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Running head: Repeatability of metabolic rate

Title: Repeatability of metabolic rate is lower for animals living under field versus laboratory conditions

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Summary statement: Individual metabolic rates are generally repeatable, but repeatability not only declines with time interval between measurements but is also lower for animals living under field versus more stable laboratory conditions.

SUMMARY

Metabolic rate has been linked to multiple components of fitness and is both heritable and repeatable to a certain extent. However, its repeatability can differ among studies, even after controlling for the time interval between measurements. Some of this variation in repeatability may be due to the relative stability of the environmental conditions in which the animals are living between measurements. We compared published repeatability estimates for basal, resting, and maximum metabolic rate from studies of endotherms living in the laboratory versus those living in the wild during the interval between measurements. We found that repeatability declines over time, as demonstrated previously, but show for the first time that estimates from free-living animals are also considerably lower than those from animals living under more stable laboratory conditions.

INTRODUCTION

Metabolic rate is an integrative measure of the energetic cost of living and can vary considerably among individuals, populations, and species (Burton et al., 2011; White and Kearney, 2013). Metabolic rate has been linked to growth, reproduction, and survival (Burton et al., 2011). As such, it is thought to be an important predictor of the fitness of individuals (Burton et al., 2011), the vital rates of populations (Metz and Diekmann, 2014), and the evolutionary trajectories of species (Koteja, 2004). Metabolic rate is heritable to a certain extent, meaning that a proportion of the phenotypic variance among individuals can be attributed to additive genetic effects (Nilsson et al., 2009; Wone et al., 2009). It can also be repeatable; a proportion of the variance in multiple measurements of metabolism is explained by phenotypic differences among individuals, these differences arising due to genetic and environmental effects (Nespolo and Franco, 2007). The repeatability of metabolic rate can decline over time (White et al., 2013). However, repeatabilities also differ by up to an order of magnitude among studies (White et al., 2013), even after controlling for the time interval between measurements, but the reasons for such variation are not clear.

Most organisms live in variable environments where they can experience fluctuations in biotic and abiotic factors on both daily and seasonal time scales. Metabolic rates are flexible and can change in response to food availability (Ostrowski et al., 2006), diet quality (Naya et al., 2007), and temperature (McKechnie, 2008), but how environmental variation is expected to affect the repeatability of metabolic rates is not well understood. On the one hand, spatial and temporal environmental variability may act to reduce the repeatability of metabolic rate. Under this hypothesis, we would predict that the repeatability of metabolic rate would be lower in animals living in the wild relative to those living under laboratory conditions since wild animals are subjected to greater environmental variation. However, a recent meta-analysis found the opposite pattern in the case of behavioural traits, with higher repeatability in free-living animals than in those living in the laboratory (Bell et al., 2009). Thus, an alternative hypothesis is that greater environmental variability, by increasing the number of available micro-niches or habitats, can actually promote stable differences in metabolic rate among individuals (Araújo et al., 2011); free-living animals should therefore show higher repeatabilities for metabolic rate than laboratory animals. The third alternative is that repeatabilities do not differ between wild and laboratory conditions, as was found for heritability estimates of morphological and life-history traits across taxa (Weigensberg and Roff, 1996).

Here we examine the effect of environmental variability on the repeatability of basal, resting and maximum metabolic rate (BMR, RMR, and MMR) by using a meta-analytical approach to compare estimates of repeatability among animals kept in the laboratory versus living in the wild. Nespolo and Franco (2007) found no difference in the repeatability of whole-organism metabolic rates among laboratory-acclimated mammals derived from laboratory strains versus wild populations, but to our knowledge, the present study is the first to compare repeatability estimates between captive and free-living animals. We initially collected estimates for all taxa but could not find a single measure of repeatability for an ectotherm in the wild, so we focused our comparison exclusively on endotherms.

