

SHORT COMMUNICATION

The repeatability of metabolic rate declines with time

Craig R. White^{1,*}, Natalie G. Schimpf¹ and Phillip Cassey²

¹School of Biological Sciences, The University of Queensland, St Lucia, QLD 4072, Australia and ²School of Earth and Environmental Sciences, The University of Adelaide, Adelaide, SA 5005, Australia

*Author for correspondence (craig.white@uq.edu.au)

SUMMARY

The evolutionary causes of variation in metabolic rate within and among species are a topic of enduring interest. Variation between individuals is the raw material on which natural selection acts, and so recent years have seen an increase in the number of studies that examine the consequences of inter-individual differences in metabolic rate for organismal performance. A minimum requirement for a trait to evolve is that it must differ consistently between individuals, and these differences must be heritable. The time constancy of a trait is assessed by estimating its repeatability, which represents the ratio of the between-individual component of phenotypic variance to total phenotypic variance. A previous meta-analysis of repeatability concluded that metabolic rate is, on average, repeatable. Here, we expand on this earlier analysis by including extra data published in the intervening years and demonstrate that the repeatability of metabolic rate decreases as the interval between measurements increases.

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INTRODUCTION

Metabolic rate is one of the most widely measured physiological traits, with data available for hundreds of species of mammal (McNab, 2008), bird (McNab, 2009), reptile (White et al., 2006), amphibian (White et al., 2006), fish (Clarke and Johnston, 1999; White et al., 2012a), insect (Chown et al., 2007) and a host of other organisms (Makarieva et al., 2008; White et al., 2012b). These comparative databases have revealed considerable diversity between species, with similarly sized species differing severalfold in some cases (e.g. White and Seymour, 2004; Careau et al., 2008). Understanding the causes of this variation has been of long-standing interest (e.g. McNab and Morrison, 1963; Weathers, 1979), and modern comparative analyses have demonstrated that differences between species are associated with a range of biotic and abiotic variables (reviewed by White and Kearney, 2012).

Interest in metabolic variation also encompasses differences in metabolic rate among individuals of the same species (e.g. Biro and Stamps, 2010; Burton et al., 2011; Konarzewski and Książek, 2013). Such inter-individual variation is important because it is the raw material on which natural selection acts. A minimum requirement for a trait to evolve is that it must differ consistently between individuals, and these differences must be heritable. In order to be heritable, the time-consistency of differences between individuals must be attributable to the genetic rather than the environmental components of phenotypic variance (Falconer and Mackay, 1996; Dohm, 2002). Although measurements of heritability for metabolic rate are becoming increasingly common (e.g. Lacy and Lynch, 1979; Lynch and Sulzbach, 1984; Dohm et al., 2001; Nespolo et al., 2003; Bacigalupe et al., 2004; Konarzewski et al., 2005; Nespolo et al., 2005; Sadowska et al., 2005; Rønning et al., 2007; Nilsson et al., 2009; Tieleman et al., 2009; Wone et al., 2009; Bushuev et al., 2011;

Careau et al., 2011; Schimpf et al., 2013), comparative physiologists more typically examine the repeatability of inter-individual differences (e.g. Nespolo and Franco, 2007; Norin and Malte, 2011). Repeatability is calculated as the ratio of individual (V_I) to total phenotypic variance (V_P), and is related to heritability because V_I includes additive genetic variance (V_A) and (narrow-sense) heritability is calculated as the ratio of V_A to V_P (Wilson et al., 2010). Repeatability therefore sets an approximate upper limit to heritability under most circumstances (Dohm, 2002).

Recently, Nespolo and Franco compiled 47 estimates of the repeatability of metabolic rate and concluded that, on average, metabolic rate is a repeatable trait and that repeatability is not affected by time between measurements (Nespolo and Franco, 2007). This finding contrasts with a recent study demonstrating that the repeatability of metabolic rate declines with time (e.g. Norin and Malte, 2011), and suggests that Nespolo and Franco's conclusion should be re-examined now that more published data are available. We therefore expand the data set compiled by Nespolo and Franco using the wealth of data that have accumulated in recent years to re-examine the time dependence of the repeatability of metabolic rate.

