

Whole-animal metabolic rate is a repeatable trait: a meta-analysis

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There were several errors published in *J. Exp. Biol.* **210**, 2000-2005.

Table 1 included a number of mistakes and incorrectly cited references. Here, we present the corrected Table 1.

The following corrections have been made: (1) cases 16, 18, 42 and 45 have been removed; (2) an additional reference for case 32 (Terblanche et al., 2004a) has been added; and (3) in case 17, the original reference should have read (Fournier and Thomas, 1999) and not (Fournier et al., 1999).

The following references should have been listed in the Reference list:

- Fournier, F. and Thomas, D. W.** (1999). Thermoregulation and repeatability of oxygen-consumption measurements in winter-acclimatized North American porcupines (*Erethizon dorsatum*). *Can. J. Zool.* **77**, 194-202.
- Terblanche, J. S., Klof, C. J., Marais, E. and Chown, S. L.** (2004b). Metabolic rate in the whip-spider, *Damon annulatipes* (Arachnida: Amblypygi). *J. Insect Physiol.* **50**, 637-645.

The reference cited in the original paper as (Terblanche et al., 2004) should have been cited as (Terblanche et al., 2004b).

The authors apologize for these errors but assure readers that the results and conclusions of the original paper remain unchanged.

Table 1. Literature search for repeatability studies in metabolic rate, sorted in chronological order

| Case | Study | Variable | Subtype | EST | <i>R</i> | <i>N</i> | <i>P</i> <0.05 | <i>M_b</i> control | Time (days) | Animal | Reference |
|------|-------|----------|---------|--------|----------|----------|----------------|---------------------------------|----------------|----------------------|-------------------------------|
| 1 | 1 | MMR | LOC | P | 0.97 | 50 | Yes | Yes | 2 | Reptile | (Garland and Else, 1987) |
| 2 | 2 | SMR | | P | 0.88 | 242 | Yes | Yes | 1 | Reptile | (Garland and Bennett, 1990) |
| 3 | 2 | SMR | | τ | 0.86 | 242 | Yes | Yes | 1 | Reptile | (Garland and Bennett, 1990) |
| 4 | 3 | MMR | LOC | τ | 0.80 | 35 | Yes | Yes | 7 | Mamm _{LAB} | (Friedman et al., 1992) |
| 5 | 4 | BMR | | P | 0.93 | 74 | Yes | Yes | 1 | Mamm _{LAB} | (Hayes et al., 1992) |
| 6 | 4 | MMR | LOC | P | 0.78 | 61 | Yes | Yes | 2 | Mamm _{LAB} | (Hayes et al., 1992) |
| 7 | 5 | MMR | LOC | P | 0.40 | 50 | Yes | Yes | 18 | Mamm _{WILD} | (Chappell et al., 1995) |
| 8 | 5 | MMR | THER | P | 0.38 | 34 | No | Yes | 18 | Mamm _{WILD} | (Chappell et al., 1995) |
| 9 | 5 | MMR | LOC | P | 0.47 | 21 | Yes | Yes | 700 | Mamm _{WILD} | (Chappell et al., 1995) |
| 10 | 5 | MMR | THER | P | 0.02 | 19 | Yes | Yes | 700 | Mamm _{WILD} | (Chappell et al., 1995) |
| 11 | 6 | FMR | | τ | 0.26 | 11 | Yes | Yes | 40 | Mamm _{WILD} | (Berteaux et al., 1996) |
| 12 | 7 | SMR | | P | 0.85 | 6 | Yes | Yes | 3 | Insect | (Ashby, 1997) |
| 13 | 8 | RMR | | τ | 0.69 | 30 | Yes | Yes | 21 | Mamm _{WILD} | (Hayes et al., 1998) |
| 14 | 8 | MMR | THER | τ | 0.74 | 30 | Yes | Yes | 21 | Mamm _{WILD} | (Hayes and O'Connor, 1999) |
| 15 | 9 | BMR | | τ | 0.35 | 17 | Yes | Yes | 30 | Bird | (Bech et al., 1999) |
| 17 | 11 | RMR | | P | 0.83 | 10 | Yes | Yes | 12 | Mamm _{WILD} | (Fournier and Thomas, 1999) |
| 19 | 13 | SMR | | P | 0.38 | 23 | Yes | Yes | 3 | Insect | (Chappell and Rogowitz, 2000) |
| 20 | 14 | MMR | LOC | P | 0.69 | 16 | Yes | Yes | 3 | Insect | (Rogowitz and Chappell, 2000) |
| 21 | 14 | MMR | LOC | P | 0.19 | 22 | No | Yes | 3 | Insect | (Rogowitz and Chappell, 2000) |
| 22 | 15 | SMR | | P | 0.68 | 28 | Yes | No | 119 | Fish | (Mccarthy, 2000) |
| 23 | 16 | SMR | | P | 0.68 | 12 | Yes | No | 35 | Fish | (Virani and Rees, 2000) |
| 24 | 17 | FMR | | τ | 0.64 | 32 | Yes | Yes | 1 | Bird | (Fyhn et al., 2001) |
| 25 | 18 | BMR | | τ | 0.84 | 28 | Yes | Yes | 8 | Bird | (Horak et al., 2002) |
| 26 | 18 | BMR | | τ | 0.65 | 13 | Yes | Yes | 120 | Bird | (Horak et al., 2002) |
| 27 | 19 | SMR | | P | 0.53 | 85 | Yes | Yes | 30 | Insect | (Nespolo et al., 2003b) |
| 28 | 20 | SMR | | τ | 0.22 | 13 | Yes | Yes | 25 | Insect | (Marais and Chown, 2003) |
| 29 | 21 | BMR | | τ | 0.66 | 10 | Yes | No | 21 | Bird | (Tieleman et al., 2003) |
| 30 | 21 | BMR | | τ | 0.48 | 8 | Yes | No | 21 | Bird | (Tieleman et al., 2003) |
| 31 | 21 | BMR | | τ | 0.57 | 7 | Yes | No | 21 | Bird | (Tieleman et al., 2003) |
| 32 | | SMR | | τ | 0.60 | 7 | Yes | Yes | 7 | Insect | (Terblanche et al., 2004a) |
| | 22 | SMR | | τ | 0.74 | 9 | Yes | Yes | 14 | Insect | (Terblanche et al., 2004b) |
| 33 | 23 | BMR | | τ | 0.56 | 64 | Yes | Yes | 30 | Mamm _{WILD} | (Labocha et al., 2004) |
| 34 | 24 | MMR | THER | P | 0.77 | 7 | Yes | Yes | 4 | Mamm _{LAB} | (Chappell et al., 2004) |
| 35 | 24 | RMR | | P | 0.76 | 7 | Yes | Yes | 4 | Mamm _{LAB} | (Chappell et al., 2004) |
| 36 | 25 | MMR | THER | P | 0.48 | 20 | Yes | Yes | 6 | Mamm _{LAB} | (Rezende et al., 2004) |
| 37 | 25 | MMR | THER | P | 0.82 | 19 | Yes | Yes | 28 | Mamm _{LAB} | (Rezende et al., 2004) |
| 38 | 26 | BMR | | P | 0.72 | 40 | Yes | Yes | 5 | Mamm _{LAB} | (Ksiazek et al., 2004) |
| 39 | 27 | BMR | | τ | 0.57 | 35 | Yes | Yes | 913 | Bird | (Ronning et al., 2005) |
| 40 | 28 | MMR | LOC | P | 0.42 | 48 | Yes | Yes | 1 | Mamm _{LAB} | (Rezende et al., 2005) |
| 41 | 28 | MMR | THER | P | 0.134 | 47 | No | Yes | 1 | Mamm _{LAB} | (Rezende et al., 2005) |
| 43 | 28 | MMR | LOC | τ | 0.82 | 48 | Yes | Yes | 1 | Mamm _{LAB} | (Rezende et al., 2005) |
| 44 | 28 | MMR | THER | τ | -0.098 | 47 | No | Yes | 1 | Mamm _{LAB} | (Rezende et al., 2005) |
| 46 | 29 | BMR | | τ | 0.6 | 89 | Yes | Yes | 3 | Mamm _{WILD} | (Sadowska et al., 2005) |
| 47 | 30 | BMR | | P | 0.006 | 85 | No | Yes | 60 | Mamm _{WILD} | (Russell and Chappell, 2006) |