MATERIALS AND METHODS

We used ISI Web of Knowledge and Google Scholar to survey the literature for metabolic rate and estimates of its repeatability, consistency, or stability. We also used data from previous meta-analyses (Nespolo and Franco, 2007; White et al., 2013) but verified their estimates from the original sources. Only those estimates of repeatability that controlled for changes in body mass and reproductive status across measurements were included. For each study, we recorded the value of the repeatability estimate, the interval duration between metabolic measurements, and whether that interval occurred in the wild or in the laboratory (location). In cases where the interval duration was not published, the authors were contacted to provide an estimate. The intervals between measurements were averaged when a combined estimate of repeatability was given for more than two successive measures of metabolism. We used combined estimates of all individuals in a study when available except in cases where estimates were given for multiple different interval durations. We also recorded the study taxa (bird versus mammal), type of metabolic trait measured (BMR, RMR or MMR), statistic used to assess repeatability (Pearson's versus the intra-class correlation coefficient), and type of oxygen analyser employed (paramagnetic, zirconia-cell or fuel-cell) since they too could influence estimates of repeatability.

We collected 106 estimates of repeatability from 39 studies (birds=16, mammals=23; Table S1). With one exception where conditions were not specified, all studies controlled for both temperature and humidity and evaluated BMR and RMR within the thermoneutral zone of the organism. However, they differed in terms of the location of the animal during the interval between successive measurements. In fifteen of these studies (38%), the subjects were wild animals that were only temporarily and briefly brought into the laboratory for metabolic rate measurements; they were thus living in the wild in the interim between successive measurements of metabolism. In the remaining studies, the estimates were derived from animals living permanently under laboratory conditions.

Correlation coefficients are typically non-normally distributed, so estimates were converted to effect sizes using the Fisher's Z-transformation (Hedges and Olkin, 1985). A funnel plot of effect size versus the number of individuals in a study was symmetrical, indicating there was no publication bias in these repeatability estimates (Fig. S1). Given that multiple measures from a single study are not independent, we used a re-sampling approach (White et al., 2013) to examine whether repeatability differs between animals living in the wild versus the laboratory, while accounting for effects of interval duration, study taxa, metabolic trait, repeatability statistic, and oxygen analyser type. For each re-sampling iteration, we randomly selected a single repeatability estimate with equal probability from each study and ran the model using only those measures. We repeated this procedure 20,000 times to ensure that all combinations of repeatability estimates were used. 20,000 iterations were more than adequate to obtain convergence on the re-sampled parameter estimates (Fig. S2). Estimates for each parameter were considered statistically significant when their 95% confidence interval (CI) did not overlap with zero.

RESULTS AND DISCUSSION

Repeatability estimates from studies conducted on laboratory-housed animals ranged from -0.20 to 0.93, while those from animals living between measurements in the wild ranged from -0.10 to 0.88 (Fig. 1). Repeatability declined with increasing interval duration (median: -0.22, 95% CI: -0.36 to -0.08; Fig. 2, 3), but did not differ among metabolic traits, taxa, repeatability statistics, or oxygen analysers (Table S2, Fig. S3). However, those estimates obtained from animals living in the wild were significantly lower than those from animals retained in the laboratory (median difference: -0.23, 95% CI: -0.38 to -0.07; Fig. 2, 3). Effect sizes from free-living animals (median: 0.42, 95% CI: 0.30 to 0.54) were roughly 35% lower than those from laboratory-housed animals (median: 0.65, 95% CI: 0.52 to 0.80) when evaluated at the mean interval duration of 75 days. These results demonstrate that the repeatability of metabolic rate not only declines with time, as shown previously (White et al., 2013), but that it can be even further reduced when animals are living in the wild during the interim between measurements.

Disparities in repeatability between animals living in the wild versus captivity may arise because of possible differences in their respective measurement errors. However, standardization of laboratory conditions, equipment, and experimental protocols did not appear to differ among studies conducted on free-living versus laboratory-housed animals. Thus, it is unlikely that metabolic rates of free-living animals were less repeatable because of any difference in the method of measurement. Rather, lower metabolic repeatability in free-living animals is likely due to differences among individuals in how their body composition changes over time and/or in how their metabolic rates respond to environmental variation. Body components such as organ masses and fat stores influence metabolic rate but can change over time in the wild (Swanson, 2010). While poorly studied, reaction norms of metabolic rates can also differ among individuals in their intercept as well as their slope (Auer et al., 2015a; Careau et al., 2014). Thus, repeatability of metabolic rates may be lower in more variable environments because individuals either differ in the type and magnitude of environmental change they encounter over time or how they respond to the same change in conditions.

