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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Figures
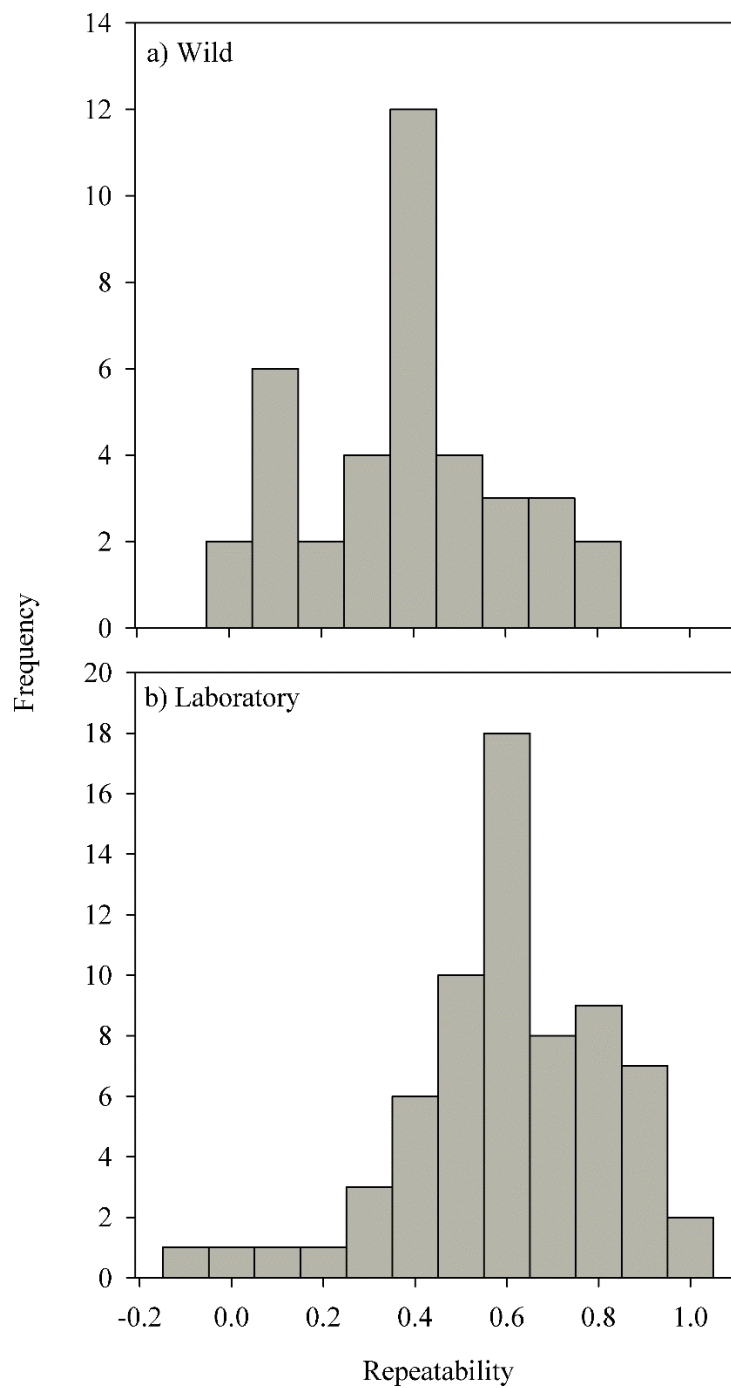
Fig 1. Frequency distributions of repeatability estimates of metabolic rate from studies conducted on animals a) free-living in the wild and b) housed in the laboratory. Data are 106 published estimates from 39 studies of birds and mammals.