Var, variable: MMR, maximum metabolic rate; BMR, basal metabolic rate; SMR, standard metabolic rate; FMR, field metabolic rate; RMR, resting metabolic rate; LOC, locomotory; THER, thermoregulatory. EST, estimator: P, Pearson product-moment correlation (r_P in text); τ , intraclass correlation coefficient; *R*, magnitude of repeatability estimate; *N*, number of individuals; *P*, probability; *M_b*, body mass; Mamm_{WILD}, mammal from a wild population; Mamm_{LAB}, mammal from a laboratory population.

Whole-animal metabolic rate is a repeatable trait: a meta-analysis

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Summary

Repeatability studies are gaining considerable interest among physiological ecologists, particularly in traits affected by high environmental/residual variance, such as whole-animal metabolic rate (MR). The original definition of repeatability, known as the intraclass correlation coefficient, is computed from the components of variance obtained in a one-way ANOVA on several individuals from which two or more measurements are performed. An alternative estimation of repeatability, popular among physiological ecologists, is the Pearson product–moment correlation between two consecutive measurements. However, despite the more than 30 studies reporting repeatability of MR, so far there is not a definite synthesis indicating: (1) whether repeatability changes in different types of animals; (2) whether some kinds of metabolism are more repeatable than others; and most important, (3) whether metabolic rate is significantly repeatable. We

performed a meta-analysis to address these questions, as well as to explore the historical trend in repeatability studies. Our results show that metabolic rate is significantly repeatable and its effect size is not statistically affected by any of the mentioned factors (i.e. repeatability of MR does not change in different species, type of metabolism, time between measurements, and number of individuals). The cumulative meta-analysis revealed that repeatability studies in MR have already reached an asymptotical effect size with no further change either in its magnitude and/or variance (i.e. additional studies will not contribute significantly to the estimator). There was no evidence of strong publication bias.

Key words: repeatability, heritability, meta-analysis, energy metabolism, intraclass correlation coefficient, effect size.

Introduction

In evolutionary terms, traits are organism's attributes that in some way reflect biological performance, and which ultimately have an impact on fitness (Arnold, 1983). The operational definition of a trait involves an instrument and a measurement scale. A crucial concept in this definition is repeatability: the time-consistency of a trait, which is measured by the intraclass correlation coefficient $\tau = \sigma^2_A / (\sigma^2_A + \sigma^2_e)$ where σ^2_A is the between-individual component of variance and σ^2_e is the residual variance component when multiple measurements are performed in the same individuals (i.e. within individual variation). Between-individual variance equals genetic variance (σ^2_G) + general environmental variance (σ^2_E). In turn, phenotypic variance equals $\sigma^2_G + \sigma^2_E + \sigma^2_e$. Then, τ can also be decomposed as $\tau = (\sigma^2_G + \sigma^2_E) / \sigma^2_P$ (Lessels and Boag, 1987; Falconer and Mackay, 1997). Since this measurement includes genetic variance, repeatability appears not only to give insight into the time-consistency of a trait (i.e. its 'qualification' to be treated as a trait) but also to set the upper limit for heritability (the ratio between genetic variance and phenotypic variance) (Lessels and Boag, 1987; Falconer

and Mackay, 1997; Roff, 1997; Lynch and Walsh, 1998; Dohm, 2002).

