Individual variation in metabolic reaction norms over ambient temperature causes low correlation between basal and standard metabolic rate

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ABSTRACT
Basal metabolic rate (BMR) is often assumed to be indicative of the energy turnover at ambient temperatures ($T_a$) below the thermoneutral zone (SMR), but this assumption has largely remained untested. Using a new statistical approach, we quantified the consistency in nocturnal metabolic rate across a temperature range in zebra finches ($N=3213$ measurements on 407 individuals) living permanently in eight outdoor aviaries. Foraging conditions were either benign or harsh, and body mass and mass-adjusted BMR (BMR$_m$) and SMR (SMR$_m$) were lower in individuals living in a harsh foraging environment. The correlation between SMR$_m$ at different $T_a$ was high ($r=0.91$), independent of foraging environment, showing that individuals are consistently ranked according to their SMR$_m$. However, the correlations between BMR$_m$ and SMR$_m$ were always lower (average: $r=0.29$; range: $0<r<0.50$), in particular in the benign foraging environment. Variation in metabolic response to lower $T_a$ at least in part reflected differential body temperature ($T_b$) regulation: early morning $T_b$ was lower at low $T_a$ and more so in individuals with a weaker metabolic response to lower $T_a$. Our findings have implications for the use of BMR in the estimation of time-energy budgets and comparative analyses: we suggest that the use of metabolic rates at ecologically relevant $T_a$ such as the easily tractable SMR, will be more informative than the use of BMR as a proxy for energy turnover.

KEY WORDS: BMR, SMR, Repeatability, Foraging, Daily energy expenditure, Body temperature

INTRODUCTION
Energy is an essential resource for reproduction and survival (Boutin, 1990; Martin, 1987; Prevedello et al., 2013; Ruffino et al., 2014). The energy an individual spends daily on all activities is called the daily energy expenditure (DEE) and includes all processes such as self-maintenance, thermoregulation and behaviour. Measuring DEE is highly relevant but often practically demanding. A component of energy turnover that is more tractable and often quantified is basal metabolic rate (BMR), i.e. the minimum energy expenditure of a post-absorptive adult animal measured during the rest phase at thermoneutral temperature (IUPS Thermal Commission, 2001; McNab, 1997). Thermoneutral temperature is defined as the ambient temperature ($T_a$) at which body temperature ($T_b$) regulation is achieved without regulatory changes in metabolic heat production or evaporative water loss (IUPS Thermal Commission, 2001). BMR has been studied in association with many traits such as growth, reproduction, personality, oxidative stress, senescence and survival (reviewed in Biro and Stamps, 2010; Burton et al., 2011; Glazier, 2015). It is often implicitly assumed that individual variation in BMR is representative of individual variation in DEE. However, the correlation between DEE and BMR is generally weak in birds and mammals ($0<r<0.23$; Careau et al., 2012; Fyhnp and others, 2001; Meerlo et al., 1997; Speakman et al., 2003; Tieleman et al., 2008; Wiersma and Tinbergen, 2003). Thus, the assumption that individual variation in BMR reflects variation in DEE, and hence can be interpreted as an index of total energy turnover, is not well supported.

Multiple hypotheses can be formulated to explain why BMR and DEE are only weakly correlated. The hypothesis we investigated here is that the low correlation between BMR and DEE is at least in part due to the fact that BMR is measured at thermoneutrality, while DEE is measured at $T_a$ as experienced in natural environments, which are often below thermoneutrality. As BMR represents a considerable proportion of an individual’s energy expenditure (~30%; e.g. Careau et al., 2012; Daan et al., 1990), we would expect a positive association between BMR and standard metabolic rate (SMR), i.e. metabolic rate below thermoneutrality but otherwise in identical conditions. However, SMR is more influenced than BMR by $T_b$ and insulation. These could associate positively with BMR, for example because individuals with poor insulation need an enhanced thermoregulatory machinery to maintain $T_b$, causing an indirect positive association between BMR and SMR. Conversely, $T_b$ and insulation might differ between individuals to such an extent that BMR and SMR will correlate poorly. To the best of our knowledge, the association between BMR and SMR remains unknown. To investigate individual variation in this relationship, we repeatedly measured BMR and SMR in a small passerine, the zebra finch, in the same individuals and under the same conditions except that $T_a$ was below the thermoneutral zone during SMR measurements. If individual differences in thermoregulatory response to a lower $T_a$ are small relative to the average response, individual variation in BMR will be strongly correlated with SMR. In this case, BMR and SMR can be considered different expressions of the ‘same’ trait. Alternatively, individuals may differ in their thermoregulatory response to the extent that the correlation between BMR and SMR is weak or absent. In this case, BMR and SMR are uncoupled and this would at least partly explain the low correlations observed between BMR and DEE.

When multiple traits of an individual are measured multiple times, phenotypic correlations between traits can arise via two ways...
Potential correlations between variables are affected by the variables’ repeatability. For example, when repeatability of a trait is zero, between-individual correlations with that trait will also be zero. Furthermore, repeatability is relevant in evolutionary terms because consistent differences between individuals are a minimum requirement for natural selection to act upon (Falconer and Mackay, 1996). Hence, here we first quantified the repeatability of body mass, BMR and SMR of zebra finches at $T_a$ ranging from 5 to 39°C (Fig. 2). We then investigated the within- and between-individual correlations between metabolic rates at different $T_a$. When exposed to a lower $T_a$, homoeothermic organisms balance three interrelated physiological factors: metabolic rate, insulation and $T_b$ (Geiser, 2004; McNab, 1980). For example, large differences between $T_a$ and $T_b$ increase heat loss, and one way to minimize this loss is by down-regulating $T_b$ (Angilletta et al., 2010; Geiser, 2004; Körtner et al., 2000). Thus, $T_b$ adjustments can be an important determinant of metabolic responses to lower $T_a$. To investigate the role of temperature regulation, we measured $T_b$ of a subset of individuals at multiple $T_a$ and correlated individual metabolic reaction norms over $T_a$ with changes in $T_b$.