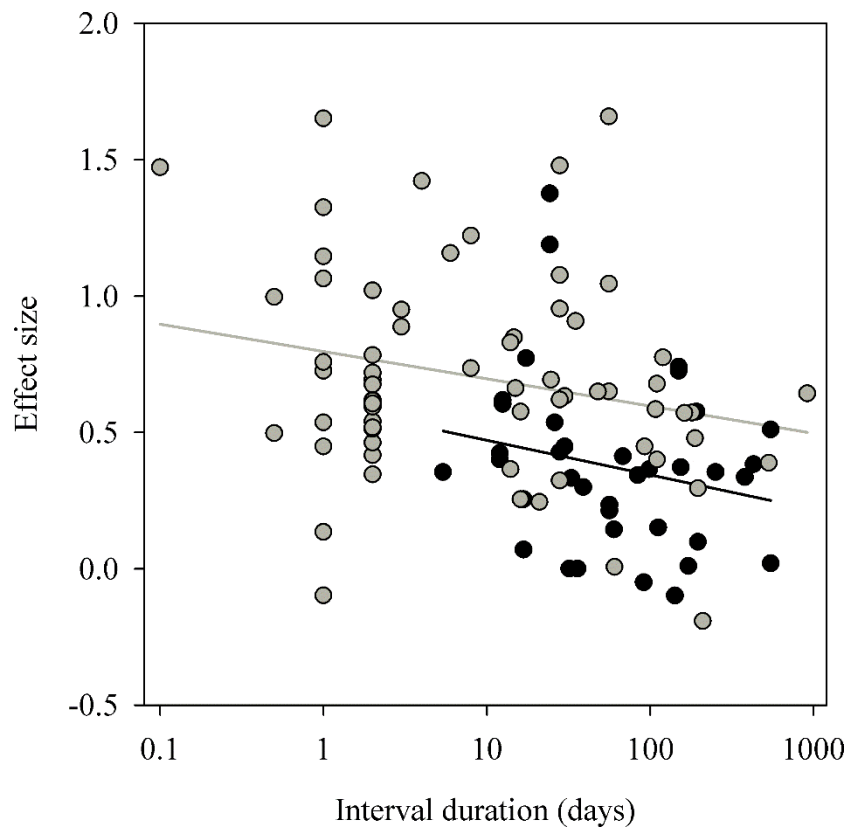
Fig 2. Z-transformed effect sizes of metabolic rate repeatability as a function of the interval duration between repeated measurements of metabolic rate conducted on animals free-living in the wild (●) versus housed under laboratory conditions (◎). Data are 106 published estimates from 39 studies of birds and mammals.
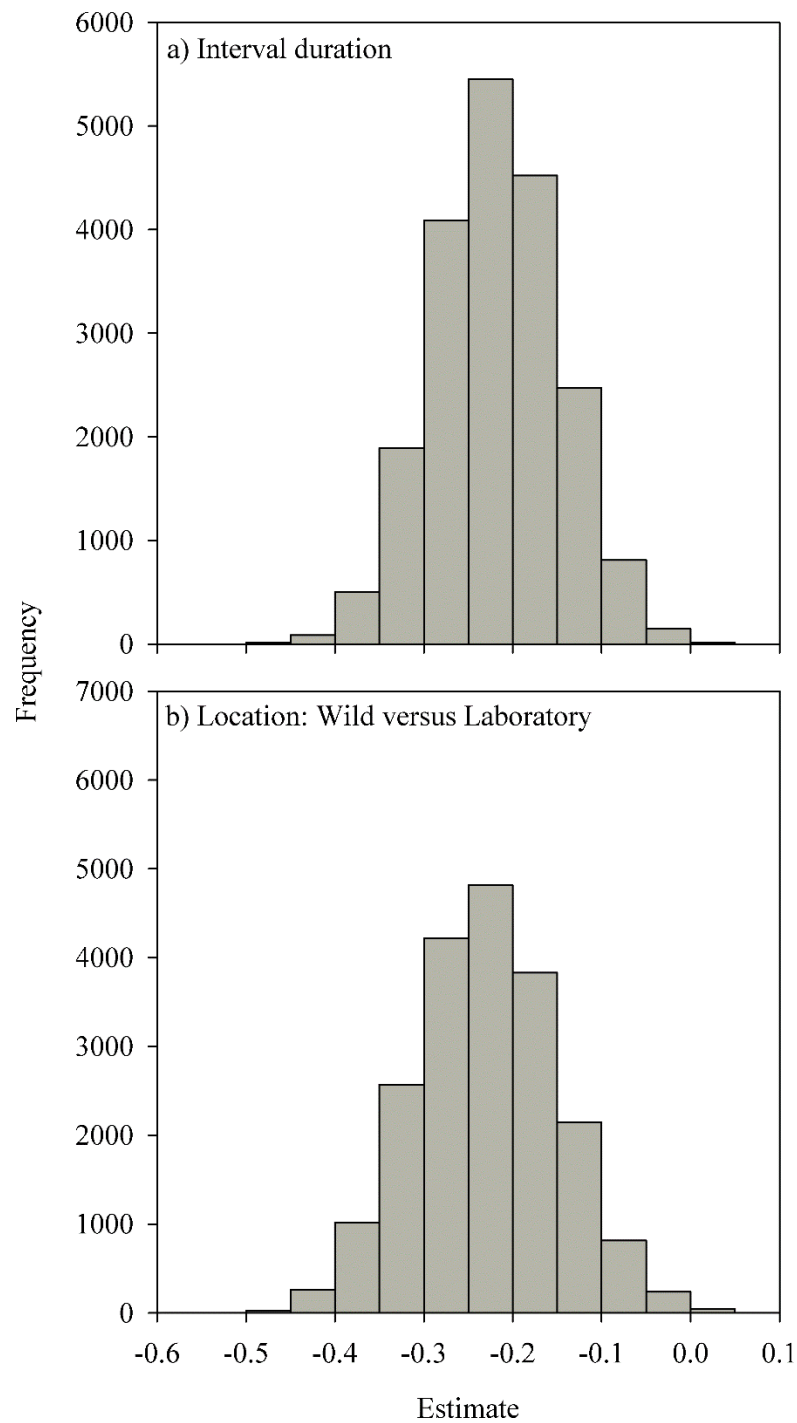
Fig 3. Frequency distributions of estimates for effects of a) $\log_{10}$-transformed interval duration and b) location on Z-transformed effect sizes of metabolic rate repeatability. Estimates for location are given as the difference between those obtained from wild versus captive laboratory populations (negative values indicate lower repeatability in the wild). Data are 106 published estimates from 39 studies of birds and mammals.