The ease of repeatability computations (and the difficulty of quantitative genetic studies) makes this quantity of great interest for organismal biologists interested in the evolutionary significance of traits, but especially important for physiological ecologists working with metabolic rate (MR) in whole animals. In such studies, the adaptive significance of MR is frequently quoted (e.g. McNab, 2002). However, MR is usually measured by flow-through respirometry, a technique that includes considerable residual variation (i.e. error variance). The most accurate modern flow-through respirometers have a minimum of 10–20% measurement error (Konarzewski et al., 2005), which also holds for isotopic methods for field metabolic rate (Speakman, 2004).

Logistically, the measurement of MR is not as straightforward as other kind of traits such as morphology, life histories or even behavior. It requires the researcher to capture animals, move them into the laboratory, and usually to acclimate them for a number of days or weeks. On the other hand, and depending on the desired metabolic variable,

respirometric trials are usually combined with certain imposed conditions to animals (e.g. cold, warm, treadmill running, noradrenaline injection, fasting period). In summary, because of the very nature of the technique, MR is a trait with high residual variance (see Konarzewski et al., 2005), and consequently repeatability of MR is important to ecological and evolutionary physiologists.

The repeatability of metabolic rate has been inferred from the intraclass correlation coefficient and multiple measurements. Also, a commonly used repeatability estimation is the Pearson–moment correlation from two consecutive measurements ($r_p = \sigma_{x,y} / \sigma_x \sigma_y$; where $\sigma_{x,y}$ is the covariance between the first and the second measurements, x and y , and $\sigma_x \sigma_y$ is the product of both standard deviations) (Lynch and Walsh, 1998). Although variance-components and τ can also be computed from two measurements, for practical reasons authors have specialized in r_p when two measurements are available, or in τ when multiple measurements are performed (see Table 1).

We performed meta-analysis on repeatability of metabolic rate to answer the following questions:

- (1) Does repeatability change in different types of animals?
- (2) Are some kinds of metabolic rates more repeatable than others?
- (3) What is the effect of elapsed time between measurements on repeatability?
- (4) Does repeatability of metabolic rate from laboratory and wild populations differ?

Materials and methods

Literature survey

We searched the literature in order to find published studies that measured repeatability of MR in animals. We recorded the magnitude of the estimator, number of individuals measured and the time elapsed between measurements, in days. We found 30 studies, from which we extracted 47 estimators that were classified according to the organisms measured (we found studies on birds, mammals, insects, reptiles and fish) and according to the standard nomenclature for metabolic measurement: locomotory maximum metabolic rate (MMR_{LOC}), standard metabolic rate (SMR), field metabolic rate (FMR), resting metabolic rate (RMR), thermoregulatory maximum metabolic rate (MMR_{THERM}) and basal metabolic rate (BMR) (Table 1). For small mammals, studies were also classified as from laboratory or wild populations. After removing a few studies where body mass M_b was not controlled ($N=5$, see Table 1), the resulting effect size was almost identical, so we present results including those studies (see also Konarzewski et al., 2005).

Statistics

Conventional statistical methods were performed using Statistica 6.0 whereas the meta-analytical techniques were performed using MetaWin 2.1 (Rosenberg et al., 2000). We first computed effect size and its variances applying the

Fisher's Z-transformation. Then, we computed the mean effect size for the sample, its 95% confidence intervals, bootstrapped confidence intervals and general heterogeneity by the Q-statistic, which is distributed as χ^2 with $N-1$ degrees of freedom (d.f.) (Rosenberg et al., 2000). We specifically tested the categorical structure of the data: type of variable (six levels), type of organism (five levels), and type of population (only in rodents; two levels). Both type of variable and type of organism were considered random factors since they do not account for all possible levels, and population (lab/wild) was considered fixed. We decomposed the total heterogeneity (Q_T) into the heterogeneity explained by the model (Q_M) and error heterogeneity (Q_E) in a similar fashion to one-way analysis of variance (Rosenberg et al., 2000). These procedures allowed us to test whether (1) different kinds of MR have a significant effect on published repeatabilities, (2) different kinds of animals have a significant effect on published repeatabilities and (3) whether, in the case of small mammals, laboratory and wild populations differ in their repeatability estimation.

In several cases we used more than one estimator from a single study, which could potentially violate the assumption of independence of meta-analyses (i.e. the within-study variance could be larger than the among-study variance due to methodological similarities) (Rosenberg et al., 2000). To test for such a possible effect, we performed a preliminary analysis with those studies that reported more than one estimator and tested whether they had a categorical effect on repeatability. This preliminary result showed that the 'study' effect was non-significant ($Q_M=3.63$; $Q_E=9.99$; $P_{\chi^2}=0.60$; $P_{rand}=0.58$). In addition, we performed a cumulative meta-analysis in order to assess the chronological trend in the effect sizes. This analysis permits determination of whether the present effect sizes were attained at some point in the past (further studies being essentially redundant) (Rosenberg et al., 2000). Finally, we assessed publication bias graphically by funnel plots, and also by fail-safe numbers. This last procedure computes the number of non-significant, unpublished or missing studies that would need to be added to a meta-analysis in order to change the results from significant to non-significant. Specifically, we applied the Rosenthal method (Rosenberg et al., 2000), which computes the number of additional studies with a mean effect size of zero needed to reduce the combined significance to an alpha level set equal to 0.05. Additionally, we computed the Orwin method (Rosenberg et al., 2000), which computes the number of additional studies needed to reduce an observed mean effect size to a minimum effect of 0.2.