Repeatability and trait correlations are inherently specific to a population and its environment. The birds used in this study lived in captivity, which may alter metabolism and possibly its repeatability relative to that of free-living animals (e.g. Auer et al., 2016). One essential difference between captive and free-living populations is that food can usually be accessed at negligible costs in captivity, which is not usually true for free-living animals (Beaulieu, 2016; Briga and Verhulst, 2015a), and this can have physiological and demographic consequences (e.g. Briga et al., 2017; Robb et al., 2008). To broaden the range of environments and increase the ecological relevance of our study, we housed the birds in outdoor aviaries, and permanently exposed half of our population to high foraging costs through a manipulation of flight cost per food reward (Koetsier and Verhulst, 2011). Increased foraging costs generally result in lower BMR (reviewed in Wiersma and Verhulst, 2005), and in zebra finches this effect was stronger at lower temperatures, i.e. on SMR (Wiersma and Verhulst, 2005). However, whether foraging costs affect the association between BMR and SMR is unknown. Thus, we experimentally manipulated foraging costs and compared BMR and SMR repeatability and correlations in a ‘benign’ environment versus a ‘harsh’ semi-natural environment.

**MATERIALS AND METHODS**

**Birds and housing**

The birds we studied are part of a long-term experiment investigating the relationships between foraging costs and survival (Briga and Verhulst, 2015b; Briga et al., 2017). Birds were housed in eight unisex outdoor aviaries (L×W×H: 320×150×225 cm) located in Groningen, The Netherlands (53°13′0″N, 6°33′0″E). Foraging costs were manipulated as described by Koetsier and Verhulst (2011). In brief, in each aviary a food box was attached to the ceiling, with holes in the sides from which food (tropical seed mixture) could be obtained. In the benign foraging environment (four aviaries) the food box had perches beneath the holes, while in the harsh foraging environment (also four aviaries) these were...
removed, forcing birds to fly and hover for seeds. Water, grit and cuttlebone were provided ad libitum and birds received 1.25 g of fortified canary food ('eggfood', Bologna, Hedel, The Netherlands) per individual per week given in three portions. Each aviary contained an approximately equal number of birds (15–25) and we kept bird density within a limited range by regularly adding birds to replace those that died. All birds had been reared in either small or large broods with in most cases two or six young. The manipulated brood sizes were within the natural range for zebra finches in the wild (Zann, 1996) and in captivity (Griffith et al., 2017). The brood size manipulation did not affect mass-adjusted BMR/SMR (Briga, 2016) and will therefore not be further considered here. All methods and experimental protocols were carried out under the approval of the Animal Experimentation Ethical Committee of the University of Groningen, licence 5150A. All methods were carried out in accordance with these approved guidelines.

Body mass and body size
Between December 2007, when the experiment started, and December 2015, we collected 15,443 mass measurements on 597 individuals. Birds were weighed almost monthly, up to 95 times (Fig. S1A) between the ages of 0.4 and 9.4 years. We used this whole dataset to estimate treatment effects. However, to consistently estimate repeatability, within- and between-individual variances (see below) based on the same individuals, we selected those individuals with at least two measurements (N=15,418 measurements on 572 individuals). Size measurements, tarsus and head+bill, were taken after reaching maturity, on average at age 133±33 days (mean±s.d.), and averaged after transformation to a standard normal distribution to obtain one estimate of structural body size.

Metabolic rate
Overnight energy expenditure was measured using an open-flow respiriometer situated in a dark climate-controlled room kept at the desired $T_a$. Up to 16 individuals per night were taken from the aviaries on average at 18:10 h (±1:17 h s.d.), weighed (±0.1 g) and randomly assigned to one of 16, 1.5 l metabolic chambers in a dark climate room. Measurements lasted until the morning, such that birds were in a post-absorptive state, thus meeting the requirements for BMR (IUPES Thermal Commission, 2001; McNab, 1997) and this was consistent for SMR as well. Rooms were kept and continuously monitored at the above-mentioned temperatures with multiple PT100 temperature sensors, one located in the room recording continuously and one in each metabolic chamber recording at each metabolic rate measurement. Technical specification of the equipment can be found in Bouwhus et al. (2011). In brief, the air flow through the metabolic chambers was controlled at 25 l h⁻¹ by mass-flow controllers (5850S, Brooks, Rijswijk, The Netherlands) calibrated with a bubble flow meter. Air was dried using a molecular sieve (3 Å; Merck, Darmstadt, Germany) and analysed by a paramagnetic oxygen analyser (Servomex Xentra 4100, Crowborough, UK). During measurements, each metabolic chamber or reference outdoor air was sampled every 8 min for 60 s to stabilise measurement levels. In each sampling, we measured $O_2$ concentration and oxygen consumption was calculated using equation 6 of Hill (1972). An energy equivalent of 19.7 kJ l⁻¹ oxygen consumed was used to calculate energy expenditure in watts. Metabolic rate was taken to be the minimum value of a 30 min running average, which included 3–6 measurements per individual. The first measurement hour was excluded to minimize potential effects of handling stress and the incomplete mixing of air in the metabolic chamber. Birds were weighed before and after the respirometer measurement and body mass for the metabolic rate analyses was taken to be the average of the two values.

Between December 2007 and April 2013, we collected 3213 metabolic rate measurements from 407 birds. Metabolic rate measurements were obtained at $T_a$ ranging from 5 to 39°C (Fig. 2), but most measurements were centred on three $T_a$ of 36°C (range 32–39°C; Fig. S2) for BMR and 26°C (±3°C) and 12°C (±3°C) for SMR (Table 1). We refer to the metabolic rates at these three $T_a$ categories as BMR, SMR26 and SMR12, respectively. Measurements were concentrated in spring and autumn. Birds were measured up to 25 times (Fig. S1B) between the ages of 0.4 and 7.2 years. To estimate treatment and seasonal effects, we used this whole dataset, avoiding any possible bias by selecting data subsets. For the repeatability analyses, we used data subsets as described in Table 1. In brief, to estimate repeatability, within- and between-individual variances based on the same individuals and correlations, we selected those individuals with at least two measurements (Table 1).

$T_b$
During autumn–winter 2011, we measured $T_b$ at the end of respirometry measurements (N=550; mean time 09:46 h, ±0:38 h s.d.) of 189 individuals using an Omega® Thermocouple Thermometer Type T smoothed with Johnson & Johnson® lubrication gel. Handling time during measurements was ≤50 s and the temperature reading was obtained within 5 s of the probe entering the cloaca, at which time $T_b$ was stable. $T_b$ increased as birds were subsequently measured in the climate-controlled room and hence we included measurement order as a covariate in all analyses. In analyses with $T_b$ as predictor, we used order-adjusted values.