MATERIALS AND METHODS

Measures of repeatability estimated using either Pearson's correlation coefficients or variance components were compiled from the peer-reviewed literature (see supplementary material Table S1). The data presented by Nespolo and Franco (Nespolo and Franco, 2007) were included in the compilation, but the original sources were used; their data were supplemented with more recently published information. Only studies that accounted for variation in body size between individuals when calculating the repeatability of

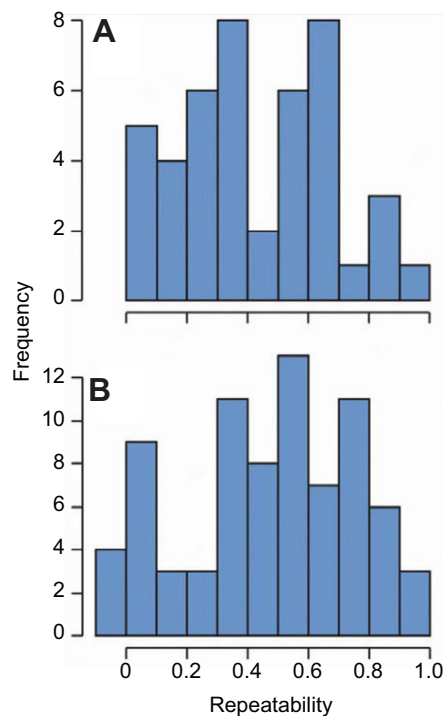


Fig. 1. Frequency distributions of the intra-class correlation coefficient (repeatability) of metabolic rate for (A) ectotherms and (B) endotherms ($N=44$ and 78 for ectotherms and endotherms, respectively). The interval between measurements varied from 7 h to 244 days for ectotherms, and 2 h to 915 days for endotherms.

metabolic rate were included in the dataset. In total, we located 122 estimates of repeatability from 37 studies. Because estimates of population correlation coefficients cannot be considered to have come from a normal distribution except when the population correlation coefficient is zero, a normally distributed estimate of

effect size was calculated from estimates of repeatability using Fisher's Z -transformation (Zar, 2010).

To minimize the bias that might arise from including multiple non-independent effect sizes from a single study, we adopted a re-sampling methodology that randomly chose (with uniform probability) only one effect size from any one study following previous methods (Blackburn et al., 2009; White et al., 2013). This re-sampling procedure was completed a total of 100 times, and for each re-sample we calculated the Pearson's correlation coefficient (r) between the Z -transformed effect size and the log-transformed duration between measurements of metabolic rate. The frequency distribution of the 100 correlation estimates was then compared with the null expectation that average $r=0$. The association was regarded as significantly negative if less than 5% of the re-sampled estimates of r were greater than zero (i.e. a one-tailed test of significance, with α set at 0.05). Estimates of repeatability for endotherms (birds and mammals, $N=78$ estimates; 40 for resting metabolic rate, 2 for field metabolic rate and 36 for maximum metabolic rate) and ectotherms (all other species, $N=44$ estimates; 31 for resting metabolic rate and 13 for maximum metabolic rate) were analysed separately.

RESULTS AND DISCUSSION

The frequency distributions of compiled repeatability estimates were similar for ectotherms and endotherms, spanning the ranges 0.02 to 0.93 for ectotherms (Fig. 1A) and -0.10 to 0.98 for endotherms (Fig. 1B), and decreased significantly with the interval between measurements for both ectotherms and endotherms (Fig. 2A,B). Correlation coefficients (r) of the relationship between repeatability and log-transformed time were negative for 99 of 100 re-sampled test statistics for ectotherms ($P=0.01$, Fig. 2C), and were always negative (100 out of 100) for endotherms ($P<0.01$, Fig. 2D), demonstrating that the repeatability of metabolic rate declines with time for both groups.