Results

Although the reviewed studies were remarkably uneven regarding organism type (insects: 7 cases, 16.7%; mammals: 25 cases, 59.5%; birds: 7 cases, 16.7%; reptiles: 3 cases, 7.1%; see Table 1) and metabolic rate type (SMR: 7 cases, 16.7%; MMR : 20 cases, 47.6%; BMR/RMR: 14 cases, 33.3%; FMR: 1 case, 2.4%; see Table 1), the use of the Pearson product–moment correlation and intraclass correlation appear

balanced (Pearson product–moment correlation: 23 cases, 54.8%; intraclass correlation: 19 cases, 45.2%; see Table 1). Published repeatabilities were leftward biased (Fig. 1), but did

not significantly depart from normality ($d=0.124$; $P=0.2$; Kolmogorov–Smirnov test), with mean=0.57 and s.d.=0.26 (Fig. 1). The funnel plot showed that there was a non-

Table 1. Literature search for repeatability studies in metabolic rate, sorted in chronological order

| Case | Study | Variable | Subtype | EST | R | N | P<0.05 | M_b control | Time (days) | Animal | Reference |
|------|-------|----------|---------|--------|--------|-----|--------|------------------|----------------|----------------------|-------------------------------|
| 1 | 1 | MMR | LOC | P | 0.97 | 50 | Yes | Yes | 2 | Reptile | (Garland and Else, 1987) |
| 2 | 2 | SMR | | P | 0.88 | 242 | Yes | Yes | 1 | Reptile | (Garland and Bennett, 1990) |
| 3 | 2 | SMR | | τ | 0.86 | 242 | Yes | Yes | 1 | Reptile | (Garland and Bennett, 1990) |
| 4 | 3 | MMR | LOC | τ | 0.80 | 35 | Yes | Yes | 7 | Mamm _{LAB} | (Friedman et al., 1992) |
| 5 | 4 | BMR | | P | 0.93 | 74 | Yes | Yes | 1 | Mamm _{LAB} | (Hayes et al., 1992) |
| 6 | 4 | MMR | LOC | P | 0.78 | 61 | Yes | Yes | 2 | Mamm _{LAB} | (Hayes et al., 1992) |
| 7 | 5 | MMR | LOC | P | 0.40 | 50 | Yes | Yes | 18 | Mamm _{WILD} | (Chappell et al., 1995) |
| 8 | 5 | MMR | THER | P | 0.38 | 34 | No | Yes | 18 | Mamm _{WILD} | (Chappell et al., 1995) |
| 9 | 5 | MMR | LOC | P | 0.47 | 21 | Yes | Yes | 700 | Mamm _{WILD} | (Chappell et al., 1995) |
| 10 | 5 | MMR | THER | P | 0.02 | 19 | Yes | Yes | 700 | Mamm _{WILD} | (Chappell et al., 1995) |
| 11 | 6 | FMR | | τ | 0.26 | 11 | Yes | Yes | 40 | Mamm _{WILD} | (Berteaux et al., 1996) |
| 12 | 7 | SMR | | P | 0.85 | 6 | Yes | Yes | 3 | Insect | (Ashby, 1997) |
| 13 | 8 | RMR | | τ | 0.69 | 30 | Yes | Yes | 21 | Mamm _{WILD} | (Hayes et al., 1998) |
| 14 | 8 | MMR | THER | τ | 0.74 | 30 | Yes | Yes | 21 | Mamm _{WILD} | (Hayes and O'Connor, 1999) |
| 15 | 9 | BMR | | τ | 0.35 | 17 | Yes | Yes | 30 | Bird | (Bech et al., 1999) |
| 16 | 10 | MMR | THER | P | 0.39 | 34 | Yes | Yes | 68 | Mamm _{WILD} | (Hayes et al., 1998) |
| 17 | 11 | RMR | | P | 0.83 | 10 | Yes | Yes | 12 | Mamm _{WILD} | (Fournier et al., 1999) |
| 18 | 12 | MMR | LOC | P | 0.31 | 68 | Yes | Yes | 70 | Bird | (Chappell et al., 1999) |
| 19 | 13 | SMR | | P | 0.38 | 23 | Yes | Yes | 3 | Insect | (Chappell and Rogowitz, 2000) |
| 20 | 14 | MMR | LOC | P | 0.69 | 16 | Yes | Yes | 3 | Insect | (Rogowitz and Chappell, 2000) |
| 21 | 14 | MMR | LOC | P | 0.19 | 22 | No | Yes | 3 | Insect | (Rogowitz and Chappell, 2000) |
| 22 | 15 | SMR | | P | 0.68 | 28 | Yes | No | 119 | Fish | (Mccarthy, 2000) |
| 23 | 16 | SMR | | P | 0.68 | 12 | Yes | No | 35 | Fish | (Virani and Rees, 2000) |
| 24 | 17 | FMR | | τ | 0.64 | 32 | Yes | Yes | 1 | Bird | (Fyhn et al., 2001) |
| 25 | 18 | BMR | | τ | 0.84 | 28 | Yes | Yes | 8 | Bird | (Horak et al., 2002) |
| 26 | 18 | BMR | | τ | 0.65 | 13 | Yes | Yes | 120 | Bird | (Horak et al., 2002) |
| 27 | 19 | SMR | | P | 0.53 | 85 | Yes | Yes | 30 | Insect | (Nespolo et al., 2003b) |
| 28 | 20 | SMR | | τ | 0.22 | 13 | Yes | Yes | 25 | Insect | (Marais and Chown, 2003) |
| 29 | 21 | BMR | | τ | 0.66 | 10 | Yes | No | 21 | Bird | (Tieleman et al., 2003) |
| 30 | 21 | BMR | | τ | 0.48 | 8 | Yes | No | 21 | Bird | (Tieleman et al., 2003) |
| 31 | 21 | BMR | | τ | 0.57 | 7 | Yes | No | 21 | Bird | (Tieleman et al., 2003) |
| 32 | 22 | SMR | | τ | 0.74 | 9 | Yes | Yes | 14 | Insect | (Terblanche et al., 2004) |
| 33 | 23 | BMR | | τ | 0.56 | 64 | Yes | Yes | 30 | Mamm _{WILD} | (Labocha et al., 2004) |
| 34 | 24 | MMR | THER | P | 0.77 | 7 | Yes | Yes | 4 | Mamm _{LAB} | (Chappell et al., 2004) |
| 35 | 24 | RMR | | P | 0.76 | 7 | Yes | Yes | 4 | Mamm _{LAB} | (Chappell et al., 2004) |
| 36 | 25 | MMR | THER | P | 0.48 | 20 | Yes | Yes | 6 | Mamm _{LAB} | (Rezende et al., 2004) |
| 37 | 25 | MMR | THER | P | 0.82 | 19 | Yes | Yes | 28 | Mamm _{LAB} | (Rezende et al., 2004) |
| 38 | 26 | BMR | | P | 0.72 | 40 | Yes | Yes | 5 | Mamm _{LAB} | (Ksiazek et al., 2004) |
| 39 | 27 | BMR | | τ | 0.57 | 35 | Yes | Yes | 913 | Bird | (Ronning et al., 2005) |
| 40 | 28 | MMR | LOC | P | 0.42 | 48 | Yes | Yes | 1 | Mamm _{LAB} | (Rezende et al., 2005) |
| 41 | 28 | MMR | THER | P | 0.134 | 47 | No | Yes | 1 | Mamm _{LAB} | (Rezende et al., 2005) |
| 42 | 28 | MMR | LOC | P | 0.49 | 48 | Yes | Yes | 1 | Mamm _{LAB} | (Rezende et al., 2005) |
| 43 | 28 | MMR | LOC | τ | 0.82 | 48 | Yes | Yes | 1 | Mamm _{LAB} | (Rezende et al., 2005) |
| 44 | 28 | MMR | THER | τ | -0.098 | 47 | No | Yes | 1 | Mamm _{LAB} | (Rezende et al., 2005) |
| 45 | 28 | MMR | LOC | τ | 0.87 | 48 | Yes | Yes | 1 | Mamm _{LAB} | (Rezende et al., 2005) |
| 46 | 29 | BMR | | τ | 0.6 | 89 | Yes | Yes | 3 | Mamm _{WILD} | (Sadowska et al., 2005) |
| 47 | 30 | BMR | | P | 0.006 | 85 | No | Yes | 60 | Mamm _{WILD} | (Russell and Chappell, 2006) |