Statistical analyses
The repeatability is the proportion of phenotypic variance attributed to between-individual variance (Nakagawa and Schielzeth, 2010).

Table 1. Description of the metabolic rate dataset at ambient temperature ($T_a$) ranges for which most data were collected

<table>
<thead>
<tr>
<th></th>
<th>SMR12</th>
<th>SMR26</th>
<th>BMR</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Whole population</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Temperature range (°C)</td>
<td>9–15</td>
<td>23–29</td>
<td>32–39</td>
</tr>
<tr>
<td>Date of first measurement</td>
<td>16 Apr 2008</td>
<td>19 Apr 2008</td>
<td>16 Dec 2007</td>
</tr>
<tr>
<td>Date of last measurement</td>
<td>12 Apr 2013</td>
<td>14 Apr 2013</td>
<td>15 Apr 2013</td>
</tr>
<tr>
<td>No. of birds</td>
<td>314</td>
<td>303</td>
<td>386</td>
</tr>
<tr>
<td>No. of birds with &gt;1 measurement</td>
<td>214</td>
<td>210</td>
<td>275</td>
</tr>
<tr>
<td>No. of measurements</td>
<td>976</td>
<td>821</td>
<td>1233</td>
</tr>
<tr>
<td>Mean metabolic rate (W)</td>
<td>0.48</td>
<td>0.31</td>
<td>0.22</td>
</tr>
<tr>
<td>s.d. metabolic rate (W)</td>
<td>0.063</td>
<td>0.045</td>
<td>0.027</td>
</tr>
<tr>
<td>CV metabolic rate</td>
<td>0.13</td>
<td>0.15</td>
<td>0.12</td>
</tr>
</tbody>
</table>

| **Temperature range (°C)** | 9–15 | 23–29 | 32–39 |
| **Date of first measurement** | 18 Apr 2008 | 30 Jun 2008 | 16 Dec 2007 |
| **Date of last measurement** | 9 Apr 2013 | 14 Apr 2013 | 15 Apr 2013 |
| **No. of birds with >1 measurement** | 110 | 107 | 133 |
| **No. of measurements** | 465 | 377 | 554 |

| **Harsh environment** |       |       |      |
| Date of first measurement | 24 Apr 2008 | 19 Apr 2008 | 18 Dec 2007 |
| Date of last measurement | 12 Apr 2013 | 13 Apr 2013 | 6 Apr 2013 |
| No. of birds with >1 measurement | 104 | 103 | 143 |
| No. of measurements | 411 | 351 | 569 |

Note that the whole dataset is larger and includes measurements at other $T_a$ than the intervals considered here (Fig. 2). SMR, standard metabolic rate (measured at 12 or 26°C); BMR, basal metabolic rate; CV, coefficient of variation.
These variance components can be estimated using a linear mixed model in which the between-individual variance is captured by including individual identity as a random effect and in which the phenotypic variance is the sum of the between-individual variance and the residual variance. In such models, residual variance decreases by including fixed effects, thereby increasing repeatability. Body mass repeatability estimates did not include fixed effects except when adjusting for size. Metabolic rate repeatability estimates included as linear fixed effects $T_e$, and, for mass-adjusted estimates, mass. Variance components were estimated using a Bayesian approach (Dingemanse and Dochtermann, 2013) with the R package MCMCglmm (Hadfield, 2010) using uninformative priors with flat improper priors with 1.5×10^7 iterations, 10,000 burn-in and a thinning interval of 100. This yielded Markov chain Monte Carlo (MCMC) sample sizes of at least 1000 with low levels of autocorrelation (mean $r_{\text{aut}}=0.002$ with all $r<0.1$). Bayesian results were consistent with those of the frequentist approach (with restricted maximum likelihood and maximum likelihood; results not shown), using the functions (i) lmer of the package lme4 (Bates et al., 2015), (ii) lme of the package nlme (https://CRAN.R-project.org/package=nlme) and (iii) rpt of the package rptR (Nakagawa and Schielzeth, 2010). We here report Bayesian estimates with 95% credible intervals (CI). To test for significance of repeatability, we used likelihood ratio tests with the function exactLRT in the package RLRsim (Scheipl et al., 2008). To test for differences between repeatability, we used t-tests with the number of individual identities as (conservative) sample size. Covariation between traits was analysed using a Bayesian approach with a trivariate analysis (SMR12, SMR26 and BMR) with the function MCMCglmm (Hadfield, 2010) using uninformative inverse Wishart priors. In these models, metabolic values were residuals of a linear model with mass and $T_e$ as fixed effects and with individual identity as a random effect. Repeatability and trait correlations for different foraging treatments were estimated separately by selecting data subsets. The effects of the season and foraging cost manipulation were analysed using general linear mixed models, lmer of the package lme4 (Bates et al., 2015) including individual as random effect. Residuals of all models were checked with function resid and all had a normal distribution without outliers. Effect sizes are reported as Cohen’s d (Cohen, 1988), which was estimated as the ratio of the coefficient over the standard deviation (equations 1 and 2 in Nakagawa and Cuthill, 2007). As a rule of thumb, effect sizes of 0.5 are considered as moderate (Cohen, 1988) and this was also the median effect size estimated from 43 ecological or evolutionary studies (Møller and Jennions, 2002).

**RESULTS**

**Body mass repeatability**

Repeatability of body mass was high at 0.72 (0.69<95% CI<0.74; Fig. 3B; N=15,418 measurements on 572 individuals). Body mass increased with size ($r=0.56$), and a modest part of the between-individual variation was due to variation in body size: body mass repeatability adjusted for size was 0.12 lower at 0.60 (0.57<95% CI<0.63; Fig. 3B). All estimates were significantly larger than zero (LR=11,324; $P<10^{-15}$). Hence, the zebra finches in our population can be characterized by their body mass and size-adjusted body mass.

Birds exposed to high foraging costs weighed on average 15.0 g, which was 4% (0.64 g, effect size $d=0.41$) lighter than birds with low foraging costs (Fig. 3A; $F_{1,580}=43$, $P<10^{-18}$), and this difference persisted when controlling for size ($F_{1,471}=44$, $P<10^{-19}$). Thus, high foraging costs negatively affected body mass.