The finding that metabolic rate is repeatable, but that repeatability declines with time, has implications for studies that test for

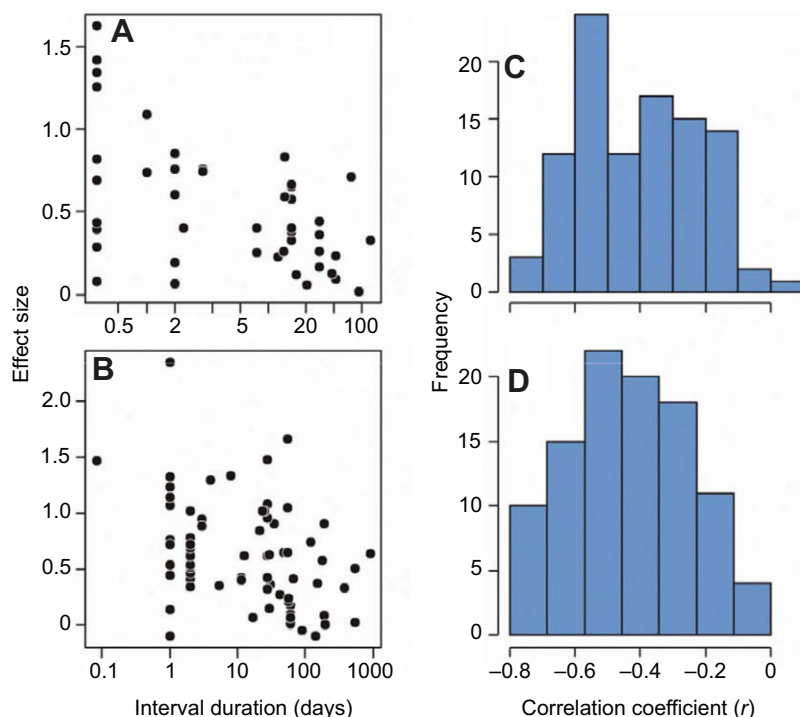


Fig. 2. Relationship between Z -transformed effect sizes and the interval between successive measurements of metabolic rate for (A) ectotherms and (B) endotherms on a log scale, and frequency distributions of the 100 re-sampled correlation coefficients between effect size and the time (log-transformed) between measurements for (C) ectotherms and (D) endotherms.

phenotypic associations between metabolic rate and other traits (e.g. Konarzewski and Diamond, 1995; Geluso and Hayes, 1999; Nespolo et al., 2002; Schimpf et al., 2012). As metabolic rate measured at one point in time may not represent the metabolic rate of the same individual at another point in time, such studies should endeavour to minimize the interval between measurements of the traits of interest. It is also important to bear in mind that low long-term repeatability of metabolic rate does not necessarily indicate that metabolic rates will not evolve by selection, because repeatability does not always set the upper limit to heritability (Dohm, 2002), and most studies have found that metabolic rate shows low to moderate heritability (see White and Kearney, 2013). A more robust approach to determining the possible importance of trait associations for responses to selection is to design experiments that test for genetic associations among traits [see e.g. Wilson et al. (Wilson et al., 2010) for a guide to applying such approaches in the context of ecological studies]. Such quantitative genetic approaches are possible when, for example, data are available for many individuals of known relatedness, and the examination of genetic associations among traits provides insight into the possible consequences of selection on one trait for the correlated evolution of others.

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AUTHOR CONTRIBUTIONS

C.R.W. and N.G.S. collected the data; C.R.W. and P.C. analysed the data; and C.R.W., N.G.S. and P.C. wrote the paper.

COMPETING INTERESTS

No competing interests declared.