Var, variable: MMR, maximum metabolic rate; BMR, basal metabolic rate; SMR, standard metabolic rate; FMR, field metabolic rate; RMR, resting metabolic rate; LOC, locomotory; THER, thermoregulatory. EST, estimator: P, Pearson product–moment correlation (r_P in text); τ , intraclass correlation coefficient; R, magnitude of repeatability estimate; N, number of individuals; P, probability; M_b , body mass; Mamm_{WILD}, mammal from a wild population; Mamm_{LAB}, mammal from a laboratory population.

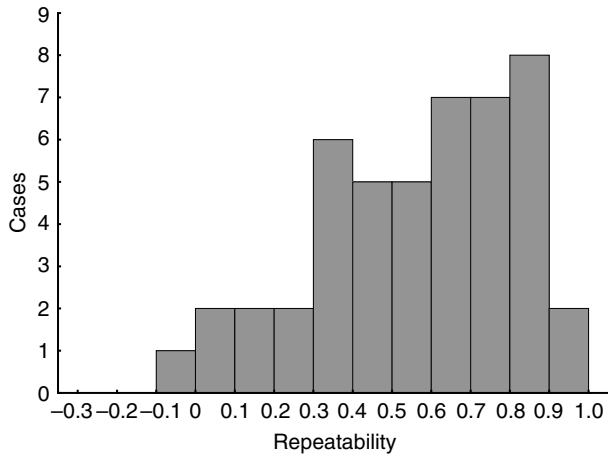


Fig. 1. Frequency histogram of published repeatabilities reviewed in this study (see Table 1 for details).

significant correlation between sample size and the magnitude of repeatability estimation ($R=0.164$; $P=0.27$; Fig. 2). The mean effect size (E) was significantly different from zero ($E=0.746$; bootstrap 95%CI: 0.626-0.873) and heterogeneity was non-significant ($Q_{total}=32.71$; d.f.=46; $P=0.96$), which suggest that data do not have a subjacent structure. Also, there was no effect of time between measurements and the size-effect of repeatability ($Q=33.5$; d.f.=39; $P=0.72$). Although this result renders it unnecessary to test the effect of the categorical factors that we were interested in, we performed it and as expected, we found non-significant effects of all categories (data not shown). In other words, our meta-analysis does not provide enough evidence to reject the hypotheses that repeatability of MR does not change with type of animal, metabolic measurement, time between measurements and laboratory or wild populations. However, the fact that only one study in FMR was found does not permit any conclusion to be made regarding the potential differences between this variable and the other categories. The cumulative meta-analysis showed

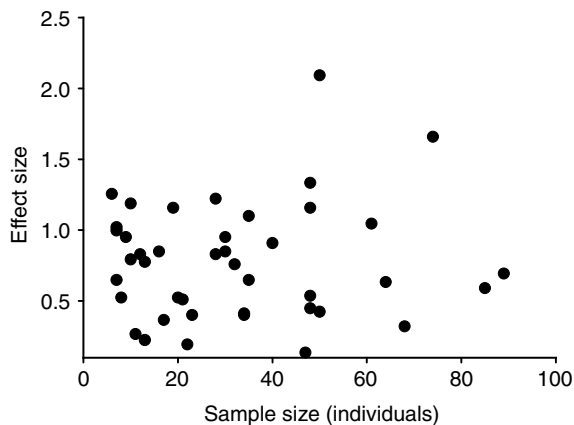


Fig. 2. Funnel plot showing the relationship between effect size and sample size. For resolution purposes, two cases with $N=242$ (Garland and Bennett, 1990), which did not change the regression results, were excluded from the graph.