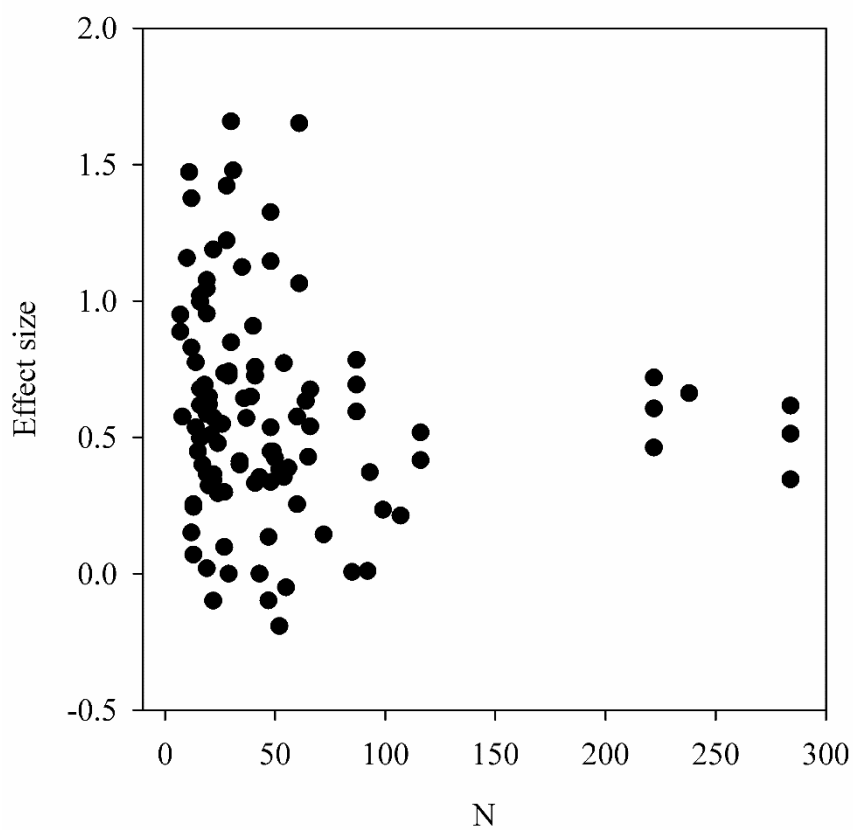
Fig. S1. Effect size versus the number of individuals in each study (N). Data are 106 Fisher's Z-transformed effect sizes of the repeatability of metabolic rate (basal, resting, or maximum) derived from 39 studies on birds and mammals.