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Table S1. Estimates of repeatability of metabolic rate for a range of animals

Variable	Repeatability	N	Interval (days)	Animal	Group	Reference
MMR	0.538	50	2	Reptile	Ectotherm	Garland and Else, 1987
RMR	0.796	242	1	Reptile	Ectotherm	Garland and Bennett, 1990
RMR	0.38	23	2.5	Insect	Ectotherm	Chappell and Rogowitz, 2000
MMR	0.64	22	2	Insect	Ectotherm	Rogowitz and Chappell, 2000
MMR	0.64	22	4	Insect	Ectotherm	Rogowitz and Chappell, 2000
MMR	0.69	22	2	Insect	Ectotherm	Rogowitz and Chappell, 2000
MMR	0.067	21	2	Insect	Ectotherm	Rogowitz and Chappell, 2000
MMR	0.63	21	4	Insect	Ectotherm	Rogowitz and Chappell, 2000
MMR	0.19	21	2	Insect	Ectotherm	Rogowitz and Chappell, 2000
RMR	0.53	85	30	Insect	Ectotherm	Nespolo et al., 2003
RMR	0.22	13	25	Insect	Ectotherm	Marais and Chown, 2003
RMR	0.28	7	0.3	Insect	Ectotherm	Terblanche et al., 2004
RMR	0.37	7	0.3	Insect	Ectotherm	Terblanche et al., 2004
RMR	0.87	7	0.3	Insect	Ectotherm	Terblanche et al., 2004
RMR	0.93	7	0.3	Insect	Ectotherm	Terblanche et al., 2004
RMR	0.41	6	0.3	Insect	Ectotherm	Terblanche et al., 2004
RMR	0.08	7	0.3	Insect	Ectotherm	Terblanche et al., 2004
RMR	0.89	7	0.3	Insect	Ectotherm	Terblanche et al., 2004
RMR	0.85	7	0.3	Insect	Ectotherm	Terblanche et al., 2004
RMR	0.60	7	0.3	Insect	Ectotherm	Terblanche et al., 2004
RMR	0.67	6	0.3	Insect	Ectotherm	Terblanche et al., 2004
RMR	0.68	26	30	Fish	Ectotherm	Maciak and Konarzewski, 2010
RMR	0.017	30	183	Fish	Ectotherm	Seppänen et al., 2010
RMR	0.314	24	244	Fish	Ectotherm	Seppänen et al., 2010
RMR	0.255	29	29	Insect	Ectotherm	Schimpf et al, unpublished
RMR	0.121	34	39.8	Insect	Ectotherm	Schimpf et al, unpublished
RMR	0.121	86	94.7	Insect	Ectotherm	Schimpf et al, unpublished
RMR	0.057	32	51.875	Insect	Ectotherm	Schimpf et al, unpublished
RMR	0.625	17	1	Insect	Ectotherm	Schimpf et al, unpublished
RMR	0.61	15	152.5	Arachnid	Ectotherm	Lardies et al., 2008
RMR	0.38	44	15	Snail	Ectotherm	Artacho and Nespolo, 2009
RMR	0.25	33	15	Snail	Ectotherm	Artacho and Nespolo, 2009
RMR	0.569	33	35	Fish	Ectotherm	Norin and Malte, 2011
RMR	0.579	33	35	Fish	Ectotherm	Norin and Malte, 2011