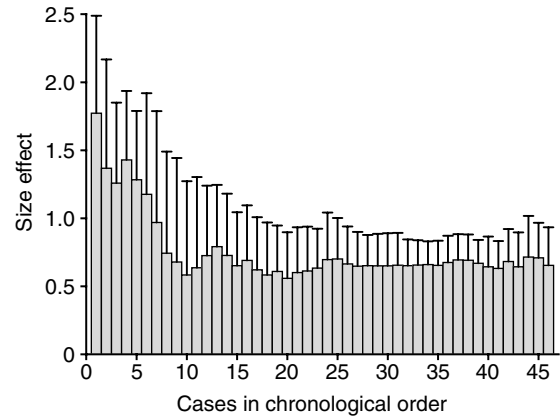


Fig. 3. Cumulative effect sizes in repeatability estimations (see Table 1). Error bars represent 95% confident intervals.

that the asymptotic effect size was approximately attained between cases 26 and 30 (Fig. 3, see also Table 1). Fail-safe numbers resulted high (Rosenthal=1442.7; Orwin=128.4) which, together with the funnel plot (Fig. 2), suggests that publication bias, if it existed, would have had a negligible effect on the magnitude of repeatability.

Discussion

To the best of our knowledge, this is the first synthetic analysis about repeatability of whole-animal metabolism. The principal outcome of our meta-analysis is that whole animal metabolism is significantly repeatable, with a magnitude that fluctuates between 0.60 and 0.80. Also, we found that repeatability, measured by either the Pearson product-moment correlation or the intraclass correlation coefficient, does not change. According to our results, repeatability is not affected by different types of animals, or by differences between laboratory and wild populations. However, the possibility that biological, meaningful effects existed but the analyses lacked sufficient statistical power to detect them is always present. Finally, the cumulative meta-analysis showed that repeatability studies have reached an asymptotic state needing no further improvement either on the precision or the magnitude of the estimator.

Are repeatability studies useful?

According to Falconer and Mackay [(Falconer and Mackay, 1997) p. 136], repeatability or the intraclass correlation coefficient (τ) has four main uses (in this order): (1) to show how much is to be gained by the repetition of measurements, (2) to set the upper limit of the ratios σ_G/σ_P or σ_A/σ_P , (3) to predict the future performance from past records, and (4) to give light on the nature of the environmental variance. For evolutionary purposes, statements (2) and (4) are the most important and have attracted the interest of several organismal/evolutionary biologists over recent decades (Lessels and Boag, 1987; Bennett, 1987; Hayes and Jenkins,

1997) (see also references therein). However the second statement, or the capacity of repeatability to estimate the upper bound of heritability, appears as the more attractive application of repeatability since it allows assessment of the response to selection in a trait [as the possibility of phenotypic correlations being good estimators of genetic correlations (see Cheverud, 1988)]. However, at least regarding physiological traits in animals, Hayes and Jenkins (Hayes and Jenkins, 1997) toned down this assertion, indicating that repeatability has some utility as a preliminary screening tool to determine whether some more detailed genetic analyses are warranted. These authors, and subsequent ones, pointed out that the capacity of repeatability to predict the upper bound of heritability is rather unrealistic in natural populations (Hayes and Jenkins, 1997; Dohm, 2002; Konarzewski et al., 2005). In fact, the reviewed literature permits qualitative evaluation of the predictive power of repeatability from studies on same traits and organisms. For instance, Chappell et al. (Chappell et al., 1995) computed the (long term) repeatability of thermoregulatory MMR in Belding's ground squirrels. According to their estimation (Table 1), the repeatability of MMR was non-significant and its magnitude was 0.38, which means that heritability of thermoregulatory MMR should not surpass ~ 0.40 . However, Nespolo et al. (Nespolo et al., 2005) computed a significant narrow-sense heritability of thermoregulatory MMR of 0.69 in the leaf-eared mouse. Similarly, in house mice, fairly high repeatabilities for BMR (over 0.70, see Table 1) have been reported (Hayes et al., 1992; Ksiazek et al., 2004), but this trait appears to exhibit very low (non-significant) additive genetic variance in the leaf-eared mouse (Nespolo et al., 2003a; Nespolo et al., 2005). Recently, using large sample sizes (see Table 1), a near-zero repeatability in BMR was reported in the deer mouse (Russell and Chappell, 2006), but a heritability of BMR equal to 0.40 was computed in the bank vole (Sadowska et al., 2005). Repeatability thus looks confusing in its capacity to predict the upper bound of heritability. The question remains, however, that different procedures, species or even manipulations could have yielded qualitatively different repeatability and/or heritability estimations. To date, we have found only two studies where both repeatability and narrow-sense heritability were computed in exactly the same metabolic rate, animal (bank voles) and experimental conditions (Labocha et al., 2004; Sadowska et al., 2005). These authors designed a multi-generation quantitative genetic design where several metabolic rates were computed in thousands of individuals. They reported a mean repeatability (across generations) of BMR of 0.50 (see Labocha et al., 2004; Sadowska et al., 2005) and a narrow-sense heritability of this trait of 0.40 (Sadowska et al., 2005); a repeatability of thermoregulatory MMR of 0.45 and a narrow-sense heritability of this trait of 0.43; and a repeatability of swim-induced MMR (a proxy of locomotory MMR) of 0.50 and a narrow-sense heritability of this trait of 0.40. Thus, in these cases repeatability was a good predictor of the upper bound of heritability since the former was consistently greater than the latter in all traits. These examples only confirm, however, that

the conditions for repeatability to be the upper limit of heritability are fairly restrictive (Dohm, 2002).

Our results suggest that repeatability of MR is remarkably homogeneous. From this fact, together with our discussion about the operational definition of traits, environmental variance and the inherent uncertainty of instruments for MR measurements (see also Konarzewski et al., 2005) we can conclude and support previous authors in their conclusions suggesting that the main contribution of repeatability studies is the determination of environmental variance in MR. Hence, the homogeneous results we found in MR repeatabilities would be a consequence of the homogeneity in the method for MR measurements. A corollary of this assertion is that probably, as the technique improves, energy metabolism will exhibit progressive higher repeatabilities (although the cumulative meta-analysis suggested that this has not happen so far). In biological terms, however, metabolic rate could be considered a repeatable trait.