Environmental conditions can affect between- and within-individual variance of traits, potentially making repeatability values conditional on the environment. The mass of birds living with high foraging costs was characterized by smaller between- and within-individual variance relative to birds living with low foraging costs (Table S1; $t_{469}=2.56$, $P=0.011$). However, between- and within-individual variance components changed to the same extent, and hence repeatability estimates of body mass and size-adjusted body mass were similar in the two environments ($t=0.70$ and 0.60, respectively; Fig. 3B). Thus, environmental quality did not affect the repeatability of body mass, but individuals in a harsh environment experienced smaller body mass variation between and within individuals.

**Metabolic rate repeatability**

Metabolic rate decreased from 5 to 32°C (Fig. 2), consistent with the classic literature (Scholander et al., 1950). Note that with decreasing metabolic rate, s.d. also decreased (Table 1). This decrease in s.d. was proportional to the decrease in mean value as the coefficients of variation remained similar across all $T_e$ (Table 1). Between 32 and 39°C, metabolic rate was steady (Fig. 2). We identified this $T_e$ range as the zebra finches' thermoneutral zone (Fig. S2), confirming earlier results (Calder, 1964) with a 10-fold larger dataset. Thus, the associations between metabolic rate and $T_e$ were consistent with those described in the classic literature.

Repeatability of whole-organism BMR was 0.54 (0.47<95% CI<0.58; LR=379, $P<10^{-15}$; Fig. 4B; Table S2), within the range of previously published results (Nespolo and Franco, 2007; Versteegh et al., 2008; White et al., 2013). Whole-organism metabolic rate is to a large extent determined by body mass ($r=0.61$). When body mass was added to the statistical model, repeatability of mass-adjusted BMR (BMR$_{ma}$) was halved to 0.27 (0.22<95% CI<0.35; LR=94, $P<10^{-15}$; Fig. 4B; Table S2). Similarly, for SMR, the repeatability of whole-organism values was 0.39 (0.33<95% CI<0.43; LR=451, $P<10^{-15}$), which was larger than that for mass-adjusted values (SMR$_{ma}$), which was 0.28 (0.24<95% CI<0.35; LR=248, $P<10^{-15}$;
The repeatability of BMRm and SMRm was very similar at 0.27 and 0.28, respectively (Fig. 4B; Table S2). For SMRm within narrower Ta ranges (SMRm12 and SMRm26), the repeatability was slightly higher at 0.30 and 0.40, respectively (Fig. 4B; both LR>102, P<10−15). Thus, the zebra finches in our population can be characterized by their BMRm as well as by their SMRm. Because the high repeatability of body mass often inflates metabolic rate repeatability (Fig. 4B,D,E), we further discuss results for mass-adjusted values only. Whole-organism results were mostly identical (results not shown).

In accordance with earlier studies in non-migratory birds (McKechnie, 2008), we found BMRm and SMRm to vary seasonally. BMRm and SMRm were, respectively, 0.011 and 0.025 W g−1 higher in spring than in autumn (Fig. 4C; BMRm: F1,1001=108, P<10−15; SMRm: F1,1880=153, P<10−15), or an effect size d=0.5 for both traits. Seasonal mass-adjusted metabolic rate change within individuals may exceed that between individuals (e.g. Bouwhuis et al., 2011). This would result in higher metabolic rate repeatability within season (in different years) compared with the mass-adjusted metabolic rate repeatability estimated with seasons pooled. For BMRm, spring and autumn repeatability were within the same range as year-round repeatability (0.26 and 0.18 versus 0.27, respectively; Fig. 4D; t443<1.46, P>0.14). For SMRm, autumn repeatability was within the same range as year-round repeatability (0.24 versus 0.28; Fig. 4D), but spring repeatability was higher (0.40; Fig. 4D; t530=2.6, P<0.0095). Thus, birds showed seasonal adjustments in metabolic rate and these adjustments were consistent between individuals except for SMRm in spring.

Increases in foraging effort often lead to energy-saving decreases in BMRm (reviewed in Wiersma and Verhulst, 2005). Indeed, BMRm and SMRm were lower in birds experiencing higher foraging costs (Fig. 4E; BMRm: F1,338=28, P<10−6; SMRm: F1,271=82, P<10−15), with the effect being more pronounced on SMRm (0.030 W g−1 or an effect size d=0.60) than on BMRm (0.009 W g−1 or an effect size d=0.42; Fig. 4E; F1,3002=112, P<10−15). The negative effect of foraging costs on SMRm also became more pronounced at lower Ta (F1,1692=4.7, P=0.03). Thus, birds from harsh environments lowered their minimal energy expenditure, and this became more pronounced with colder Ta.

Repeatability of BMRm and SMRm was, respectively, 23% and 48% higher in the low foraging cost environment than in the high foraging cost environment (BMRm: 0.26 versus 0.20; SMRm: 0.31 versus 0.16; Fig. 4F; Table S2), but these differences were at best marginally significant (t309<1.83, P>0.07). For BMRm, the lower repeatability arose as a result of lower between-individual variance in the high foraging cost environment, while the within-individual variance was environment independent (Table S2). For SMRm, the high foraging cost birds were characterized by lower between- and within-individual variance, but none of these patterns were significant (Table S2; t309<1.60, P>0.11). Thus, birds in a benign environment had a higher repeatability of metabolic rate, but the effect of environment was not significant.
Metabolic rate correlations and reaction norms at multiple $T_a$

The phenotypic correlation between $\text{SMR}_{m12}$ and $\text{SMR}_{m26}$ was moderate at 0.43 (Table 2; Fig. S3C; $t_{577}=11.45$, $P<10^{-15}$). Surprisingly, the phenotypic correlations between $\text{BMR}_m$ and either $\text{SMR}_{m12}$ or $\text{SMR}_{m26}$ were substantially lower (0.14<$r<$0.22; Table 2; Fig. S3C; $t_{577}=3.46$, $P<0.0006$). These patterns were consistent in both foraging environments (Table 2). Thus, $\text{SMR}_m$ values at different $T_a$ correlate better with each other than with $\text{BMR}_m$.

Phenotypic correlations in datasets with multiple observations per individual are the combined result of between- and within-individual correlations (Fig. 1) and here we tease apart these components. The between-individual correlation between $\text{SMR}_{m12}$ and $\text{SMR}_{m26}$ was higher than the phenotypic correlation and remained close to 1 in both foraging cost groups (0.80<$r<$0.91; Table 2). In contrast, the within-individual correlation between $\text{SMR}_{m12}$ and $\text{SMR}_{m26}$ was low (0.04<$r<$0.25; Table 2) and significantly positive only in the low foraging cost group (Table 2). Hence, the phenotypic correlation between $\text{SMR}_{m12}$ and $\text{SMR}_{m26}$ arose as a result of high between-individual correlation. Thus, individuals can be ranked consistently by their mean $\text{SMR}_m$ over the whole sub-thermoneutral $T_a$ range (Fig. 5A).