RMR	0.517	33	35	Fish	Ectotherm	Norin and Malte, 2011
RMR	0.163	33	70	Fish	Ectotherm	Norin and Malte, 2011
RMR	0.416	33	70	Fish	Ectotherm	Norin and Malte, 2011
RMR	0.093	33	105	Fish	Ectotherm	Norin and Malte, 2011
MMR	0.316	33	35	Fish	Ectotherm	Norin and Malte, 2011
MMR	0.362	33	35	Fish	Ectotherm	Norin and Malte, 2011
MMR	0.38	33	35	Fish	Ectotherm	Norin and Malte, 2011
MMR	0.253	33	70	Fish	Ectotherm	Norin and Malte, 2011
MMR	0.346	33	70	Fish	Ectotherm	Norin and Malte, 2011
MMR	0.225	33	105	Fish	Ectotherm	Norin and Malte, 2011
MMR	0.787	61	1	Mammal (L)	Endotherm	Hayes et al., 1992
MMR	0.4	50	11.5	Mammal (W)	Endotherm	Chappell and Bachman, 1995
MMR	0.38	34	11.5	Mammal (W)	Endotherm	Chappell and Bachman, 1995
MMR	0.47	21	547.5	Mammal (W)	Endotherm	Chappell and Bachman, 1995
MMR	0.02	19	547.5	Mammal (W)	Endotherm	Chappell and Bachman, 1995
FMR	0.261	11	42	Mammal (W)	Endotherm	Berteaux et al., 1996
RMR	0.69	30	21	Mammal (W)	Endotherm	Hayes et al., 1998
MMR	0.39	34	68	Mammal (W)	Endotherm	Hayes and O'Conner, 1999
RMR	0.35	17	30.3	Bird	Endotherm	Bech et al., 1999
FMR	0.64	32	1	Bird	Endotherm	Fyhn et al., 2001
RMR	0.86	28	4	Bird	Endotherm	Hörak et al., 2002
RMR	0.87	28	8	Bird	Endotherm	Hörak et al., 2002
RMR	0.63	14	120	Bird	Endotherm	Hörak et al., 2002
RMR	0.56	64	30	Mammal (W)	Endotherm	Labocha et al., 2004
MMR	0.64	41	1	Mammal (L)	Endotherm	Chappell et al., 2004
MMR	0.77	16	2	Mammal (L)	Endotherm	Chappell et al., 2004
MMR	0.74	7	3	Mammal (L)	Endotherm	Chappell et al., 2004
RMR	0.62	41	1	Mammal (L)	Endotherm	Chappell et al., 2004
RMR	0.55	16	2	Mammal (L)	Endotherm	Chappell et al., 2004
RMR	0.71	7	3	Mammal (L)	Endotherm	Chappell et al., 2004
MMR	0.792	19	28	Mammal (L)	Endotherm	Rezende et al., 2004
MMR	0.78	19	56	Mammal (L)	Endotherm	Rezende et al., 2004
MMR	0.741	19	28	Mammal (L)	Endotherm	Rezende et al., 2004
MMR	0.312	20	28	Mammal (L)	Endotherm	Rezende et al., 2004
MMR	0.572	20	56	Mammal (L)	Endotherm	Rezende et al., 2004
MMR	0.551	20	28	Mammal (L)	Endotherm	Rezende et al., 2004
RMR	0.72	40	35	Mammal (L)	Endotherm	Książek et al., 2004
RMR	0.567	36	915	Bird	Endotherm	Rønning et al., 2005
RMR	0.571	39	48	Bird	Endotherm	Rønning et al., 2005