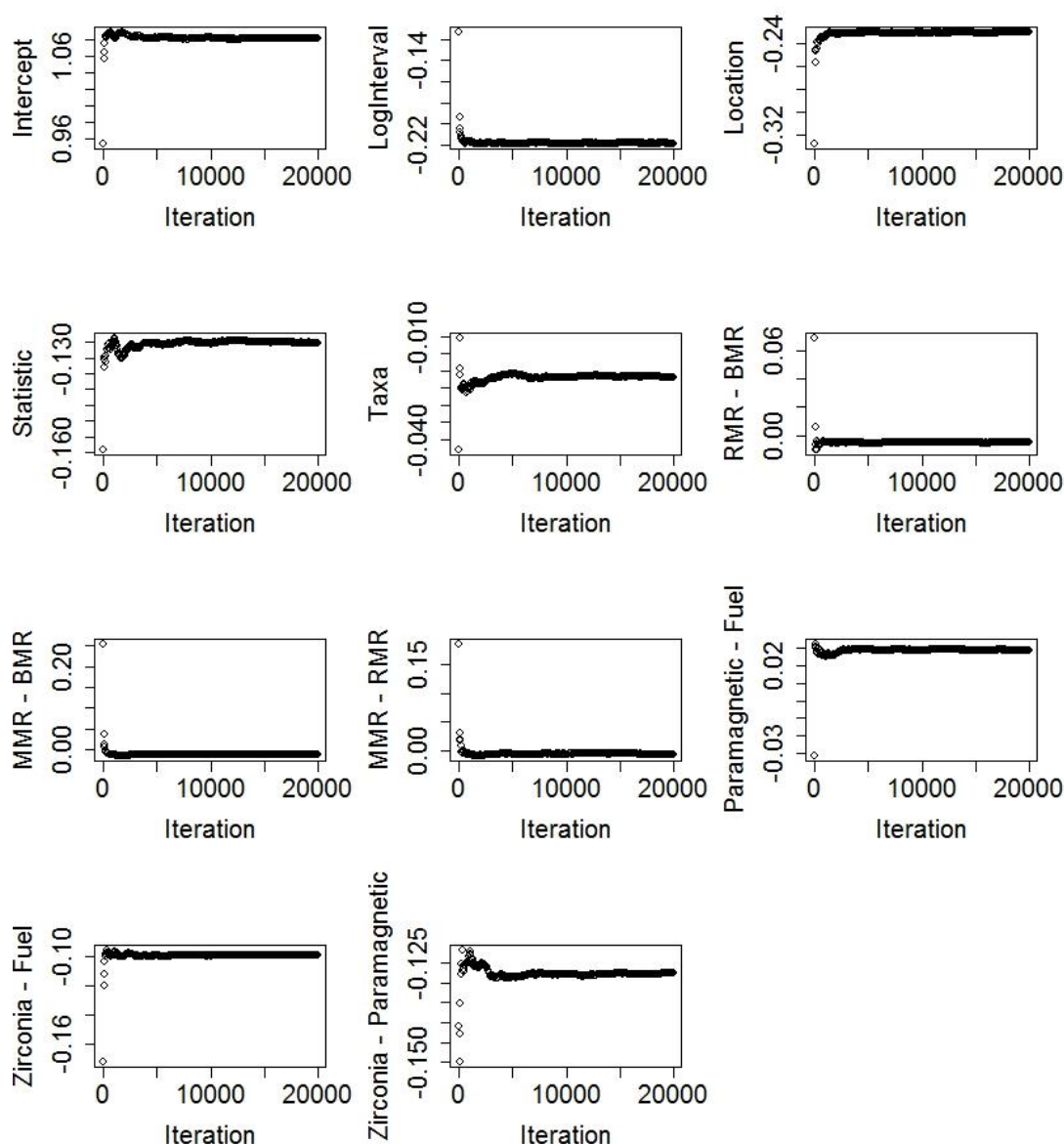
Fig. S2. Convergence of parameter estimates after successive re-sampling (iteration) of 106 Fisher's Z transformed effect sizes for estimates of basal, resting, and maximum metabolic rates (BMR, RMR and MMR, respectively) derived from 39 studies. Estimates for location, study taxa, and repeatability statistic are given as the difference between levels of each categorical predictor: wild minus laboratory populations, mammals minus birds, and intra-class minus Pearson's correlation coefficient, respectively. Estimates for metabolic traits are given as the difference between traits: RMR minus BMR, MMR minus BMR, and MMR minus RMR. Estimates for oxygen analyser are given as the difference between types: zirconia-cell minus fuel-cell, paramagnetic minus fuel-cell, and paramagnetic minus zirconia-cell.