There is some evidence that metabolic reaction norms are under selection (Bartheld et al., 2015; Terblanche et al., 2009), so the lower repeatability estimates obtained in the wild do not necessarily indicate that metabolic rates will not evolve. However, the differences in repeatabilities that we report do have implications for the level of inference that can be made from laboratory estimates to the temporal consistency of metabolism in the wild. Lower repeatabilities in free-living individuals also mean that phenotypic correlations between their metabolism and other organismal traits may be influenced more by within-individual relative to among-individual variation. As such, we may not be able to predict the long-term fitness prospects of individuals from a single measure of their metabolism.

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Competing interests None declared.

Author contributions S.K.A. collated the data; S.K.A. and R.D.B. analysed the data. S.K.A. drafted the manuscript that was then revised by all authors.

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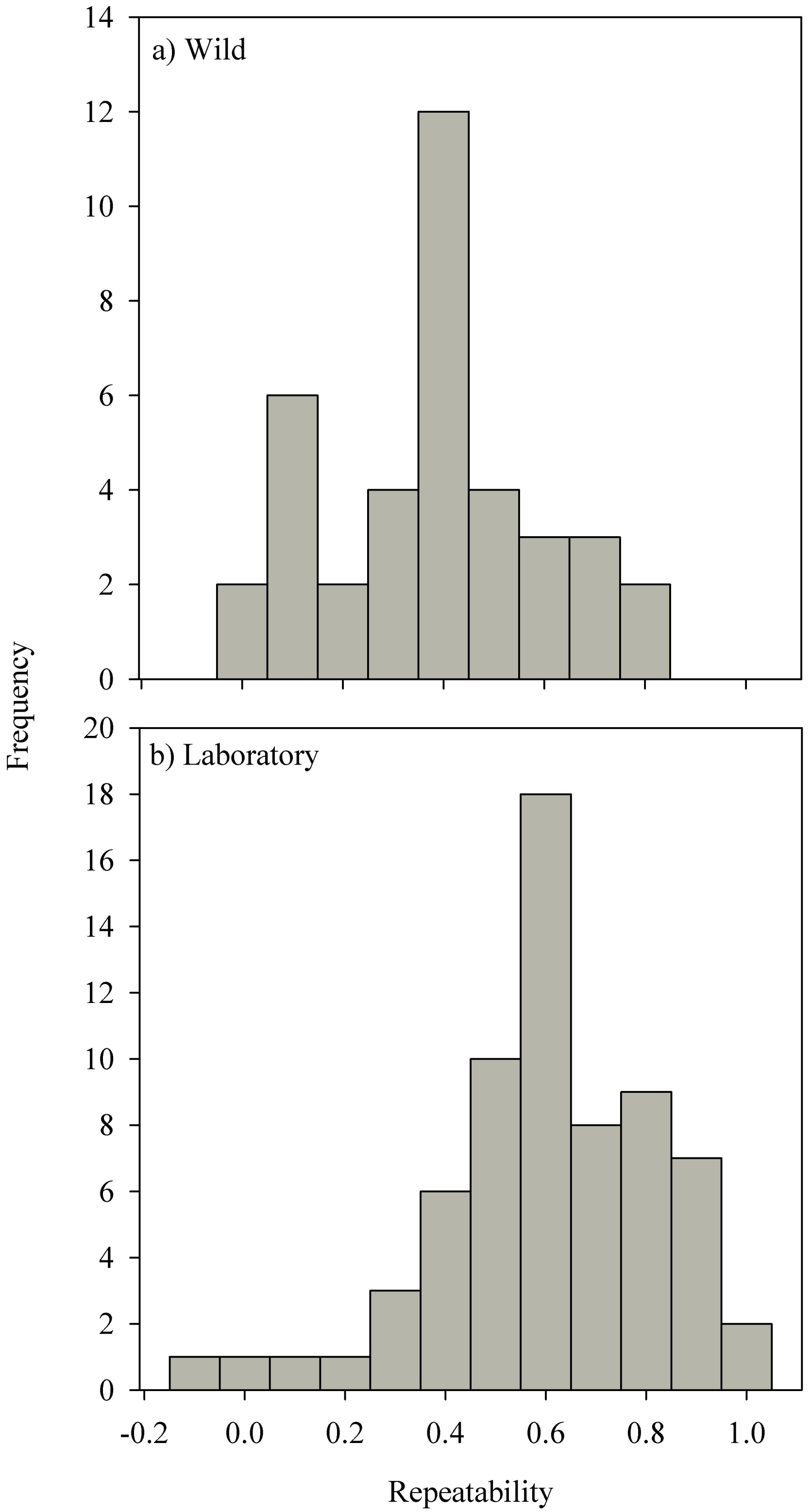
Figures