In contrast with the findings for $\text{SMR}_{m12}$ and $\text{SMR}_{m26}$, correlations between $\text{BMR}_m$ and any of the $\text{SMR}_m$ values were weak and their 95% CI often overlapped with zero between and within individuals and in both foraging cost groups (Table 2). Hence, the weak phenotypic correlations between $\text{BMR}_m$ and any of the $\text{SMR}_m$ values arose as a result of weak between- and weak within-individual correlations. Thus, the ranking of individuals according to their mean $\text{BMR}_m$ differs from the ranking according to their mean $\text{SMR}_m$ (Fig. 5A).

The high correlation between $\text{SMR}_{m12}$ and $\text{SMR}_{m26}$ indicates that individuals can be characterized by their metabolic reaction norms over sub-thermoneutral $T_a$. Statistically, an individual reaction norm can be quantified by a random slope. We hence ran a random slope model with $\text{SMR}_m$ data, including $T_a$ and mass as fixed effects and individual identity as a random effect and we quantified the improvement in model fit by inclusion of random slopes was larger in the low foraging cost environment (SMR: $\Delta \text{AIC}c=-6.8$; $\text{SMR}_m$: $\Delta \text{AIC}c=-3.3$). Thus, individuals can be characterized by their metabolic reaction norms over sub-thermoneutral $T_a$ (Fig. 5B) and this is most pronounced in a benign environment.

![Fig. 5. $\text{SMR}_{m12}$ and $\text{SMR}_{m26}$ associate better with each another than with $\text{BMR}_m$](image-url)
and for BMR (Fig. S4A; harsh foraging environment. Thermoneutral T_a was lower than in birds foraging in benign environments (reviewed in Geiser, 2004; Vuarin and Henry, 2014). We confirmed this pattern at T_a=12°C (Fig. 6; F_{1,113}=9.24, P=0.0029) and at thermoneutral T_a (T_a=36°C; Fig. 6; F_{1,147}=9.22, P=0.0028), but not at T_a=26°C (Fig. 6; F_{1,124}=0.36, P=0.55). The environment×T_a interaction was significant (F_{2,350}=3.36, P=0.036). Thus, individuals in harsh environments maintained either the same or lower night-time T_b depending on T_a.

There are multiple solutions to balancing metabolic rate, insulation and T_b (McNab, 1980). Thermal physics predicts that, everything else remaining equal, individuals with low SMR_m also have a lower T_b (McNab, 1980). Indeed, this was the case at T_a=12°C (Fig. S4A; r=0.22; F_{1,184}=9.0, P=0.003). However, this association was absent at T_a=26°C (Fig. S4A; F_{1,124}=0.09, P=0.77) and for BMR (Fig. S4A; r=0.05; F_{1,172}=0.11, P=0.74). These results were consistent for both foraging cost groups (F_{1,122}=2.63, P=0.11). The difference in the association between T_b and mass-adjusted metabolic rate at different T_a values was significant (F_{2,481}=3.04, P=0.05), with the association becoming stronger with decreasing T_a.

We next investigated whether the weak between-individual correlation between BMR_m and SMR_m was associated with individual differences in T_b response to sub-thermoneutral T_a. We tested whether individual responses of mass-adjusted metabolic rate and T_b to colder T_a were correlated. Indeed, when comparing mass-adjusted metabolic rate and T_b between T_a of 36 and 12°C, individuals with the largest increases in mass-adjusted metabolic rate maintained the highest T_b (Fig. 7; r=0.21; F_{1,123}=5.46, P=0.02) for both foraging cost groups (Fig. 7; F_{1,119}=0.29, P=0.59). Between 26 and 12°C, we found a significant association for birds in the low foraging cost environment (Fig. S4B; F_{1,59}=7.45, P=0.008), but not for birds in the high foraging cost environment (Fig. S4B; F_{1,41}=0.16, P=0.69) and this difference was significant (F_{1,101}=4.34, P=0.04). Between 36 and 26°C, we found little evidence for positive association between mass-adjusted metabolic rate and T_b responses (Fig. S4C; r=−0.24; F_{1,84}=2.56, P=0.11). Hence, we found some evidence that when facing sub-thermoneutral T_a, some individuals maintain a higher mass-adjusted metabolic rate and T_b than others. Thus, the weak between-individual correlations between BMR_m and SMR_m (Table 2) are in part due to individual differences in T_b regulation in response to sub-thermoneutral T_a.

**DISCUSSION**

Body mass, BMR_m and SMR_m were repeatable traits in our study population (Fig. 3B, Fig. 4B). BMR_m at different T_a correlated almost perfectly between individuals (Table 2, Fig. 5A,B). In contrast, correlations between BMR_m and SMR_m were always weaker (Table 2, Fig. 5A,B). Thus, individuals with high BMR_m do not necessarily have high SMR_m and our results better fit the scenario in Fig. S3B over that in Fig. S3A. Individual variation in metabolic reaction norms can have various causes (McNab, 1980) and here we showed a role for differential T_b regulation: individuals with the steeper metabolic reaction norms maintained a higher T_b at low ambient temperatures (Fig. 7). Thus, BMR_m was a weak indicator of the energy turnover at sub-thermoneutral T_a and this was in part due to individual variation in T_b regulation.

Repeatability is likely to be environment specific, and thus the fact that our birds lived in captivity may have affected our findings. A major difference between captive and free-living populations is Fig. 6. T_b is lower at lower T_a and this is more pronounced for birds in the harsh foraging environment. Boxplots show median, and 25–75 and 5–95 (black vertical lines) percentiles, N=550 measurements on 189 individuals.

T_b

Birds decreased their T_b in response to lower T_a (Fig. 6; F_{2,314}=313, P<10−15). Previous studies have shown that T_b is lower in individuals from harsh foraging environments (reviewed in Geiser, 2004; Vuarin and Henry, 2014). We confirmed this pattern at T_a=12°C (Fig. 6; F_{1,133}=9.24, P=0.0029) and at thermoneutral T_a (T_a=36°C; Fig. 6; F_{1,147}=9.22, P=0.0028), but not at T_a=26°C (Fig. 6; F_{1,124}=0.36, P=0.55). The environment×T_a interaction was significant (F_{2,350}=3.36, P=0.036). Thus, individuals in harsh environments maintained either the same or lower night-time T_b depending on T_a.