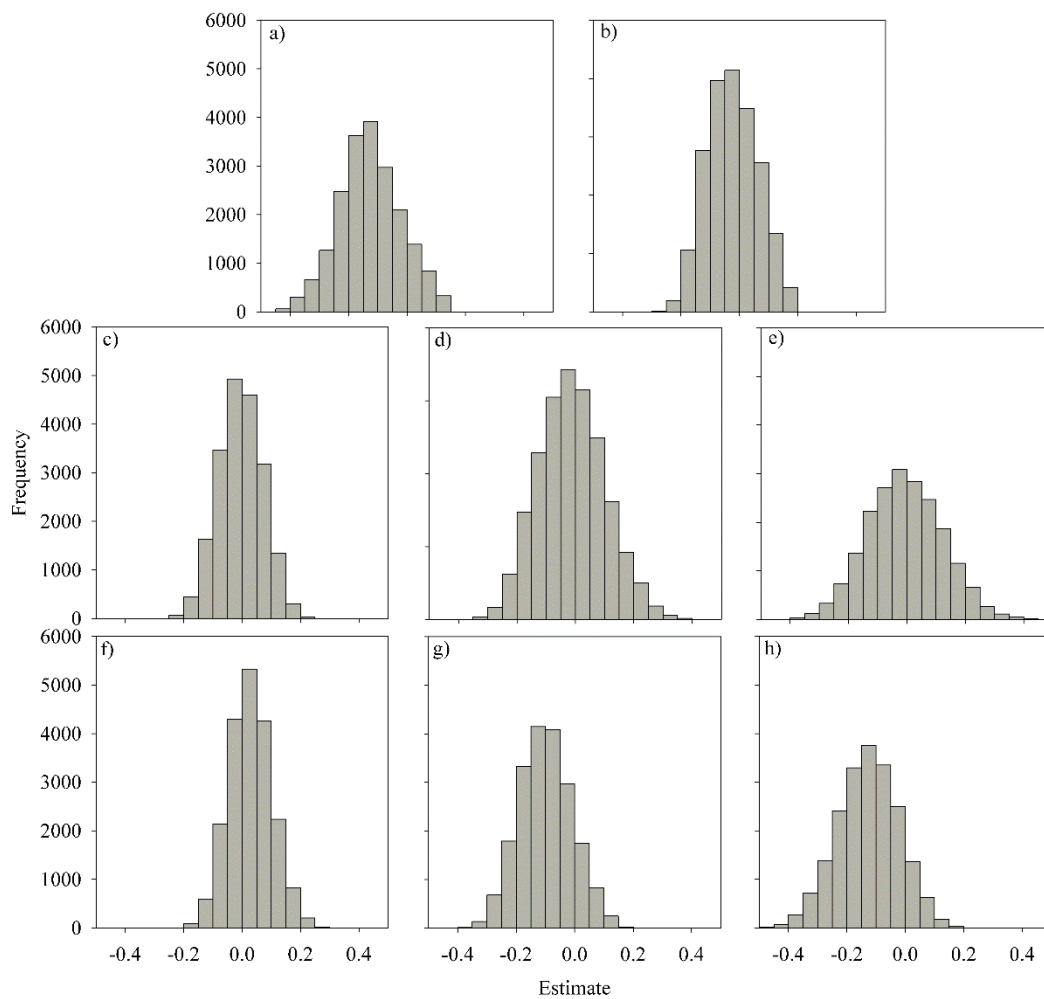
Fig. S3. Frequency distributions of parameter estimates obtained by re-sampling repeatedly from a dataset of 106 Fisher's Z transformed effect sizes for estimates of basal, resting, and maximum metabolic rates (BMR, RMR and MMR, respectively) derived from 39 studies. A single estimate was selected randomly from each study for each replicate. Estimates for repeatability statistic and study taxa and are given as the difference between levels of each categorical predictor: a) intra-class minus Pearson's correlation coefficient and b) mammals minus birds. Estimates for metabolic traits are given as the difference between traits: c) RMR minus BMR, d) MMR minus BMR, and e) MMR minus RMR. Estimates for oxygen analysers are given as the difference between types: f) zirconia-cell minus fuel-cell, g) paramagnetic minus fuel-cell, and h) paramagnetic minus zirconia-cell. Estimates for each parameter were considered statistically significant when their 95% confidence interval (CI) did not overlap with zero (Table S2). See main text for effects of location and interval duration.

