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SHORT COMMUNICATION

The repeatability of metabolic rate declines with time

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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

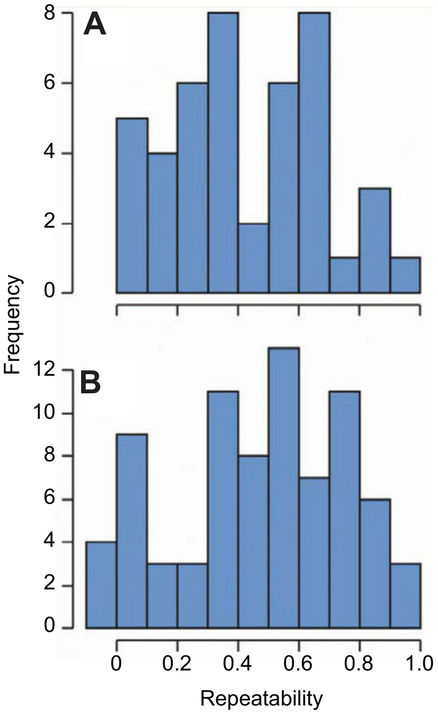

Fig. 1. Frequency distributions of the intra-class correlation coefficient (repeatability) of metabolic rate for (A) ectotherms and (B) endotherms (N=44 and 78 for ecotherms and endotherms, respectively). The interval between measurements varied from 7 h to 244 days for ectotherms, and 2 h to 915 days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

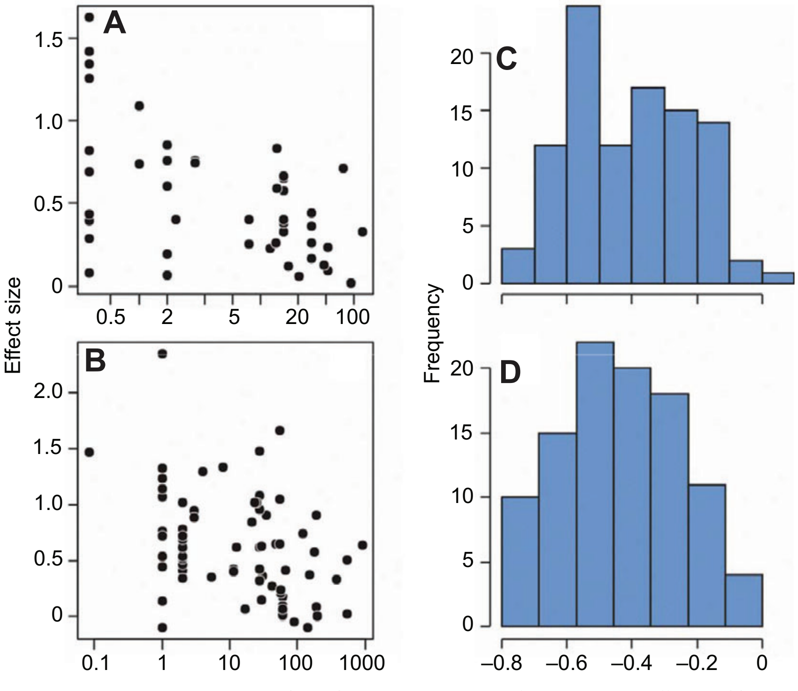

Fig 2. Relationship between Z-transformed effect sizes and the interval between successive measurements of metabolic rate for (A) ectotherms and (B) endotherms on a log scale, and frequency distributions of the 100 re-sampled correlation coefficients between effect size and the time (log-transformed)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