MMR	0.844	47	1	Mammal (L)	Endotherm	Rezende et al., 2005
MMR	0.42	48	1	Mammal (L)	Endotherm	Rezende et al., 2005
MMR	0.134	47	1	Mammal (L)	Endotherm	Rezende et al., 2005
MMR	0.982	47	1	Mammal (L)	Endotherm	Rezende et al., 2005
MMR	0.816	48	1	Mammal (L)	Endotherm	Rezende et al., 2005
MMR	-0.098	47	1	Mammal (L)	Endotherm	Rezende et al., 2005
RMR	0.49	48	1	Mammal (L)	Endotherm	Rezende et al., 2005
RMR	0.868	48	1	Mammal (L)	Endotherm	Rezende et al., 2005
RMR	0.492706	66	2	Mammal (W)	Endotherm	Sadowska et al., 2005
RMR	0.548447	284	2	Mammal (W)	Endotherm	Sadowska et al., 2005
RMR	0.599836	87	2	Mammal (W)	Endotherm	Sadowska et al., 2005
RMR	0.616453	222	2	Mammal (W)	Endotherm	Sadowska et al., 2005
MMR	0.39342	116	2	Mammal (W)	Endotherm	Sadowska et al., 2005
MMR	0.472356	284	2	Mammal (W)	Endotherm	Sadowska et al., 2005
MMR	0.532445	87	2	Mammal (W)	Endotherm	Sadowska et al., 2005
MMR	0.431666	222	2	Mammal (W)	Endotherm	Sadowska et al., 2005
MMR	0.476033	116	2	Mammal (W)	Endotherm	Sadowska et al., 2005
MMR	0.588353	66	2	Mammal (W)	Endotherm	Sadowska et al., 2005
MMR	0.333231	284	2	Mammal (W)	Endotherm	Sadowska et al., 2005
MMR	0.654189	87	2	Mammal (W)	Endotherm	Sadowska et al., 2005
MMR	0.540366	222	2	Mammal (W)	Endotherm	Sadowska et al., 2005
RMR	0.007	85	60.5	Mammal (W)	Endotherm	Russell and Chappell, 2007
RMR	0.003	59	60.5	Mammal (W)	Endotherm	Russell and Chappell, 2007
RMR	0.059	61	60.5	Mammal (W)	Endotherm	Russell and Chappell, 2007
RMR	0.099	26	60.5	Mammal (W)	Endotherm	Russell and Chappell, 2007
RMR	0.177	13	60.5	Mammal (W)	Endotherm	Russell and Chappell, 2007
RMR	0.014	26	60.5	Mammal (W)	Endotherm	Russell and Chappell, 2007
RMR	0.061	72	60.5	Mammal (W)	Endotherm	Russell and Chappell, 2007
RMR	0.404	65	28	Bird	Endotherm	Broggi et al., 2009
RMR	0.356	93	154	Bird	Endotherm	Broggi et al., 2009
RMR	0.324	48	380	Bird	Endotherm	Broggi et al., 2009
RMR	0.77	22	25.01	Mammal (W)	Endotherm	Larivée et al., 2010
RMR	0.77	11	23.3	Mammal (W)	Endotherm	Larivée et al., 2010
RMR	0.09	27	192.2	Mammal (W)	Endotherm	Larivée et al., 2010
RMR	-0.001	15	195.34	Mammal (W)	Endotherm	Larivée et al., 2010
RMR	0.72	12	192.1	Mammal (W)	Endotherm	Larivée et al., 2010
RMR	0.55	13	12.5	Mammal (W)	Endotherm	Szafrańska et al., 2007
RMR	0.07	19	16.8	Mammal (W)	Endotherm	Szafrańska et al., 2007
RMR	-0.099	22	142.3	Mammal (W)	Endotherm	Bozinovic, 2007
RMR	0.34	43	5.4	Mammal (W)	Endotherm	Boratyński and Koteja, 2009
RMR	0.23	99	56.4	Mammal (W)	Endotherm	Boratyński and Koteja, 2009
MMR	0.34	54	5.4	Mammal (W)	Endotherm	Boratyński and Koteja, 2009
MMR	0.21	107	56.4	Mammal (W)	Endotherm	Boratyński and Koteja, 2009
RMR	0.143	72	30	Bird	Endotherm	Bouwhuis et al., 2011
RMR	-0.05	55	91.5	Bird	Endotherm	Bouwhuis et al., 2011
MMR	0.9	11	0.083	Bird	Endotherm	Chappell et al., 1996
MMR	0.901	31	28	Bird	Endotherm	Chappell et al., 1996
MMR	0.93	30	56	Bird	Endotherm	Chappell et al., 1996
MMR	0.517	22	180	Bird	Endotherm	Chappell et al., 1996

RMR, resting metabolic rate; FMR, field metabolic rate; MMR, maximum metabolic rate; L, lab; W, wild.

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