Table S1. Estimates of repeatability for metabolic rates of endotherms

Study	Location	Metabolic trait	Taxa	Oxygen analyser	Statistic	Repeatability estimate	Interval (days)	Sample size	Reference
1	Lab	MMR	Mammal	Zirconia-cell	τ	0.809	1.0	35	(Friedman et al., 1992)
2	Lab	BMR	Mammal	Zirconia-cell	r	0.929	1.0	61	(Hayes et al., 1992)
2	Lab	MMR	Mammal	Zirconia-cell	r	0.787	1.0	61	(Hayes et al., 1992)
3	Wild	MMR	Mammal	Zirconia-cell	r	0.020	547.5	19	(Chappell et al., 1995)
3	Wild	MMR	Mammal	Zirconia-cell	r	0.380	12.0	34	(Chappell et al., 1995)
3	Wild	MMR	Mammal	Zirconia-cell	r	0.400	12.0	50	(Chappell et al., 1995)
3	Wild	MMR	Mammal	Zirconia-cell	r	0.470	547.5	21	(Chappell et al., 1995)
4	Lab	MMR	Bird	Zirconia-cell	r	0.900	0.1	11	(Chappell et al., 1996)
4	Lab	MMR	Bird	Zirconia-cell	r	0.901	28.0	31	(Chappell et al., 1996)
4	Lab	MMR	Bird	Zirconia-cell	r	0.930	56.0	30	(Chappell et al., 1996)
4	Lab	MMR	Bird	Zirconia-cell	r	0.517	180.0	22	(Chappell et al., 1996)
4	Lab	MMR	Bird	Zirconia-cell	r	-0.190	210.0	52	(Chappell et al., 1996)
5	Wild	MMR	Bird	Zirconia-cell	r	0.150	112.0	12	(Swanson and Weinacht, 1997)
6	Lab	RMR	Mammal	Zirconia-cell	τ	0.690	14.7	30	(Hayes et al., 1998)
7	Wild	BMR	Bird	Paramagnetic	τ	0.350	98.6	19	(Bech et al., 1999)
7	Wild	BMR	Bird	Paramagnetic	τ	0.520	192.5	8	(Bech et al., 1999)
8	Wild	MMR	Mammal	Zirconia-cell	r	0.390	68.0	34	(Hayes and O'Connor, 1999)
9	Lab	BMR	Bird	CO_2 only	r	0.890	4.0	28	(Hõrak et al., 2002)
9	Lab	BMR	Bird	CO_2 only	r	0.840	8.0	28	(Hõrak et al., 2002)
9	Lab	BMR	Bird	CO_2 only	r	0.650	120.0	14	(Hõrak et al., 2002)
10	Lab	RMR	Mammal	Zirconia-cell	r	0.620	1.0	41	(Chappell et al., 2004)
10	Lab	MMR	Mammal	Zirconia-cell	r	0.640	1.0	41	(Chappell et al., 2004)
10	Lab	RMR	Mammal	Zirconia-cell	r	0.550	2.0	16	(Chappell et al., 2004)
10	Lab	MMR	Mammal	Zirconia-cell	r	0.770	2.0	16	(Chappell et al., 2004)
10	Lab	RMR	Mammal	Zirconia-cell	r	0.710	3.0	7	(Chappell et al., 2004)
10	Lab	MMR	Mammal	Zirconia-cell	r	0.740	3.0	7	(Chappell et al., 2004)
11	Lab	BMR	Mammal	Zirconia-cell	r	0.720	35.0	40	(Książek et al., 2004)
12	Lab	BMR	Mammal	Zirconia-cell	τ	0.560	30.0	64	(Labocha et al., 2004)

13	Lab	MMR	Mammal	Zirconia-cell	r	0.312	28.0	20	(Rezende et al., 2004)
13	Lab	MMR	Mammal	Zirconia-cell	r	0.551	28.0	20	(Rezende et al., 2004)
13	Lab	MMR	Mammal	Zirconia-cell	r	0.792	28.0	19	(Rezende et al., 2004)
13	Lab	MMR	Mammal	Zirconia-cell	r	0.741	28.0	19	(Rezende et al., 2004)
13	Lab	MMR	Mammal	Zirconia-cell	r	0.780	56.0	19	(Rezende et al., 2004)
13	Lab	MMR	Mammal	Zirconia-cell	r	0.572	56.0	20	(Rezende et al., 2004)
14	Lab	RMR	Mammal	Zirconia-cell	r	0.490	1.0	48	(Rezende et al., 2005)
14	Lab	RMR	Mammal	Zirconia-cell	τ	0.868	1.0	48	(Rezende et al., 2005)
14	Lab	MMR	Mammal	Zirconia-cell	τ	-0.098	1.0	47	(Rezende et al., 2005)
14	Lab	MMR	Mammal	Zirconia-cell	r	0.134	1.0	47	(Rezende et al., 2005)