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Repeatability is likely to be environment specific, and thus the fact that our birds lived in captivity may have affected our findings. A major difference between captive and free-living populations is
that food can often be accessed at negligible costs in captivity, which is not usually the case for free-living animals (e.g. Beaulieu, 2016; Briga and Verhulst, 2015a). To better mimic natural conditions, we therefore experimentally increased foraging costs, which decreased life expectancy up to 15% (Briga et al., 2017). A unique aspect of our study is that we carried out this manipulation for life, and hence our findings reflect long-term adjustments to foraging conditions. Individuals living with high foraging costs had lower body mass, BMR<sub>m</sub> and SMR<sub>m</sub> (Fig. 3A, Fig. 4A), consistent with shorter-term studies of birds (Bautista et al., 1998; Deerenberg et al., 1998; Koetsier and Verhulst, 2011; Wiersma and Verhulst, 2005) and mammals (Day and Bartness, 2001; Perrigo, 1987; Schubert et al., 2009; Vaanholt et al., 2007). The standardized effect size <i>d</i> of foraging costs on mass-adjusted metabolic rate was approximately 0.5, which appears a reasonably large effect (Moller and Jennions, 2002). However, to establish the biological significance of this finding, we need to know how the observed effect sizes translate into differences in lifespan and/or reproductive success.

The effect of increased foraging costs was more pronounced on SMR<sub>m</sub> than on BMR<sub>m</sub>, in agreement with the findings of Wiersma and Verhulst (2005). The increasing effect of foraging costs with lower temperature is probably due to increased use of energy-saving mechanisms at lower <i>T<sub>a</sub></i>, such as night-time hypothermia (Fig. 6), which appears to be a general response to increased foraging costs or food shortage (Angilletta et al., 2010; Daan et al., 1989; Geiser, 2004; McKechnie and Lovegrove, 2002; Vuarin and Henry, 2014). That more energy is saved when foraging costs are increased is not surprising, because an increase in thermoregulatory requirements leads to a knock-on increase in energy expenditure in hard foraging conditions, because more energy needs to be expended to gather the extra energy for thermoregulation. Thus, we predict that diurnal energy expenditure will increase faster in response to decreasing ambient temperature when foraging costs are high, but this remains to be tested.

**Repeatability**

The repeatability of whole-organism metabolic rate in the range 0.4–0.5 found here are consistent with the existing literature, with most repeatabilities ranging between 0.3 and 0.8 (Auer et al., 2016; Nespolo and Franco, 2007; Versteegh et al., 2008; White et al., 2013). Our repeatability of mass-adjusted metabolic rate, ranging between 0.3 and 0.4, is also consistent with earlier studies in birds, although perhaps on the lower range relative to that found in earlier zebra finch studies, which was between 0.3 and 0.6 (Careau et al., 2014; Ronning et al., 2005; Verhulst et al., 2006; Vezina and Williams, 2005). Two aspects of our study are likely to have contributed to this difference. Firstly, our dataset covers a larger time range (up to 5.5 years), which deflates trait repeatability (Auer et al., 2016; White et al., 2013). Secondly, our birds were housed outdoors and thus exposed to a wider range of environmental variation than birds housed indoors. Thus, the repeatability of our metabolic rate measurements is within the range one would expect based on earlier studies.

How environmental quality affects trait repeatability is not well known. Heritability, i.e. the proportion of phenotypic variance due to additive genetic effects, was shown to increase weakly but significantly with environmental quality (Charmantier and Garant, 2005; Visscher et al., 2008; but see Rowinski and Rogell, 2017). Hence, a positive association is sometimes expected between repeatability and environmental quality. We did in fact find the expected difference for BMR<sub>m</sub> and SMR<sub>m</sub>, but the error around our estimates was such that this difference was only marginally significant despite a considerable sample size. However, for body mass and SMR<sub>m</sub> there was also an environmental effect on within-individual variance, being higher in the benign environment (significant for body mass, the trait with the largest sample size). This contrasts with the expectation for repeatability because, everything else remaining equal, large within-individual variance decreases repeatability. Indeed, the repeatability of body mass was independent of environmental quality because within- and between-individual variance both changed significantly and to the same extent. Our findings imply that there is no general prediction regarding the effect of environmental quality on trait repeatability.

**Weak metabolic correlations: causes and implications**

To the best of our knowledge, this study is the first to quantify the correlation between BMR<sub>m</sub> and SMR<sub>m</sub>. Intraspecific correlations between BMR (or BMR<sub>m</sub>) and other measures of energy expenditure, such as DEE and maximum metabolic rate (MMR; which is a special case of SMR when measured at very low <i>T<sub>a</sub></i> because it is not sustainable) were often found to be weak in endothermic species (DEE: Careau et al., 2012; Fyhnn et al., 2001; Meerlo et al., 1997; Speakman et al., 2003; Tieleman et al., 2008; Wiersma and Tinbergen, 2003; cold-induced MMR: Chappell and Bachman, 1995; Petit et al., 2013; Swanson et al., 2012; Vézina et al., 2006; Wiersma et al., 2007a; Zhang et al., 2015). Why these correlations are weak is not well known. BMR<sub>m</sub> is largely determined by central organs, while insulation and <i>T<sub>r</sub></i> will in addition be important for energetic expenditure at sub-thermoneutral <i>T<sub>a</sub></i> (such as SMR<sub>m</sub>, DEE and MMR; Daan et al., 1989; Daan et al., 1990; Suarez and Darveau, 2005; Vézina et al., 2006; Wiersma et al., 2012; Zhang et al., 2015). That there are different drivers of variation in BMR<sub>m</sub> (central organ mass and cellular activity) and SMR<sub>m</sub> (insulation and <i>T<sub>r</sub></i>) is likely to contribute to weakening the correlation between BMR<sub>m</sub> and SMR<sub>m</sub>. Here, we showed that individual differences in thermoregulation (<i>T<sub>r</sub></i>) in response to low temperature caused a low correlation between BMR<sub>m</sub> and SMR<sub>m</sub> and the same effect is likely to weaken correlations with DEE and MMR. There are, however, more drivers of variation for the weak correlation between BMR and DEE or MMR; in particular, additional variance due to variation in activity level is likely to be important. The extent to which thermoregulation explains the weak correlation between BMR and DEE can be verified by testing how much better SMR at ecologically relevant temperatures correlates with DEE or MMR. There are, however, more drivers of variation for the weak correlation between BMR and DEE or MMR; in particular, additional variance due to variation in activity level is likely to be important. The extent to which thermoregulation explains the weak correlation between BMR and DEE can be verified by testing how much better SMR at ecologically relevant temperatures correlates with DEE or MMR.