On the error measurement in MR records

Given that MR is a consequence of an unmeasured variable known as energy metabolism, the error in its measurement, as discussed above, is inherent to the instrument used. Several authors have recognized this problem and some alternative methods have been proposed to determine energy metabolism with more precision. One of them is the calculation of latent variables in multivariate statistical analyses such as structural equation modeling (Hayes and Shonkwiler, 1996), where different measurable consequences of energy metabolism (e.g. oxygen consumption, CO₂ production, heat production, food consumption) can be measured, and a 'latent' variable could be constructed from the resulting covariance structure. In a similar fashion, repeatability can be treated with factor analysis, a related statistical method that considers each repeated measurement of MR as observable indicators of an underlying true factor or latent variable (Hayes and Jenkins, 1997). It is very surprising to find that few authors have applied such comprehensive quantitative approaches in further studies of MR repeatability. It would appear that physiological ecologists have avoided using these approaches to improve the precision of MR measurements in a similar way to the persistent use of mass-specific MR unities, despite the fact that many authors have shown how misleading is to use them as a body mass standardization (see Hayes, 1996; Christians, 1999; Packard and Boardman, 1999; Hayes, 2001).

In summary, our analysis provides synthetic evidence to suggest that whole animal metabolic rate is repeatable and calls for new directions in order to determine precisely the sources of this inter-individual variation in energy metabolism. We feel that organismal biologists have not fully recognized the wide possibilities of quantitative methods such as meta-analysis. Meta-analytic procedures could be applied not only to physiological traits but also to biomechanics, life history evolution, behavior and any field where sufficient published information has accumulated around specific questions or hypotheses.

