theory predicts that they should be higher. This result indicates that the voles were rarely resting for more than 10 min. If we used an average of several consecutive minutes, which is usual practice (Hayes *et al.* 1992*b*), the estimates would be upwardly biased and would bear a larger random error. Obviously, this may not apply to other animals, such as laboratory mice (Hayes *et al.* 1992*a*; Dohm *et al.* 2001), that remain resting for longer intervals.

Average BMR, after adjusting for differences in body mass, was consistent across two generations and across a one month interval within a generation. More importantly, at the level of individual variation, BMR was highly repeatable across the one month interval. The coefficient of intraclass correlation, ρ_i, was 0.70 for the absolute log-transformed BMR and 0.56 for mass-independent values. Thus, not only was a population average consistent over time, but also individual differences were largely preserved over at least one month—a substantial interval for the voles, which rarely survive for more than 1 year (Petrusewicz 1983).

The values of BMR, as estimated in this study, provide a meaningful measure of a physiological characteristic of the organism, and can be used to test hypotheses concerning the relationships between minimum rates of energy turnover and other physiological, behavioural or ecological traits. This conclusion may seem trivial to those who have routinely used BMR values in comparative studies, but empirical evidence supporting such a conclusion has been scarce (Bech *et al.* 1999; Horak *et al.* 2002).

To our knowledge, the only estimate of the repeatability of BMR (or actually of a resting metabolic rate (RMR) close to BMR) in a non-domestic mammal has been reported for captive Merriam's kangaroo rats (Hayes *et al.* 1997). Repeatability, measured across a 21 day interval,

was 0.69 for absolute RMR and 0.68 for mass-independent values. Similar values were reported for mass-specific BMR (i.e. per gram body mass) in captive greenfinches (0.89 across 4 days and 0.65 across 130 days; Horak *et al*. 2002; note, however, that the repeatability of mass-specific values reflects to some extent a repeatability of body mass). In both of the studies, the animals were trapped in the field, but they were maintained in the laboratory between the two measurements of BMR. In kittiwakes repeatability was measured in free-living individuals, which were captured for the measurement of BMR, released and recaptured for a repeated trial a month or a year later (Bech *et al.* 1999). Repeatability of mass-independent BMR was lower, between 0.35 and 0.52 depending on the time interval and season. However, as the studies differed in the animal used, the measurement technique, the method of evaluating BMR and the interval between trials, it may be premature to infer that laboratory studies overestimate the repeatability found in natural situations.

An important advantage of laboratory studies is that genealogy is easy to record, and—after accumulating sufficient data—heritability of the traits can be estimated. The data reported here are not yet sufficient to obtain a reliable estimate of heritability, but they suggest it is not very high. A doubled value of the coefficient of intraclass correlation for siblings usually provides an upwardly biased estimator of heritability (Lynch & Walsh 1998), and the coefficient reported here did not differ significantly from zero. This result is consistent with low estimates of the heritability of BMR reported for laboratory house mouse (*Mus domesticus*; Dohm *et al.* 2001) and in the leaf-eared mouse (*Phyllotis darwini*; Nespolo *et al*. 2003*b*). However, both the results reported by Nespolo *et al*. (2003*b*) and our findings are based on samples that are too small to come to a firm conclusion.

A finding of low heritability of a physiological trait could result from low repeatability of its estimates (e.g. caused by high random error of the measurement). However, as repeatability of BMR estimates in the voles is reasonably high, a plausible alternative explanation could be that the trait has been subject to selection leading to reduced additive genetic variation. Thus, two objectives should be given priority in future studies on variation in BMR:

(i) estimating heritability of the trait in more wild species of birds and mammals; and
(ii) testing whether BMR is related to major fitness components—survival chance and reproductive success—in free-living individuals.

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