Between-individual correlations between SMR<sub>m</sub>12 and SMR<sub>m</sub>26 were high, and this observation was confirmed by the random slope analyses. In contrast, between-individual correlations between BMR<sub>m</sub> and SMR<sub>m</sub> were low. This finding may be due to individual differences in conductance (heat loss over the T<sub>a</sub>–T<sub>r</sub> gradient; McNab, 1980), with better insulated individuals showing a weaker metabolic rate response to lower <i>T<sub>r</sub></i>. Alternatively, the heterogeneity in metabolic rate response may be due to variation in <i>T<sub>r</sub></i> response to lower <i>T<sub>a</sub></i>. Our data (Figs 6 and 7) indicate that at least part of the heterogeneity in metabolic rate response can be attributed to the latter effect. Unfortunately, our data prevent us from estimating conductance directly because SMR and DEE were measured at different times (night and morning, respectively). In European kestrels *Falco tinnunculus*, a food rationing-induced decline in <i>T<sub>r</sub></i> was substantially larger at night than in the morning (Daan et al., 1989), indicating the error introduced when calculating conductance using metabolic rate and <i>T<sub>r</sub></i> measured at different times. Hence, the correlation between BMR<sub>m</sub> and SMR<sub>m</sub> is low at least in part due to individual differences in <i>T<sub>r</sub></i> regulation, and
individual variation in conductance may have further contributed to this finding, but this remains to be tested. BMR is often used to characterize energy consumption or minimum cost of self-maintenance of individuals or species. Our finding that BMR and SMR are poorly correlated raises the question whether BMR or SMR is most suitable for this purpose. When individuals are the unit of analysis, for example when relating an individual’s minimum energy expenditure to life-history traits (e.g. Burton et al., 2011; Nilsson and Nilsson, 2016), SMR may be preferable because heat loss is an inevitable determinant of an individual’s minimum levels of energy expenditure and animals spend much of their time at sub-thermoneutral $T_a$. Because SMRs at all sub-thermoneutral $T_a$ correlate almost perfectly with each other (Table 2), it appears that individual differences in SMR are equally well characterized at any sub-thermoneutral $T_a$. However, when species are the unit of analysis, the problem is more intricate because species live at different $T_a$ (Wiersma et al., 2007a,b, 2012). A possible solution might be to quantify SMR a standard number of degrees below the thermoneutral zone. Conversely, at the interspecific level, BMR and SMR may be well correlated, in which case using either BMR or SMR should make little difference for the results, but this needs to be verified. 

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Competing interests
The authors declare no competing or financial interests.

Author contributions
Conceptualization: M.B., S.V.; Methodology: M.B., S.V.; Software: M.B.; Validation: M.B.; Formal analysis: M.B., S.V.; Investigation: M.B., S.V.; Resources: M.B.; Data curation: M.B., S.V.; Writing - original draft: M.B.; Writing - review & editing: M.B., M.B.; Formal analysis: M.B., S.V.; Investigation: M.B., S.V.; Resources: M.B.; Data curation: M.B., S.V.; Writing - review & editing: M.B., M.B.; Methodology: M.B., S.V.; Software: M.B.; Validation: M.B.; Formal analysis: M.B., S.V.; Investigation: M.B., S.V.; Resources: M.B.; Data curation: M.B., S.V.; Writing - original draft: M.B.

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Supplementary information
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References
Auer, S. K., Bassar, R. D., Salin, K. and Metcalfe, N. B. (2016). Repeatability of metabolic rate is lower for animals living under field versus laboratory conditions. J. Physiol. 219, 631-634.


Fig. S1. Distribution of number of measurements per bird

Number of birds with a count of their body mass measurements (A) and their metabolic rate measurements (B). Note the different scales on the X-axes.
Table S1. Body mass variance components and repeatability
Variance components and repeatability estimates (±95% CI) for the body mass traits shown in Fig. 3.

<table>
<thead>
<tr>
<th>Dataset</th>
<th>Variance Between-individual</th>
<th>Variance Within-individual</th>
<th>Repeatability</th>
</tr>
</thead>
<tbody>
<tr>
<td>Whole population</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Body mass</td>
<td>1.75 (1.54-1.96)</td>
<td>0.70 (0.68-0.71)</td>
<td>0.72 (0.69-0.74)</td>
</tr>
<tr>
<td>Size-adjusted</td>
<td>1.06 (0.91-1.19)</td>
<td>0.69 (0.68-0.71)</td>
<td>0.60 (0.57-0.64)</td>
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<td>Benign environment</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Body mass</td>
<td>2.07 (1.76-2.46)</td>
<td>0.83 (0.80-0.86)</td>
<td>0.72 (0.68-0.84)</td>
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<tr>
<td>Size-adjusted</td>
<td>1.10 (0.93-1.36)</td>
<td>0.83 (0.81-0.87)</td>
<td>0.57 (0.52-0.62)</td>
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<tr>
<td>Harsh environment</td>
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<td></td>
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<tr>
<td>Body mass</td>
<td>1.22 (1.00-1.43)</td>
<td>0.55 (0.54-0.57)</td>
<td>0.69 (0.65-0.72)</td>
</tr>
<tr>
<td>Size-adjusted</td>
<td>0.77 (0.65-0.94)</td>
<td>0.54 (0.53-0.57)</td>
<td>0.58 (0.54-0.64)</td>
</tr>
</tbody>
</table>
**Fig. S2. Association between ambient temperature and basal metabolic rate in the thermoneutral zone**

The thermoneutral zone of the zebra finch was previously identified as ranging from 29.5°C till 40°C and the minimum oxygen consumption was measured at 34.9°C (Calder, 1964). Yet, these estimates were based on 72 measurements and larger datasets may find a different thermoneutral zone. In our data, using Tₐ ranges as identified in Calder (1964) we found a quadratic association between MR and Tₐ with the minimum BMR occurring at 34.8°C (Tₐ; F=4.2 p<10⁻⁴; Tₐ²; F=5.6 p<10⁻⁷; N=1233 measurements on 386 birds). This minimum is consistent with the earlier results of Calder et al. (1964). However, within this Tₐ range the distribution of BMR around the minimum would be asymmetric (Fig. S2) with a difference between maximum and minimum BMR of 0.027W (or 1 SD BMR, Table 1). Here, we chose a narrower and more symmetric distribution of BMR around the minimum of 34.8°C and, given the distribution of our data, determined the thermoneutral zone between 32°C and 39°C (Fig. S2). Hence, although we used a dataset that was over ten times as large as what was used previously, we identified a thermoneutral zone that is overall very consistent with that of earlier studies.