14	Lab	MMR	Mammal	Zirconia-cell	r	0.420	1.0	48	(Rezende et al., 2005)
14	Lab	MMR	Mammal	Zirconia-cell	τ	0.816	1.0	48	(Rezende et al., 2005)
15	Lab	BMR	Bird	Paramagnetic	τ	0.567	915.0	36	(Rønning et al., 2005)
15	Lab	BMR	Bird	Paramagnetic	τ	0.571	48.0	39	(Rønning et al., 2005)
16	Lab	BMR	Mammal	Zirconia-cell	τ	0.493	2.0	66	(Sadowska et al., 2005)
16	Lab	BMR	Mammal	Zirconia-cell	τ	0.548	2.0	284	(Sadowska et al., 2005)
16	Lab	BMR	Mammal	Zirconia-cell	τ	0.600	2.0	87	(Sadowska et al., 2005)
16	Lab	BMR	Mammal	Zirconia-cell	τ	0.616	2.0	222	(Sadowska et al., 2005)
16	Lab	MMR	Mammal	Zirconia-cell	τ	0.393	2.0	116	(Sadowska et al., 2005)
16	Lab	MMR	Mammal	Zirconia-cell	τ	0.432	2.0	222	(Sadowska et al., 2005)
16	Lab	MMR	Mammal	Zirconia-cell	τ	0.472	2.0	284	(Sadowska et al., 2005)
16	Lab	MMR	Mammal	Zirconia-cell	τ	0.532	2.0	87	(Sadowska et al., 2005)
16	Lab	MMR	Mammal	Zirconia-cell	τ	0.333	2.0	284	(Sadowska et al., 2005)
16	Lab	MMR	Mammal	Zirconia-cell	τ	0.476	2.0	116	(Sadowska et al., 2005)
16	Lab	MMR	Mammal	Zirconia-cell	τ	0.540	2.0	222	(Sadowska et al., 2005)
16	Lab	MMR	Mammal	Zirconia-cell	τ	0.588	2.0	66	(Sadowska et al., 2005)
16	Lab	MMR	Mammal	Zirconia-cell	τ	0.654	2.0	87	(Sadowska et al., 2005)
17	Lab	RMR	Bird	Fuel-cell	τ	0.626	8.0	27	(Vézina and Williams, 2005)
17	Lab	RMR	Bird	Fuel-cell	τ	0.516	162.0	37	(Vézina and Williams, 2005)
17	Lab	RMR	Bird	Fuel-cell	τ	0.445	188.0	24	(Vézina and Williams, 2005)
17	Lab	RMR	Bird	Fuel-cell	τ	0.287	196.0	24	(Vézina and Williams, 2005)
18	Wild	BMR	Mammal	Zirconia-cell	r	-0.099	142.0	22	(Bozinovic, 2007)

19	Lab	BMR	Mammal	Zirconia-cell	r	0.007	60.5	85	(Russell and Chappell, 2007)
20	Wild	RMR	Mammal	Fuel-cell	r	0.540	12.5	19	(Szafrańska et al., 2007)
20	Wild	RMR	Mammal	Fuel-cell	τ	0.550	12.5	19	(Szafrańska et al., 2007)
20	Wild	RMR	Mammal	Fuel-cell	τ	0.070	16.8	13	(Szafrańska et al., 2007)
20	Wild	RMR	Mammal	Fuel-cell	r	0.250	16.8	13	(Szafrańska et al., 2007)
20	Wild	RMR	Mammal	Fuel-cell	r	0.620	149.5	29	(Szafrańska et al., 2007)
20	Wild	RMR	Mammal	Fuel-cell	τ	0.630	149.5	29	(Szafrańska et al., 2007)
21	Lab	BMR	Bird	Fuel-cell	τ	0.600	24.7	18	(Versteegh et al., 2008)
22	Wild	BMR	Mammal	Fuel-cell	τ	0.340	5.4	43	(Boratyński and Koteja, 2009)
22	Wild	MMR	Mammal	Fuel-cell	τ	0.340	5.4	54	(Boratyński and Koteja, 2009)
22	Wild	BMR	Mammal	Fuel-cell	τ	0.230	56.4	99	(Boratyński and Koteja, 2009)
22	Wild	MMR	Mammal	Fuel-cell	τ	0.210	56.4	107	(Boratyński and Koteja, 2009)
23	Wild	BMR	Bird	Paramagnetic	τ	0.404	28.0	65	(Broggi et al., 2009)
23	Wild	BMR	Bird	Paramagnetic	τ	0.356	154.0	93	(Broggi et al., 2009)
23	Wild	BMR	Bird	Paramagnetic	τ	0.324	380.0	48	(Broggi et al., 2009)
24	Lab	RMR	Mammal	Fuel-cell	τ	0.240	21.0	13	(Cortes et al., 2009)
25	Lab	RMR	Mammal	Paramagnetic	r	0.580	15.0	238	(Duarte et al., 2010)
25	Lab	RMR	Mammal	Paramagnetic	r	0.380	110.0	17	(Duarte et al., 2010)