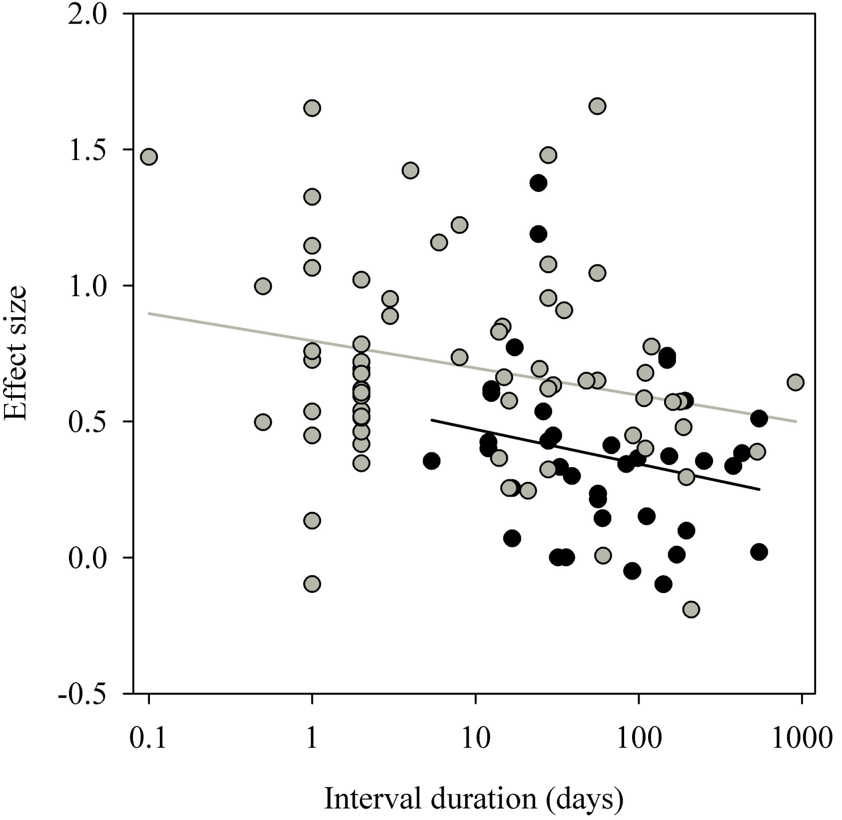
Fig 1. Frequency distributions of repeatability estimates of metabolic rate from studies conducted on animals a) free-living in the wild and b) housed in the laboratory. Data are 106 published estimates from 39 studies of birds and mammals.