Dashed line shows model results.
Table S2. Metabolic rate variance components and repeatability

Variance components and repeatability estimates (± 95% CI) for the metabolic rate traits in Fig. 4.

<table>
<thead>
<tr>
<th></th>
<th>Between-individual variance</th>
<th>Within-individual variance</th>
<th>Repeatability</th>
<th>Difference BMR-SMR</th>
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<td><strong>Whole population</strong></td>
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<tr>
<td>Whole-organism</td>
<td>BMR 0.00036 (0.00031-0.00047)</td>
<td>SMR 0.0012 (0.0010-0.0016)</td>
<td>BMR 0.00035 (0.00031-0.00038)</td>
<td>SMR 0.0021 (0.0020-0.0023)</td>
</tr>
<tr>
<td>Mass-adjusted</td>
<td>BMR 0.00013 (8.8 10⁻⁵-0.00016)</td>
<td>SMR 0.00073 (0.00057-0.00093)</td>
<td>BMR 0.00032 (0.00029-0.00036)</td>
<td>SMR 0.0018 (0.0017-0.0019)</td>
</tr>
<tr>
<td><strong>Spring data</strong></td>
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<tr>
<td>Whole-organism</td>
<td>BMR 0.00036 (0.00026-0.00046)</td>
<td>SMR 0.0016 (0.0013-0.0020)</td>
<td>BMR 0.00030 (0.00025-0.00034)</td>
<td>SMR 0.00014 (0.00012-0.00015)</td>
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<tr>
<td>Mass-adjusted</td>
<td>BMR 0.00076 (0.00053-0.00094)</td>
<td>SMR 0.00073 (0.00056-0.00099)</td>
<td>BMR 0.00027 (0.00022-0.00030)</td>
<td>SMR 0.00011 (0.000096-0.00012)</td>
</tr>
<tr>
<td><strong>Autumn data</strong></td>
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<tr>
<td>Whole-organism</td>
<td>BMR 0.00038 (0.00028-0.00052)</td>
<td>SMR 0.0011 (0.00082-0.0014)</td>
<td>BMR 0.00035 (0.00030-0.00042)</td>
<td>SMR 0.00014 (0.00012-0.00015)</td>
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<tr>
<td>Mass-adjusted</td>
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<td>SMR 0.00058 (0.00043-0.00084)</td>
<td>BMR 0.00037 (0.00012-0.00014)</td>
<td>SMR 0.0018 (0.00018-0.00022)</td>
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<tr>
<td><strong>Benign environment</strong></td>
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<tr>
<td>Whole-organism</td>
<td>BMR 0.00040 (0.00031-0.00058)</td>
<td>SMR 0.00093 (0.00065-0.0013)</td>
<td>BMR 0.00038 (0.00033-0.00044)</td>
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<td>Mass-adjusted</td>
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<td>SMR 0.00076 (0.000050-0.0011)</td>
<td>BMR 0.00033 (0.00029-0.00038)</td>
<td>SMR 0.00022 (0.00020-0.00024)</td>
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<td><strong>Harsh environment</strong></td>
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<tr>
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<td>BMR 0.00018 (0.00013-0.00026)</td>
<td>SMR 0.00049 (0.00036-0.00072)</td>
<td>BMR 0.00032 (0.00028-0.00036)</td>
<td>SMR 0.00014 (0.00013-0.00015)</td>
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<tr>
<td>Mass-adjusted</td>
<td>BMR 0.000078 (0.000044-0.00013)</td>
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<td>BMR 0.00031 (0.00027-0.00036)</td>
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<td><strong>All data</strong></td>
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<td>SMR26 0.00087 (0.00068-0.0011)</td>
<td>SMR12 0.00082 (0.00061-0.0010)</td>
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<td>Whole-organism</td>
<td>BMR 0.0012 (0.0008-0.0017)</td>
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<td>SMR 0.0008 (0.0005-0.0010)</td>
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<td>Mass-adjusted</td>
<td>BMR 0.00058 (0.00036-0.00068)</td>
<td>SMR 0.00051 (0.00036-0.00068)</td>
<td>BMR 0.0008 (0.0005-0.0010)</td>
<td>SMR 0.0008 (0.0005-0.0010)</td>
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</tbody>
</table>
Fig. S3. Phenotypic correlations between metabolic traits

Schematic (A, B) and data representations (C) of phenotypic correlations between metabolic traits. (A) Metabolic reaction norms of three individuals (1, 2 and 3) differ little in response to ambient temperature ($T_a$), generating a high between individual correlation between BMR and SMR. (B) Represents the alternative scenario, in which individuals differ in their metabolic response to a decrease in $T_a$: individuals with high BMR can have either high or low SMR, generating a low between individual correlation between BMR and SMR. (C) Data show that SMRs at various $T_a$’s correlate well with each other (C1 & C2) but that correlations between BMR and any of the SMR’s are weak (C3-C6), hence consistent with the scenario shown in (B) and not in (A).
**Fig. S4. Body temperature**

Associations between (A) mass-adjusted metabolic rate and body temperature and (B) between change in mass-adjusted metabolic rate and body temperature at various ambient temperatures (T_a). (A) Mass-adjusted metabolic rate and body temperature correlate positively at T_a=12°C, but this association decreases with increasing T_a. Dots show data, lines are results of model fits. (B) Within-individual differences in metabolic rate are not significantly correlated with differences in body temperatures when T_a declines from (A) 26°C to 12°C or (B) the thermoneutral zone to 26°C. Grey dots and dashed lines show raw data and model fit for benign environment, black triangles and full lines show raw data and model fit for harsh environment. For statistics see results section.