25	Lab	RMR	Mammal	Paramagnetic	r	0.590	110.0	16	(Duarte et al., 2010)
26	Wild	RMR	Mammal	Fuel-cell	r	0.830	24.3	22	(Larivee et al., 2010)
26	Wild	RMR	Mammal	Fuel-cell	r	0.880	24.3	12	(Larivee et al., 2010)
26	Wild	RMR	Mammal	Fuel-cell	r	0.098	196.0	27	(Larivee et al., 2010)
27	Wild	BMR	Bird	Paramagnetic	τ	0.143	60.0	72	(Bouwhuis et al., 2011)
27	Wild	BMR	Bird	Paramagnetic	τ	-0.050	91.5	55	(Bouwhuis et al., 2011)
28	Wild	MMR	Bird	Fuel-cell	r	0.648	17.4	54	(Chappell et al., 2011)
28	Wild	MMR	Bird	Fuel-cell	r	0.365	430.0	52	(Chappell et al., 2011)
29	Lab	BMR	Mammal	Fuel-cell	τ	0.680	14.0	12	(Gonzalez et al., 2012)
30	Lab	BMR	Bird	Fuel-cell	τ	0.460	0.5	16	(Kaseloo et al., 2012)
30	Lab	BMR	Bird	Fuel-cell	τ	0.760	0.5	16	(Kaseloo et al., 2012)
31	Wild	RMR	Mammal	Fuel-cell	τ	0.010	171.0	92	(Careau et al., 2013)
32	Lab	MMR	Bird	Zirconia-cell	r	0.350	14.0	22	(Swanson and King, 2013)
33	Wild	RMR	Mammal	Fuel-cell	τ	0.330	84.0	22	(Szafranska et al., 2013)

34	Lab	BMR	Bird	Fuel-cell	τ	0.250	16.1	60	(Careau et al., 2014)
34	Lab	MMR	Bird	Fuel-cell	τ	0.520	16.1	60	(Careau et al., 2014)
35	Lab	RMR	Mammal	Fuel-cell	τ	0.420	92.5	49	(Guenther et al., 2014)
36	Lab	BMR	Bird	Fuel-cell	τ	0.820	6.0	10	(Jacobs and McKechnie, 2014)
37	Lab	BMR	Mammal	Fuel-cell	τ	0.500	35.0	26	(Sichova et al., 2014)
37	Lab	BMR	Mammal	Fuel-cell	τ	0.370	533.0	56	(Sichova et al., 2014)
38	Wild	BMR	Bird	Fuel-cell	τ	0.420	30.0	15	(Cortes et al., 2015)
38	Wild	BMR	Bird	Fuel-cell	τ	0.320	33.0	41	(Cortes et al., 2015)
38	Wild	BMR	Bird	Fuel-cell	τ	0.290	39.0	27	(Cortes et al., 2015)
38	Wild	MMR	Bird	Fuel-cell	τ	0.490	26.0	14	(Cortes et al., 2015)
38	Wild	MMR	Bird	Fuel-cell	τ	0.000	32.0	43	(Cortes et al., 2015)
38	Wild	MMR	Bird	Fuel-cell	τ	0.000	36.0	29	(Cortes et al., 2015)
39	Wild	BMR	Bird	Fuel-cell	τ	0.340	252.0	28	(Mathot et al., 2015)

Metabolic trait: BMR=basal metabolic rate, RMR=resting metabolic rate; MMR=maximum metabolic rate; Statistic = Pearson's (r) or intra-class (τ) correlation coefficient.

Table S2. Parameter estimates and 95 % confidence intervals (CI) from post hoc comparisons among different levels of categorical factors in their effects on the repeatability of metabolic rate. Estimates are given for the difference between levels of each categorical predictor. See main text for effects of location and interval duration.

Predictor	Comparison	Median difference	Lower 95% CI	Upper 95% CI
Statistic	intra-class – Pearson's correlation coefficient	-0.13	-0.33	0.09
Taxa	mammal – bird	-0.03	-0.18	0.15
Metabolic trait	resting – basal metabolic rate	-0.01	-0.15	0.14
	maximum –basal metabolic rate	-0.02	-0.22	0.22
	maximum – resting metabolic rate	-0.01	-0.25	0.24
Oxygen analyser	zirconia – fuel-cell	0.03	-0.11	0.18
	paramagnetic – fuel-cell	-0.10	-0.27	0.08
	paramagnetic – zirconia-cell	-0.13	-0.34	0.07

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