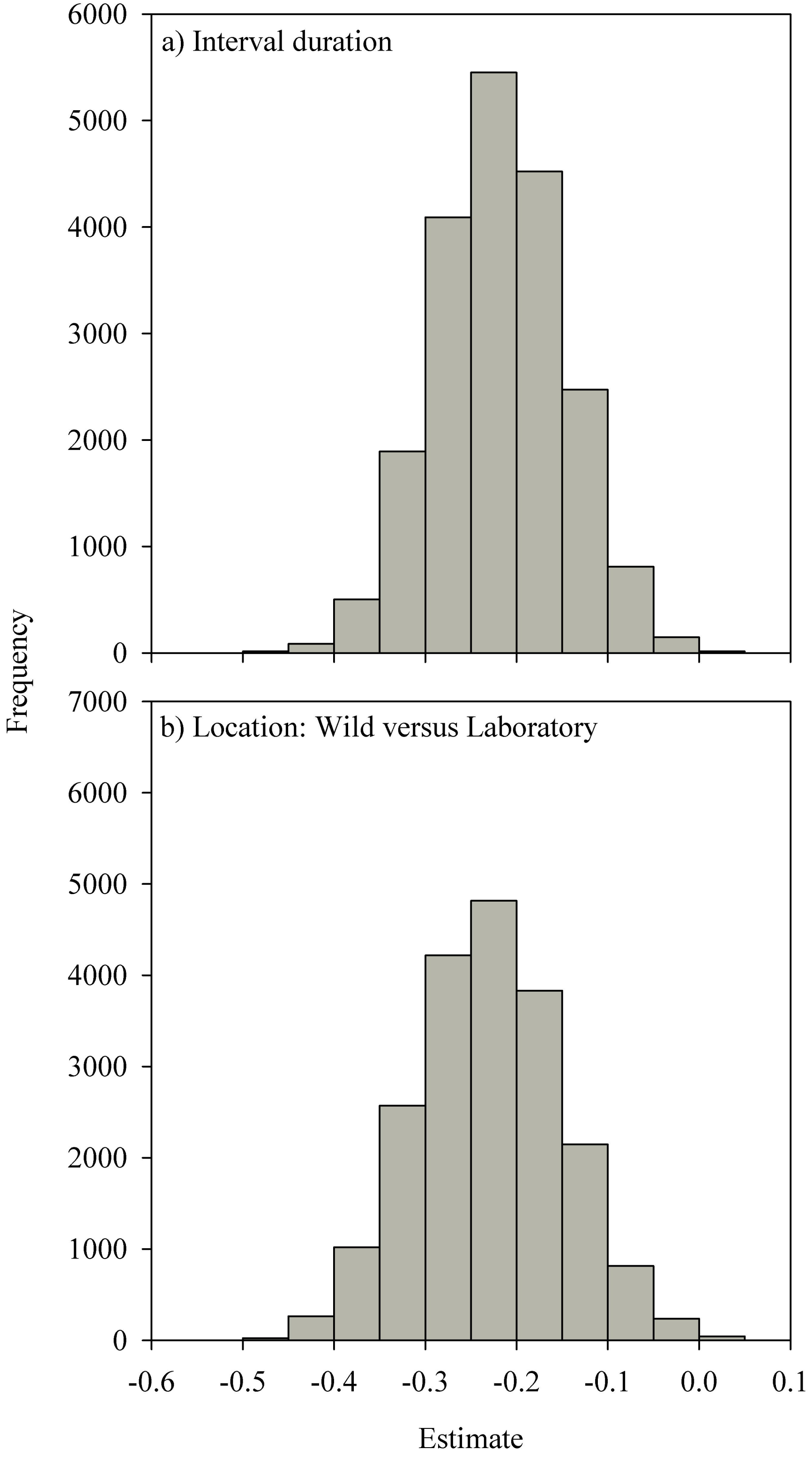
Fig 2. Z-transformed effect sizes of metabolic rate repeatability as a function of the interval duration between repeated measurements of metabolic rate conducted on animals free-living in the wild (●) versus housed under laboratory conditions (○). Data are 106 published estimates from 39 studies of birds and mammals.

Fig 3. Frequency distributions of estimates for effects of a) $\log_{10}$-transformed interval duration and b) location on Z-transformed effect sizes of metabolic rate repeatability. Estimates for location are given as the difference between those obtained from wild versus captive laboratory populations (negative values indicate lower repeatability in the wild). Data are 106 published estimates from 39 studies of birds and mammals.



a) Wild
b) Laboratory
Frequency
Repeatability
0
2
4
6
8
10
12
14
16
18
20
-0.2
0.0
0.2
0.4
0.6
0.8
1.0


2.0
1.5
1.0
0.5
0.0
-0.5
Effect size
0.1
1
10
100
1000
Interval duration (days)



a) Interval duration
b) Location: Wild versus Laboratory
Frequency
Estimate
0
1000
2000
3000
4000
5000
6000
7000
-0.6
-0.5
-0.4
-0.3
-0.2
-0.1
0.0
0.1