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References

- Arnold, S. J.** (1983). Morphology, performance, and fitness. *Am. Zool.* **23**, 347-361.
- Ashby, P. D.** (1997). Conservation of mass-specific metabolic rate among high- and low-elevation populations of the acridid grasshopper *Xanthippus corallipes*. *Physiol. Biochem. Zool.* **70**, 701-711.
- Bech, C., Langseth, I. and Gabrielsen, G. W.** (1999). Repeatability of basal metabolism in breeding female kittiwakes. *Proc. R. Soc. Lond. B Biol. Sci.* **266**, 2161-2167.
- Bennett, A. F.** (1987). Inter-individual variability: an under utilized resource. In *New Directions in Ecological Physiology* (ed. M. E. Feder, A. F. Bennett, W. W. Burggren and R. W. Huey), pp. 147-169. Cambridge: Cambridge University Press.
- 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.
- Chappell, M. A. and Rogowitz, G. L.** (2000). Mass, temperature and metabolic effects on discontinuous gas exchange cycles in eucalyptus-boring beetles (Coleoptera: Creamybycidae). *J. Exp. Biol.* **203**, 3809-3820.
- Chappell, M. A., Bachman, G. C. and Odell, J. P.** (1995). Repeatability of maximal aerobic performance in Belding's ground squirrels, *Spermophilus beldingi*. *Funct. Ecol.* **9**, 498-504.
- 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.
- Chappell, M. A., Garland, T., Rezende, E. L. and Gomes, F. R.** (2004). Voluntary running in deer mice: speed, distance, energy costs and temperature effects. *J. Exp. Biol.* **207**, 3839-3854.
- Cheverud, J. M.** (1988). A comparison of genetic and phenotypic correlations. *Evolution* **42**, 958-968.
- Christians, J. K.** (1999). Controlling for body mass effects: is part-whole correlation important? *Physiol. Biochem. Zool.* **72**, 250-253.
- Dohm, M. R.** (2002). Repeatability estimates do not always set an upper limit to heritability. *Funct. Ecol.* **16**, 273-280.
- Falconer, D. S. and Mackay, T. F. C.** (1997). *Introduction to Quantitative Genetics* (4th edn). Edinburgh: Longman.
- Fournier, F., Thomas, D. W. and Garland, T.** (1999). A test of two hypotheses explaining the seasonality of reproduction in temperate mammals. *Funct. Ecol.* **13**, 523-529.
- Friedman, W. A., Garland, T. and Dohm, M. R.** (1992). Individual variation in locomotor behavior and maximal oxygen consumption in mice. *Physiol. Behav.* **52**, 97-104.
- Fyh, M., Gabrielsen, G. W., Nordoy, E. S. and Moe, B.** (2001). Individual variation in field metabolic rate of kittiwakes (*Rissa tridactyla*) during the chick-rearing period. *Physiol. Biochem. Zool.* **74**, 343-355.
- Garland, T. and Bennett, A. F.** (1990). Quantitative genetics of maximal oxygen consumption in a garter snake. *Am. J. Physiol.* **259**, R986-R992.
- Garland, T. and Else, P. L.** (1987). Seasonal, sexual and individual variation in endurance and activity metabolism in lizards. *Am. J. Physiol.* **252**, R439-R449.
- Hayes, J. P.** (1996). Analyzing mass-independent data. *Physiol. Zool.* **69**, 974-980.
- Hayes, J. P.** (2001). Mass specific and whole-animal metabolism are not the same concept. *Physiol. Biochem. Zool.* **74**, 147-150.
- Hayes, J. P. and Jenkins, S. H.** (1997). Individual variation in mammals. *J. Mammal.* **78**, 274-293.
- Hayes, J. P. and O'Connor, C. S. O.** (1999). Natural selection on thermogenic capacity of high-altitude deer mice. *Evolution* **53**, 1280-1287.
- Hayes, J. P. and Shonkwiler, J. S.** (1996). Altitudinal effects on water fluxes of deer mice: a physiological application of structural equation modeling with latent variables. *Physiol. Zool.* **69**, 509-531.
- Hayes, J. P., Garland, T. and Dohm, M. R.** (1992). Individual variation in metabolism and reproduction of *Mus*: are energetics and life history linked? *Funct. Ecol.* **6**, 5-14.
- Hayes, J. P., Bible, C. A. and Boone, J. D.** (1998). Repeatability of mammalian physiology: evaporative water loss and oxygen consumption of *Dipodomys merriami*. *J. Mammal.* **79**, 475-485.
- Horak, P., Saks, L., Ots, I. and Kollist, H.** (2002). Repeatability of condition indices in captive greenfinches (*Carduelis chloris*). *Can. J. Zool.* **80**, 636-643.
- Konarzewski, M., Ksiazek, A. and Lapo, I. B.** (2005). Artificial selection on metabolic rates and related traits in rodents. *Integr. Comp. Biol.* **45**, 416-425.
- Ksiazek, A., Konarzewski, M. and Lapo, I. B.** (2004). Anatomic and energetic correlates of divergent selection for basal metabolic rate in laboratory mice. *Physiol. Biochem. Zool.* **77**, 890-899.
- Labocha, M. K., Sadowska, E. T., Baliga, K. and Semer, A. K.** (2004). Individual variation and repeatability of basal metabolism in the bank vole, *Clethrionomys glareolus*. *Proc. R. Soc. Lond. B Biol. Sci.* **271**, 367-372.
- Lessels, C. M. and Boag, P. T.** (1987). Unrepeatable repeatabilities: a common mistake. *Auk* **104**, 116-121.
- Lynch, M. and Walsh, B.** (1998). *Genetics and Analysis of Quantitative Traits* (1st edn). Sunderland, MA: Sinauer.
- Marais, E. and Chown, S. L.** (2003). Repeatability of standard metabolic rate and gas exchange characteristics in a highly variable cockroach, *Perisphaeria sp.* *J. Exp. Biol.* **206**, 4565-4574.
- McCarthy, I. D.** (2000). Temporal repeatability of relative standard metabolic rate in juvenile Atlantic salmon and its relation with life history variation. *J. Fish Biol.* **57**, 224-238.
- McNab, B. K.** (2002). *The Physiological Ecology of Vertebrates. A View from Energetics* (1st edn). Ithaca: Cornell University Press.
- Nespolo, R. F., Bacigalupe, L. D. and Bozinovic, F.** (2003a). Heritability of energetics in a wild mammal, the leaf-eared mouse (*Phyllotis darwini*). *Evolution* **57**, 1679-1688.
- Nespolo, R. F., Lardies, M. A. and Bozinovic, F.** (2003b). Intrapopulation variation in the standard metabolic rate of insects: repeatability thermal dependence and sensitivity (Q10) of oxygen consumption in a cricket. *J. Exp. Biol.* **206**, 4309-4315.
- Nespolo, R. F., Bustamante, D. M., Bacigalupe, L. D. and Bozinovic, F.** (2005). Quantitative genetics of bioenergetics and growth-related traits in the wild mammal, *Phyllotis darwini*. *Evolution* **59**, 1829-1837.
- Packard, G. C. and Boardman, T. J.** (1999). The use of percentages and size-specific indices to normalize physiological data for variation in body size: wasted time, wasted effort? *Comp. Biochem. Physiol.* **122A**, 37-44.
- Rezende, E. L., Chappell, M. A. and Hammond, K. A.** (2004). Cold-acclimation in *Peromyscus*: temporal effects and individual variation in maximum metabolism and ventilatory traits. *J. Exp. Biol.* **208**, 2447-2458.
- Rezende, E. L., Chappell, M. A., Gomes, F. R. and Malisch, J. L.** (2005). Maximal metabolic rates during voluntary exercise, forced exercise, and cold exposure in house mice selectively bred for high wheel-running. *J. Exp. Biol.* **207**, 195-305.
- Roff, D. A.** (1997). *Evolutionary Quantitative Genetics* (1st edn). Montreal: Chapman & Hall.
- Ronning, B., Moe, B. and Bech, C.** (2005). Long-term repeatability makes basal metabolic rate a likely heritable trait in the zebra finch *Taeniopygia guttata*. *J. Exp. Biol.* **208**, 4663-4669.
- Rogowitz, G. L. and Chappell, M. A.** (2000). Energy metabolism of eucalyptus-boring beetles at rest and during locomotion: gender makes a difference. *J. Exp. Biol.* **203**, 1131-1139.
- Rosenberg, M. S., Adams, D. C. and Gurevitch, J.** (2000). *MetaWin. Statistical Software for Meta-Analysis, ver 2.1.* (1st edn). Sunderland, MA: Sinauer Associates.
- Russell, G. A. and Chappell, M. A.** (2006). Is BMR repeatable in deer mice? Organ mass correlates and the effects of cold acclimation and natal altitude. *J. Comp. Physiol. B Biochem. Syst. Environ. Physiol.* **177**, 75-87.
- Sadowska, E. T., Labocha, M. K., Baliga, K. and Stanisiz, A.** (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.** (2004). The role of technology in the past and future development of the doubly labelled water method. *Isotopes Environ. Health Stud.* **41**, 335-343.
- Terblanche, J. S., Klok, C. J. and Chown, S. L.** (2004). Metabolic rate variation in *Glossina pallidipes* (Diptera: Glossinidae): gender, ageing and repeatability. *J. Insect Physiol.* **50**, 419-428.
- Tieleman, B. I., Williams, J. B., Buschur, M. E. and Brown, C. R.** (2003). Phenotypic variation of larks along an aridity gradient: are desert birds more flexible? *Ecology* **84**, 1800-1815.
- Virani, N. A. and Rees, B. B.** (2000). Oxygen consumption, blood lactate and inter-individual variation in the gulf killifish, *Fundulus grandis*, during hypoxia and recovery. *Comp. Biochem. Physiol.* **126A**, 397-405.